

**THE LAND CAPABILITY POTENTIAL INDEX:
A DECISION SUPPORT TOOL FOR THE MANAGEMENT
OF MISSOURI RIVER FLOODPLAIN HABITAT**

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by
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THE LAND CAPABILITY POTENTIAL INDEX: A DECISION SUPPORT TOOL FOR THE MANAGEMENT OF MISSOURI RIVER FLOODPLAIN HABITAT

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and hereby certify that, in their opinion, it is worthy of acceptance.

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DEDICATION

This thesis is dedicated to the two people that have inspired me most: Alicia and Charlotte. Alicia, your work in the field of ecology has inspired and challenged me to accomplish more. You have provided support and encouragement throughout my scientific career and the long process of my research and thesis, and you have helped me to remember why it is we do what we do. Charlotte, you have inspired me to work harder and to become a better scientist and person. I hope my example helps you to realize that you can become anything that you want to be, and that you can make yourself and the world in which we live better. Thank you both for the inspiration and love you have given me.

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
LIST OF FIGURES	viii
LIST OF TABLES	xiv
Chapter I: Introduction	1
Theory behind LCPI: a comprehensive literature review	5
Scope and terms	5
The abiotic template	8
Vannote et al. (1980).....	9
Wharton et al. (1982)	10
Brinson (1990)	11
Malanson (1993)	13
Landscape structure	14
Internal Structure	14
Direct effects of flooding.....	15
Indirect effects of flooding	16
Parker and Bendix (1996)	17
Hupp and Osterkamp (1996).....	18
Hughes (1997).....	19
Hupp (2000)	20
Flow-return interval.....	21
Herbaceous species	22
Woody species	23
Cottonwood and willow	24
Exotic species.....	26
Communities	27

Flow-return interval conclusion	28
Flow-return interval as a surrogate for other hydrologic variables.....	29
Flow Duration	30
Reflooding.....	33
Depth to groundwater.....	33
Surface water depth.....	37
Elevation and flow energy.....	38
Damage and mortality.....	39
Propagule deposition.....	40
Opportunities for establishment and growth	41
Soil deposition and sedimentation	44
Other elevation-related environmental factors	46
Soil organic matter.....	46
Nutrient deposition/soil chemistry	48
Contaminant deposition	50
Soil drainage and the water availability gradient	50
Soil oxygen availability.....	55
Elevation and water availability	57
Soil texture and water availability.....	58
Effects of variation in soil drainage on cottonwood and willow	61
Soil drainage classification reflects past conditions	63
Environmental parameters not addressed by the LCPI.....	65
Flow timing	65
Variation in flow-return interval	67
Spatial configuration	68
Terrestrial and hydrologic modification.....	70
Competition.....	71
Non-equilibrium/Succession	74

Literature review summary	77
Chapter II: Methods and Materials	81
Current distribution of LCPI Classes	82
Subdivision by ecological province.....	83
Subdivision by geomorphological segments and tributary-defined sections.....	86
Effects of tributaries	88
Variation in groundwater processes by soil drainage classes	91
Background—the Groundwater Response Factor (GWRF)	91
Sites	94
Well selection and installation.....	97
Water level data collection	102
Groundwater data analysis	104
Relationships between LCPI and vegetation	105
Background	105
Species and community data	107
GIS-derived data variables	110
Analysis of vegetation data	112
Identification of dominant environmental variables using Non-metric Multidimensional Scaling	112
Statistical tests of variation in species and community abundance between LCPI classes	113
Potential future LCPI class abundance.....	115
Chapter III: Results	119
Current distribution of LCPI Classes	119
Differences between ecological provinces	125
Differences between geomorphological segments and tributary-defined sections.....	129
Changes associated with tributary mouths	131
Potential future LCPI class abundance.....	146
Variation in groundwater processes by soil drainage classes	152
Forest City summary	152

Overton summary	156
Maximum GWRF.....	161
Lag ratio	164
Exceedance ratios	166
Comparison of shallow and deep well groundwater response to flow pulses	169
Relationships between LCPI and vegetation	170
Non-metric multi-dimensional scaling	171
All plots.....	172
Gavins	174
Platte	175
Squaw Creek	176
Fort Leavenworth.....	177
Lisbon Bottom.....	178
Jameson Island	179
Overton North	180
Overton South	181
Eagle Bluffs.....	182
St. Aubert Island.....	184
Howell Island	185
Summary of NMS results.....	186
Species frequency and abundance analyses.....	189
Exotic species.....	189
Frequency by flow-return interval	189
Cover by flow-return interval	192
Frequency by soil drainage class	196
Cover by soil drainage class	200
Native species	204
Flow-return interval	204

Soil drainage	207
Community frequency and abundance analyses	210
Flow-return interval within Big Muddy	210
Flow-return interval and plots outside of Big Muddy	217
Soil drainage within Big Muddy	220
Soil drainage outside of Big Muddy.....	226
Chapter IV: Discussion	229
Current distribution of LCPI classes	229
Ecological provinces	229
Hydrogeomorphic sections	230
Tributaries	231
Urban areas.....	232
Potential future LCPI class abundance	233
Variation in groundwater processes between soil drainage classes	236
Relationships between LCPI and vegetation	242
Non-metric Multidimensional Scaling	242
Species frequency and abundance	245
Community frequency and abundance	248
Advancement to science and management.....	251
Chapter V: Conclusions.....	252
References Cited	255

LIST OF FIGURES

FIGURE 1. BAR GRAPH OF RELATIVE AREA OF SOIL DRAINAGE CLASSES FOR EACH FLOW-RETURN INTERVAL BY RIVER SEGMENT SHOWING THAT POORLY DRAINED SOILS GENERALLY REPRESENT A LOWER PROPORTION OF TOTAL AREA ON HIGHER ELEVATION LANDS THAN ON LOWER ELEVATION LANDS.53

FIGURE 2. AREA MODELED BY THE LCPI (YELLOW) IN RELATION TO THE PRAIRIE PARKLAND (TEMPERATE) AND CENTRAL INTERIOR BROADLEAF FOREST ECOLOGICAL PROVINCES (CLELAND ET AL., 2007) 84

FIGURE 3. SECTIONS OF THE LOWER MISSOURI RIVER BASED ON GEOMORPHOLOGIC CRITERIA (JACOBSON ET AL., 2009) AND MAJOR TRIBUTARIES BELIEVED TO HAVE A STRONG EFFECT ON THE HYDROLOGIC AND SEDIMENT REGIMES OF THE RIVER (CHOJNACKI ET AL., 2012).....87

FIGURE 4. PROCESS FOR SUBDIVIDING THE STUDY AREA INTO CROSS-SECTIONS FOR ANALYSES: A) A LINE APPROXIMATING THE DIRECTIONAL TREND OF THE VALLEY WAS DRAWN WITH NODES AT 3 KM INTERVALS, B) THE NODES WERE USED TO CREATE THIESSEN POLYGONS, WHICH WERE ATTRIBUTED WITH THE MEAN VALUE OF RIVER MILE POINTS WITHIN THE POLYGON, AND C) THE LCPI MODEL WAS PARTITIONED BY INTERSECTING IT WITH THE THEISSEN POLYGON SURFACE.89

FIGURE 5. THE AREA OF THE LOWER MISSOURI RIVER MODELED BY THE LAND CAPABILITY POTENTIAL INDEX IN RELATION TO ECOLOGICAL SECTIONS (CLELAND ET AL., 2007).....91

FIGURE 6. LOCATION OF GROUNDWATER LEVEL MONITORING WELLS IN RELATION TO MAPPED SSURGO SOIL DRAINAGE CLASSES (SOIL SURVEY STAFF, 2012) AT THE FOREST CITY STUDY SITE95

FIGURE 7. LOCATION OF GROUNDWATER LEVEL MONITORING WELLS IN RELATION TO MAPPED SSURGO SOIL DRAINAGE CLASSES (SOIL SURVEY STAFF, 2012) AT THE BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE OVERTON NORTH MANAGEMENT UNIT, MISSOURI.97

FIGURE 8. SCHEMATIC REPRESENTATION OF NEWLY INSTALLED WELLS AT OVERTON AND FOREST CITY, MISSOURI.99

FIGURE 9. SITES AT WHICH DATA USED IN THIS STUDY WERE COLLECTED IN RELATION TO ECOLOGICAL PROVINCES.108

FIGURE 10. CHANGE IN RIVER STAGE ASSOCIATED WITH THE 5 YEAR FLOW-RETURN INTERVAL FROM HISTORIC (1967-2006; SOLID LINES) TO MODELED FUTURE CONDITIONS (2040-2069; DASHED LINES) ASSUMING A 16 PERCENT INCREASE IN DISCHARGE AT BOONVILLE, MISSOURI (GANGOPADHYAY ET AL., 2012).....119

FIGURE 11. MAP OF LCPI SOIL DRAINAGE CLASSES FOR THE ENTIRE LOWER MISSOURI RIVER.....120

FIGURE 12. MAP OF LCPI FLOW-RETURN INTERVALS FOR THE ENTIRE LOWER MISSOURI RIVER.121

FIGURE 13. RELATIVE AREA OF LCPI FLOW-RETURN INTERVALS BY VALLEY CROSS-SECTION FOR THE LOWER MISSOURI RIVER.123

FIGURE 14. RELATIVE AREA OF LCPI SOIL DRAINAGE CLASSES BY VALLEY CROSS-SECTION FOR THE LOWER MISSOURI RIVER.124

FIGURE 15. RELATIVE AREA OF LAND CAPABILITY POTENTIAL INDEX FLOW-RETURN INTERVALS BY ECOLOGICAL PROVINCE (CLELAND ET AL., 2007).....126

FIGURE 16. GRAPH SHOWING DECREASING RELATIVE AREA OF THE GREATER THAN 500 YEAR FLOW-RETURN INTERVAL AS DISTANCE FROM THE GAVINS POINT DAM (MILE 811) INCREASES.126

FIGURE 17. RELATIVE AREA OF LAND CAPABILITY POTENTIAL INDEX SOIL DRAINAGE CLASSES BY ECOLOGICAL PROVINCE (CLELAND ET AL., 2007).....127

FIGURE 18. RELATIVE AREA OF FLOW-RETURN INTERVALS WITHIN 40 MILES OF THE TRANSITION BETWEEN THE PRAIRIE PARKLAND (TEMPERATE) AND CENTRAL INTERIOR BROADLEAF FOREST PROVINCES SHOWING A SHIFT TO LESS FREQUENTLY FLOODED LANDS.128

FIGURE 19. RELATIVE AREA OF SOIL DRAINAGE CLASSES WITHIN 40 MILES OF THE TRANSITION BETWEEN THE PRAIRIE PARKLAND (TEMPERATE) AND CENTRAL INTERIOR BROADLEAF FOREST PROVINCES SHOWING A SHIFT TO BETTER DRAINED SOILS.	128
FIGURE 20. RELATIVE AREA OF LAND CAPABILITY POTENTIAL INDEX FLOW-RETURN INTERVALS FOR SEGMENTS OF THE LOWER MISSOURI RIVER DEFINED BY TRIBUTARIES (CHOJNACKI ET AL., 2012) AND BY GEOMORPHOLOGICAL CRITERIA (JACOBSON ET AL., 2009) (FLOW IS FROM LEFT TO RIGHT).....	130
FIGURE 21. RELATIVE AREA OF LAND CAPABILITY POTENTIAL INDEX SOIL DRAINAGE CLASSES FOR OF THE LOWER MISSOURI RIVER DEFINED BY TRIBUTARIES (CHOJNACKI ET AL., 2012) AND BY GEOMORPHOLOGICAL CRITERIA (JACOBSON ET AL., 2009) (FLOW IS FROM LEFT TO RIGHT).	131
FIGURE 22. SOIL DRAINAGE CLASSES (LEFT) AND FLOW-RETURN INTERVALS (RIGHT) AT THE MOUTH OF TH BIG SIOUX RIVER (WITHIN THE BLUE-HIGHLIGHTED VALLEY CROSS-SECTION).....	132
FIGURE 23. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE BIG SIOUX RIVER.	132
FIGURE 24. RELATIVE AREA REPRESENTED BY FLOW-RETURN INTERVALS WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE BIG SIOUX RIVER.	133
FIGURE 25. SOIL DRAINAGE CLASSES (LEFT) AND FLOW-RETURN INTERVALS (RIGHT) AT THE MOUTH OF THE PLATTE RIVER (WITHIN THE BLUE-HIGHLIGHTED VALLEY CROSS-SECTION).....	134
FIGURE 26. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE PLATTE RIVER.	134
FIGURE 27. RELATIVE AREA REPRESENTED BY FLOW-RETURN INTERVALS WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE PLATTE RIVER.	135
FIGURE 28. SOIL DRAINAGE CLASSES (LEFT) AND FLOW-RETURN INTERVALS (RIGHT) AT THE MOUTH OF THE KANSAS RIVER (WITHIN THE BLUE-HIGHLIGHTED VALLEY CROSS-SECTION).	136
FIGURE 29. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE KANSAS RIVER.	136
FIGURE 30. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE KANSAS RIVER, EXCLUDING URBAN AND OTHER HUMAN-MODIFIED SOIL TYPES.	137
FIGURE 31. RELATIVE AREA REPRESENTED BY FLOW-RETURN INTERVALS WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE KANSAS RIVER.	137
FIGURE 32. SOIL DRAINAGE CLASSES (LEFT) AND FLOW-RETURN INTERVALS (RIGHT) AT THE MOUTH OF THE GRAND RIVER (WITHIN THE BLUE-HIGHLIGHTED VALLEY CROSS-SECTION).	138
FIGURE 33. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE GRAND RIVER.	139
FIGURE 34. RELATIVE AREA REPRESENTED BY FLOW-RETURN INTERVALS WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE GRAND RIVER.	139
FIGURE 35. SOIL DRAINAGE CLASSES (LEFT) AND FLOW-RETURN INTERVALS (RIGHT) AT THE MOUTH OF THE OSAGE RIVER (WITHIN THE BLUE-HIGHLIGHTED VALLEY CROSS-SECTION).....	140
FIGURE 36. RELATIVE AREA REPRESENTED BY SOIL DRAINAGE CLASSES WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE OSAGE RIVER.	141
FIGURE 37. RELATIVE AREA REPRESENTED BY FLOW-RETURN INTERVALS WITHIN VALLEY CROSS-SECTIONS IN PROXIMITY TO THE MOUTH OF THE OSAGE RIVER.	141
FIGURE 38. COMPARISON OF CHANGES IN FLOW-RETURN INTERVAL INDEX ASSOCIATED WITH THE MOUTHS OF 5 MAJOR TRIBUTARIES OF THE MISSOURI RIVER.....	143

FIGURE 39. COMPARISON OF CHANGES IN SOIL DRAINAGE INDEX ASSOCIATED WITH THE MOUTHS OF 5 MAJOR TRIBUTARIES OF THE MISSOURI RIVER.	143
FIGURE 40. MEAN FLOW-RETURN INTERVAL INDEX AND MEAN SOIL DRAINAGE INDEX FOR TRIBUTARIES (BOTTOM) DRAINING FOUR ECOLOGICAL REGIONS.	145
FIGURE 41. MEAN FLOW-RETURN INTERVAL INDEX AND MEAN SOIL DRAINAGE INDEX FOR TRIBUTARIES (BOTTOM) DRAINING FOUR ECOLOGICAL REGIONS.	146
FIGURE 42. BAR GRAPH OF THE RELATIVE ABUNDANCE OF LCPI FLOW-RETURN INTERVALS ILLUSTRATING A SHIFT TOWARD MORE FREQUENT FLOODING BETWEEN THE FLOW REGIME UNDER DAM MANAGEMENT (1967-2006) AND THE FLOW REGIME BASED ON MODELED FUTURE CHANGES IN DISCHARGE RESULTING FROM CLIMATE CHANGE (2040-2069) (GANGOPADHYAY ET AL., 2012).	149
FIGURE 43. COMPARISON OF LCPI FLOW-RETURN INTERVAL CLASS DISTRIBUTION BETWEEN THE PERIOD OF RESERVOIR MANAGEMENT (1967-2006) AND AS MODELED BASED ON ANTICIPATED FUTURE DISCHARGE PATTERNS UNDER CLIMATE CHANGE (2040-2069; GANGOPADHYAY ET AL., 2012) FOR THE GAVINS, INCISING 1A SECTION OF THE MISSOURI RIVER (HIGHLIGHTED IN INSET).	150
FIGURE 44. COMPARISON OF LCPI FLOW-RETURN INTERVAL CLASS DISTRIBUTION BETWEEN THE PERIOD OF RESERVOIR MANAGEMENT (1967-2006; LEFT) AND AS MODELED BASED ON ANTICIPATED FUTURE DISCHARGE PATTERNS UNDER CLIMATE CHANGE (2040-2069; RIGHT; GANGOPADHYAY ET AL., 2012) FOR THE GRAND, STABLE-AGGRADING 2 SECTION OF THE MISSOURI RIVER (HIGHLIGHTED IN INSET).	151
FIGURE 45. COMPARISON OF LCPI FLOW-RETURN INTERVAL CLASS DISTRIBUTION BETWEEN THE PERIOD OF RESERVOIR MANAGEMENT (1967-2006; LEFT) AND AS MODELED BASED ON ANTICIPATED FUTURE DISCHARGE PATTERNS UNDER CLIMATE CHANGE (2040-2069; RIGHT; GANGOPADHYAY ET AL., 2012) FOR THE SIOUX, STABLE-AGGRADING 1 SECTION OF THE MISSOURI RIVER (HIGHLIGHTED IN INSET)..	151
FIGURE 46. AVERAGE DAILY ESTIMATED RIVER AND GROUNDWATER ELEVATION (M) FOR DEEP WELLS AT THE FOREST CITY SITE RELATIVE TO WATER SURFACE ELEVATION (253 M) AT WHICH OVERLAND FLOW CUTS OFF WELLS FC11 AND FC12 FROM THE REST OF THE FLOODPLAIN.	153
FIGURE 47. A LARGE FLOW PULSE FROM APRIL, 2012 AND A MODERATE FLOW PULSE FROM OCTOBER, 2013, WITH THE TYPICAL PATTERN OF GWRF FOR WELLS AT FOREST CITY, MISSOURI.	155
FIGURE 48. AVERAGE DAILY ESTIMATED RIVER AND GROUNDWATER ELEVATION (M) FOR DEEP WELLS ON THE BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE OVERTON NORTH MANAGEMENT UNIT, MISSOURI RELATIVE TO WATER ELEVATIONS AT WHICH OVERLAND FLOW OCCURS AT CHUTES AND THE LEVEE BREACH.	158
FIGURE 49. A MODERATE FLOW PULSE FROM MAY, 2012 AND A LARGE FLOW PULSE FROM MARCH, 2013, WITH THE TYPICAL PATTERN OF GWRF FOR DEEP WELLS AT OVERTON, MISSOURI.	160
FIGURE 50. MAXIMUM GROUNDWATER RESPONSE FACTOR (GWRF) AS A FUNCTION OF DISTANCE FROM THE RIVER AT FOREST CITY (TOP) AND OVERTON (BOTTOM) IN RELATION TO MODELED MAXIMUM GWRF BASED ON SIMULATIONS FOR THE MISSOURI RIVER NEAR KANSAS CITY, MISSOURI (KELLY, 2000) ..	163
FIGURE 51. POSITIVE LINEAR RELATIONSHIP BETWEEN LAG RATIO AND DISTANCE FROM THE RIVER FOR WELLS AT FOREST CITY (TOP) AND OVERTON (BOTTOM).	165
FIGURE 52. NEGATIVE RELATIONSHIP BETWEEN THE 0.25 EXCEEDANCE RATIO AND DISTANCE FROM THE RIVER AT FOREST CITY (TOP) AND OVERTON (BOTTOM).	167
FIGURE 53. NEGATIVE RELATIONSHIP BETWEEN THE 0.1 EXCEEDANCE RATIO AND DISTANCE FROM THE RIVER AT FOREST CITY (TOP) AND OVERTON (BOTTOM).	168
FIGURE 54 GRAPH OF AVERAGE HOURLY RIVER AND WELL WATER ELEVATION FOR 4 FLOOD PULSES DETECTED BY PAIRED SHALLOW AND DEEP WELLS AT OVERTON NORTH.....	170

FIGURE 55. NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR ALL PLOTS CODED BY TRIBUTARY-DEFINED RIVER SEGMENTS (TOP) (CHOJNACKI ET AL., 2012) AND FLOW-RETURN INTERVAL (BOTTOM) SHOWING AGGREGATION OF PLOTS WITH LONG FLOW-RETURN INTERVALS IN THE GAVINS SECTION. .	173
FIGURE 56. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING FOR PLOTS IN THE GAVINS SAMPLING SITE SHOWING SEPARATION OF COTTONWOOD AND SANDBAR WILLOW COMMUNITIES (LEFT) FROM OTHER COMMUNITIES ALONG A FLOW-FREQUENCY GRADIENT.	174
FIGURE 57. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS IN THE PLATTE SAMPLING SITE SHOWING SEPARATION OF COTTONWOOD-WILLOW FORESTS (RIGHT) FROM OTHER COMMUNITIES (LEFT) ALONG A FLOW-FREQUENCY GRADIENT AND FROM SANDBAR WILLOW COMMUNITIES (REAR) ALONG AN AVAILABLE WATER CAPACITY GRADIENT.....	175
FIGURE 58. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS IN THE SQUAW CREEK NWR SAMPLING SITE SHOWING BLACK WILLOW, POND, AND SILVER MAPLE COMMUNITIES WITH POOR SOIL DRAINAGE, SHORT FLOW-RETURN INTERVALS, AND LOW AVAILABLE WATER CAPACITY (LEFT OF GRAPH).	176
FIGURE 59. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS IN THE FT. LEAVENWORTH SAMPLING SITE SHOWING A SHIFT FROM COTTONWOOD COMMUNITIES TO BOX-ELDER AND ELM FORESTS AS ONE MOVES CLOSER TO THE RIVER AND FURTHER FROM ROADS (LEFT TO RIGHT ALONG AXIS 1).	177
FIGURE 60. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR SPECIES AT LISBON BOTTOM SHOWING THAT COTTONWOOD-WILLOW FORESTS AND ALL WOODY SPECIES ARE LESS DOMINANT AT LOCATIONS WITH POORER SOIL DRAINAGE (LOWER RIGHT OF GRAPH).	179
FIGURE 61. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR JAMESON ISLAND SHOWING DOMINANCE BY COTTONWOOD-WILLOW FORESTS AND DIRECTION OF INCREASE FOR THOSE VARIABLES MOST CORRELATED WITH ORDINATION RESULTS (SOIL DRAINAGE AND AVAILABLE WATER CAPACITY IN THE TOP 50 CM OF SOIL).	180
FIGURE 62. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS AT OVERTON NORTH SHOWING THAT BETTER DRAINED SOILS CLOSER TO THE RIVER (LEFT OF THE ORDINATION ORIGIN) ARE DOMINATED BY COTTONWOOD AND WILLOW COMMUNITIES.	181
FIGURE 63. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS AT OVERTON SOUTH SHOWING THAT BETTER DRAINED SOILS CLOSER WITH LESS FREQUENT FLOODING ARE DOMINATED BY COTTONWOOD COMMUNITIES.	182
FIGURE 64. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS AT EAGLE BLUFFS CONSERVATION AREA, MISSOURI, SHOWING COTTONWOOD-WILLOW FORESTS ON SOILS WITH LOWER AVAILABLE WATER CAPACITY FARTHER FROM THE RIVER THAN OTHER COMMUNITIES.	183
FIGURE 65. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR SPECIES AT EAGLE BLUFFS CONSERVATION AREA, MISSOURI, SHOWING THE AFFINITY OF WILLOWS (<i>SALIX</i> spp.) AND COTTONWOOD (<i>POPULUS DELTOIDES</i>) FOR SOILS WITH LOWER AVAILABLE WATER CAPACITY (LEFT OF ORIGIN) AND OF NEARLY ALL OTHER WOODY SPECIES FOR SOILS WITH HIGHER AVAILABLE WATER CAPACITY (RIGHT OF ORIGIN).	184
FIGURE 66. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS AT St. AUBERT ISLAND SHOWING A TRANSITION FROM EPHEMERAL POND THROUGH COTTONWOOD COMMUNITIES TO BOX ELDER COMMUNITIES AS FLOW-RETURN INTERVAL INCREASES (CROSSES INDICATE CENTROID FOR COMMUNITY TYPE WITH MATCHING COLOR).	185
FIGURE 67. GRAPH OF NON-METRIC MULTIDIMENSIONAL SCALING RESULTS FOR PLOTS AT HOWELL ISLAND CONSERVATION AREA, MISSOURI, SHOWING HIGHER ELEVATIONS OCCUPIED BY BOX ELDER AND COTTONWOOD-WILLOW FORESTS. ADDITIONALLY, DISTANCE FROM THE RIVER SEPARATES BOX-ELDER AND ASH COMMUNITIES (FARTHER FROM RIVER) FROM SILVER MAPLE COMMUNITIES (CLOSER TO RIVER).	186

FIGURE 68. RELATIVE FREQUENCY OF EXOTIC SPECIES SAMPLING POINTS AND EXOTIC SPECIES OCCURRENCES AMONGST FLOW-RETURN INTERVALS.	190
FIGURE 69. PROBABILITY THAT THE INDICATED EXOTIC SPECIES WILL OCCUPY LAND WITH A GIVEN FLOW-RETURN INTERVAL.	191
FIGURE 70. PROBABILITY THAT THE EXOTIC SPECIES WILL OCCUPY LAND WITH THE GIVEN FLOW-RETURN INTERVAL IN THE PRAIRIE PARKLAND (TEMPERATE) PROVINCE (TOP) AND THE CENTRAL INTERIOR BROADLEAF FOREST PROVINCE (BOTTOM).	192
FIGURE 71. BAR GRAPH OF MEAN COVER FOR SIX EXOTIC SPECIES BY FLOW-RETURN INTERVAL CLASS.	193
FIGURE 72. QUANTILE DISTRIBUTION FOR SPECIES WITH SIGNIFICANT DIFFERENCES IN THE DISTRIBUTION OF COVER VALUES BETWEEN FLOW-RETURN INTERVALS.....	195
FIGURE 73. PROBABILITY COVER FOR THE INDICATED EXOTIC SPECIES WILL EXCEED 15 PERCENT ON THE FLOW-RETURN INTERVAL.	196
FIGURE 74. RELATIVE FREQUENCY OF EXOTIC SPECIES SAMPLING POINTS AND EXOTIC SPECIES OCCURRENCES AMONGST SOIL DRAINAGE CLASSES.....	197
FIGURE 75. PROBABILITY THAT EXOTIC SPECIES WILL OCCUPY LAND WITH THE INDICATED SOIL DRAINAGE GROUP.	198
FIGURE 76. PROBABILITY THAT EXOTIC SPECIES WILL OCCUPY LAND WITH THE INDICATED SOIL DRAINAGE GROUP IN THE PRAIRIE PARKLAND (TEMPERATE) PROVINCE (TOP) AND THE CENTRAL INTERIOR BROADLEAF FOREST PROVINCE (BOTTOM).	200
FIGURE 77. BAR GRAPH OF MEAN COVER FOR SIX EXOTIC SPECIES BY LCPI SOIL DRAINAGE CLASS IN ORDER OF INCREASING ABUNDANCE AS SOIL DRAINAGE CAPACITY DECREASES.	201
FIGURE 78. QUANTILE DISTRIBUTION FOR TWO SPECIES WITH SIGNIFICANT DIFFERENCES IN THE DISTRIBUTION OF COVER VALUES BETWEEN SOIL DRAINAGE CLASSES.	202
FIGURE 79. PROBABILITY THAT EXOTIC SPECIES WILL OCCUPY LAND WITH THE INDICATED SOIL DRAINAGE.	203
FIGURE 80. RELATIVE FREQUENCY OF SAMPLING POINTS AND SPECIES GROUP OCCURRENCES AMONGST FLOW-RETURN INTERVALS.	205
FIGURE 81. PROBABILITY THAT SELECT SPECIES GROUPS WILL OCCUPY LAND WITH THE INDICATED FLOW-RETURN INTERVAL.	206
FIGURE 82. PROBABILITY THAT THE COVER OF SELECT SPECIES GROUPS WILL EXCEED 15 PERCENT ON LAND WITH THE INDICATED FLOW-RETURN INTERVAL.	207
FIGURE 83. RELATIVE FREQUENCY OF SAMPLING POINTS AND SPECIES GROUP OCCURRENCES AMONGST SOIL DRAINAGE CLASSES.....	208
FIGURE 84 PROBABILITY THAT SELECT SPECIES GROUPS WILL OCCUPY LAND WITH THE INDICATED SOIL DRAINAGE.	209
FIGURE 85. PROBABILITY THAT THE COVER OF SELECT SPECIES GROUPS WILL EXCEED 15 PERCENT ON LAND WITH THE INDICATED SOIL DRAINAGE.	210
FIGURE 86. RELATIVE FREQUENCY OF MAPPED POLYGONS AND VEGETATION COMMUNITIES ACROSS LCPI FLOW-RETURN INTERVALS FOR BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	212
FIGURE 87. RELATIVE FREQUENCY (TOP) AND RELATIVE AREA (BOTTOM) OF NATURAL COMMUNITIES WITHIN LCPI FLOW-RETURN INTERVALS BASED ON INTERSECTION OF LCPI MODEL AND MAP OF VEGETATION COMMUNITIES AT BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	215
FIGURE 88. QUANTILE DISTRIBUTION FOR VEGETATION COMMUNITIES WITH SIGNIFICANT DIFFERENCES IN THE RELATIVE MAPPED AREA BETWEEN FLOW-RETURN INTERVALS.	216
FIGURE 89. PROBABILITY OF COMMUNITY OCCURRENCE ACROSS FLOW-RETURN INTERVALS.....	217

FIGURE 90. RELATIVE FREQUENCY OF SAMPLING POINTS AND ASSOCIATED VEGETATION COMMUNITIES AMONG LCPI FLOW-RETURN INTERVALS BASED ON PLOT DATA FOR LOCATIONS OUTSIDE OF BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	219
FIGURE 91. PROBABILITY OF COMMUNITY OCCURRENCE ACROSS FLOW-RETURN INTERVALS FOR PLOTS OUTSIDE OF MAPPED PORTIONS OF BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE, MISSOURI.	220
FIGURE 92. RELATIVE FREQUENCY OF VEGETATION COMMUNITY MAPPED POLYGONS ACROSS LCPI SOIL DRAINAGE CLASSES ON BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	222
FIGURE 93. RELATIVE FREQUENCY (TOP) AND RELATIVE AREA (BOTTOM) OF NATURAL COMMUNITIES WITHIN LCPI SOIL DRAINAGE CLASSES BASED ON INTERSECTION OF LCPI MODEL AND MAP OF VEGETATION COMMUNITIES AT BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	224
FIGURE 94. QUANTILE DISTRIBUTION FOR VEGETATION COMMUNITIES WITH SIGNIFICANT DIFFERENCES IN RELATIVE MAPPED AREA BETWEEN SOIL DRAINAGE CLASSES.	225
FIGURE 95. PROBABILITY THAT THE GIVEN COMMUNITY WILL OCCUPY LAND WITH THE INDICATED FLOW-RETURN INTERVAL.	226
FIGURE 96. RELATIVE FREQUENCY OF SAMPLING POINTS AND ASSOCIATED VEGETATION COMMUNITIES AMONG LCPI SOIL DRAINAGE CLASSES BASED ON PLOT DATA FOR LOCATIONS OUTSIDE OF BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	227
FIGURE 97. PROBABILITY THAT THE GIVEN COMMUNITY WILL OCCUPY LAND WITH THE INDICATED SOIL DRAINAGE FOR PLOTS OUTSIDE OF MAPPED AREAS OF BIG MUDDY NATIONAL FISH AND WILDLIFE REFUGE.	228
FIGURE 98. DISTRIBUTION OF CHANGE IN MONTHLY DISCHARGE VALUES BETWEEN HISTORIC PERIOD (1950 TO 1999) AND FUTURE CONDITIONS (2040-2069) FOR BOONVILLE, MISSOURI FROM 112 SIMULATIONS SHOWING BROAD RANGE OF POTENTIAL OUTCOMES DEPENDING ON EMISSIONS SCENARIO, GLOBAL CIRCULATION MODEL, AND INITIAL CONDITIONS (FROM FIGURE A.1 IN GANGOPADHYAY ET AL., 2012)	236
FIGURE 99. DISTRIBUTION OF PLOTS AMONG FLOW-RETURN INTERVALS BY SAMPLE SITE ON THE MISSOURI RIVER.	243
FIGURE 100. DISTRIBUTION* OF JOHNSON GRASS (<i>SORGHUM HALEPENSE</i>) IN THE CONTERMINOUS UNITED STATES (KARTESZ, 2014).	244

LIST OF TABLES

TABLE 1. SOIL DRAINAGE CLASS DESCRIPTIONS FROM THE <i>SOIL SURVEY HANDBOOK</i> (SOIL SURVEY STAFF, 1993).....	2
TABLE 2. TRIBUTARY-DEFINED SEGMENTS AND GEOMORPHOLOGICAL ZONES OF THE LOWER MISSOURI RIVER.....	88
TABLE 3. ELEVATION ATTRIBUTES, DRAINAGE CLASSIFICATION, AND DISTANCE FROM THE RIVER FOR WELLS USED TO MONITOR GROUNDWATER ELEVATION AT FOREST CITY AND OVERTON NORTH.	102
TABLE 4. ALPHABETICAL LIST OF NON-NATIVE SPECIES SELECTED FOR DETECTION DURING 2012 VEGETATION COMMUNITY MAPPING (STRUCKHOFF, 2013).....	110
TABLE 5. SPECIES SELECTED TO REPRESENT LATE-SUCCESSIONAL COMMUNITIES	114
TABLE 6. PERCENT CHANGE IN MEAN MONTHLY DISCHARGE BETWEEN THE HISTORIC PERIOD (1950-1999) AND FUTURE (2040-2069) CONDITIONS BASED ON MODELED EFFECTS OF CLIMATE CHANGE FOR 9 GAGES WITHIN THE AREA MODELED BY THE LCPI (TABLE A.9 IN GANGOPADHYAY ET AL., 2012).....	116
TABLE 7. CHANGE IN MEAN MONTHLY DISCHARGE AND MAXIMUM MONTHLY DISCHARGE BETWEEN HISTORIC PERIOD AND AS MODELED UNDER CLIMATE CHANGE (GANGOPADHYAY ET AL., 2012)	118
TABLE 8. COMPARISON OF MEAN RELATIVE AREA FOR FLOW-RETURN INTERVAL CLASSES WITHIN 40 MILES OF THE TRANSITION BETWEEN ECOLOGICAL PROVINCES.	129
TABLE 9. COMPARISON OF MEAN RELATIVE AREA FOR SOIL DRAINAGE CLASSES WITHIN 40 MILES OF THE TRANSITION BETWEEN ECOLOGICAL PROVINCES.	129
TABLE 10. AREA (HA) OF LAND REPRESENTED BY EACH LCPI FLOW-RETURN INTERVAL CLASS IN TRIBUTARY-DEFINED SECTIONS (CHOJNACKI ET AL., 2012) AND GEOMORPHOLOGICAL ZONES (JACOBSON ET AL., 2009) DURING THE PERIOD OF RESERVOIR MANAGEMENT (1967-2012) AND AS MODELED BASED ON ANTICIPATED FUTURE DISCHARGE PATTERNS UNDER CLIMATE CHANGE (2040-2069; GANGOPADHYAY ET AL., 2012), AND THE PERCENT CHANGE BETWEEN PERIODS.	148
TABLE 11. SUMMARY GROUNDWATER DATA FOR 13 FLOW EVENTS SELECTED FOR ANALYSES AT THE FOREST CITY, MISSOURI.	154
TABLE 12. MEAN MAXIMUM GROUNDWATER RESPONSE FACTOR, LAG RATIO, AND EXCEEDANCE RATIOS FOR WELLS AT FOREST CITY, MISSOURI.....	156
TABLE 13. SUMMARY OF GROUNDWATER DATA FOR 17 DISCREET FLOW EVENTS AT OVERTON, MISSOURI.	159
TABLE 14. MEAN MAXIMUM GROUNDWATER RESPONSE FACTOR, LAG RATIO, AND EXCEEDANCE RATIOS FOR DEEP WELLS AT OVERTON NORTH, MISSOURI.....	161
TABLE 15. SUMMARY OF NON-METRIC MULTIDIMENSIONAL SCALING (NMS) RESULTS BY SITE.	188
TABLE 16. DISTRIBUTION OF SAMPLING POINTS AND EXOTIC SPECIES OCCURRENCES AMONG LCPI FLOW-RETURN INTERVALS.....	190
TABLE 17. RESULTS OF KRUSKAL-WALLIS ANALYSIS OF VARIANCE ON RANKS WITH DUNN’S MULTIPLE COMPARISON TESTS COMPARING EXOTIC SPECIES COVER BETWEEN FLOW-RETURN INTERVALS.....	194
TABLE 18. DISTRIBUTION OF EXOTIC SPECIES SAMPLING POINTS AND EXOTIC SPECIES OCCURRENCES AMONG LCPI SOIL DRAINAGE CLASSES.....	197
TABLE 19. RESULTS OF KRUSKAL-WALLIS ANALYSIS OF VARIANCE ON RANKS WITH DUNN’S MULTIPLE COMPARISON TESTS COMPARING EXOTIC SPECIES COVER BETWEEN SOIL DRAINAGE CLASSES.	202
TABLE 20. DISTRIBUTION OF SAMPLE POINTS AND LOCATIONS WHERE EXOTIC SPECIES COVER EXCEEDED 15 PERCENT.....	203

TABLE 21. DISTRIBUTION OF SAMPLING PLOTS AND SPECIES GROUP OCCURRENCES AMONG LCPI FLOW- RETURN INTERVALS.....	205
TABLE 22. DISTRIBUTION OF SAMPLING POINTS AND SPECIES GROUP OCCURRENCES AMONG LCPI SOIL DRAINAGE CLASSES.....	208
TABLE 23. DISTRIBUTION OF MAPPED VEGETATION COMMUNITIES AMONG LCPI FLOW-RETURN INTERVALS	211
TABLE 24. DISTRIBUTION OF MAPPED VEGETATION COMMUNITIES AMONG LCPI SOIL DRAINAGE CLASSES	221

THE LAND CAPABILITY POTENTIAL INDEX:
A DECISION SUPPORT TOOL FOR THE MANAGEMENT OF MISSOURI RIVER
FLOODPLAIN HABITAT

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ABSTRACT

The Land Capability Potential Index (LCPI) is a hydrogeomorphic model of potential flow-return interval and soil drainage developed as a decision support tool for the restoration and management of floodplain habitat on the lower Missouri River (Chojnacki et al., 2012). Although intended to facilitate coarse-scale assessments of land capability for planning and acquisition purposes, the LCPI captures critical abiotic variables known to affect the distribution of plant species, implying that it may be applied at a variety of scales to anticipate the distribution of plant species and communities and to inform management of floodplain vegetation. The primary purpose of this thesis is to quantify relationships between LCPI flow-return and soil drainage classes and the distribution of plants species and communities on the Missouri River floodplain. Additionally, the following themes are explored: the theory behind the LCPI, landscape factors affecting the current distribution of LCPI classes, groundwater response to changes in river stage in relation to LCPI soil drainage classes, and the potential future distribution of LCPI flow-return intervals based on predicted flow changes resulting from global climate-change.

The current distributions of flow-return intervals and soil drainage classes are explored in relation to Ecological Provinces (Bailey, 1976), river segments defined by geomorphologic characteristics (Jacobson et al., 2009) and major tributaries (Chojnacki et al., 2012), and near the mouths of major and minor tributaries. Results indicate strong and far-reaching effects of management of the Missouri River reservoir system, which results in a greater relative abundance of land with long flow-return intervals in upper portions of the river. Differences in LCPI class abundance at the ecological province level reflect these effects. Flow-return intervals tend to increase through incising sections and decrease through stable and aggrading section. Tributaries are associated with longer flow-return intervals in both ecological provinces, and with poorer soil drainage in the prairie province.

Future changes in LCPI class abundance resulting from climate change are modeled by adjusting water surface elevations for each flow-return interval based on predicted changes in discharge from the Climate Change Analysis for the Missouri River Basin (Gangopadhyay et al., 2012). Results indicate a shift toward wetter conditions throughout the area modeled by the LCPI, increasing opportunities to manage for

wetland species. The relative area of lands where cottonwood forests tend to dominate are expected to decrease in most river sections. Finally, reductions in land area with long flow-return intervals suitable for late successional species are expected throughout the modeled area, but likely will be problematic only in river sections where long flow-return intervals are already scarce.

Groundwater response to flow pulses is compared between soil drainage classes using the Groundwater Response Factor (GWRF) (Kelly, 2000) at two sites in Missouri. Comparisons of mean values for maximum GWRF and lag time to maximum GWRF indicate that more poorly drained soils have reduced and slower responses to flow pulses than better drained soils. Additionally, comparisons of the duration of time that groundwater elevation exceeds 10, 25, and 50 percent of flow pulse magnitude indicate that poorly drained soils are less likely to experience elevated groundwater following flow pulses than better drained soils. These results are inconclusive, but collectively suggest that poorly drained soils are less likely to experience soil moisture recharge as a result of elevated groundwater following flow pulses. This effect may expose poorly drained sites to a broader range of soil moisture conditions and affect plant species' distributions.

Relationships between naturally-occurring floodplain vegetation and LCPI classes in a post-agricultural setting are quantified using pre-existing plot data and contemporary vegetation community maps from 16 sites within the modeled area. Multivariate analyses indicate that LCPI classes often are more strongly correlated to the distribution of species than are other factors known to affect species distribution, including the distance to the river, roads, and levees. Chi-square analyses and analyses of variance on ranks indicate that the distributions of six exotic species (garlic mustard, Japanese hops, Johnson grass, reed canary grass, sweet clover, and velevetleaf) are significantly related to soil drainage, flow-return interval, or both. Five species groups representing herbaceous wetlands (sedges and smartweeds), early-successional woody communities (willows and cottonwood), and late-successional forests also exhibit significant relationships with LCPI classes that are consistent with the known life-history traits of constituent species. Similar analyses of mapped community distributions in relation to LCPI classes confirm the analyses of species abundance data and support the conclusion that the LCPI model is capturing abiotic variables relevant to the distribution and management of plant species and communities on the Missouri River floodplain.

Chapter I:

Introduction

The Land Capability Potential Index (LCPI) is a hydrogeomorphic model of flow-return intervals and soil drainage classes developed for the Lower Missouri River floodplain from the Gavins Point Dam near Yankton, South Dakota to the mouth of the river near St. Louis, Missouri (Chojnacki et al., 2012). The LCPI covers 811 river miles (1,305 kilometers) and 986,000 hectares of bottomlands, and was developed as a decision support tool for the restoration and management of floodplain habitat. Although intended to facilitate coarse-scale assessments of land capability for planning and acquisition purposes, the LCPI captures critical abiotic variables known to affect the distribution of plant species (see the literature review that follows), suggesting that it may be applied at a variety of scales to anticipate the distribution of plant species and communities and to inform management of floodplain vegetation. The primary goal of this thesis is to identify and describe relationships between LCPI classes and the distribution of plant species and communities on the Missouri River floodplain in a post-agricultural setting in which little or nothing has been done to specifically affect species distributions.

The methods used to develop the LCPI are provided in the U.S. Geological Survey Data Series report that accompanied the final version of the model (Chojnacki et al., 2012), and are summarized at the beginning of the “Methods and Materials” section. In brief, a nine-class flow-recurrence index (0–2, 2–5, 5–10, 10–20, 20–50, 50–100, 100–200, 200–500, and greater than 500 years) was generated based on the intersection between a digital elevation model for the floodplain and water-surface elevation models based on eight stream discharges, assuming complete connectivity of the floodplain at each water-surface elevation. Data to inform both elevation models were derived from the Upper Mississippi River System Flow Frequency Study (U.S. Army Corps of Engineers, 2004). Flow data used to estimate flow-return intervals were from the period of reservoir management, beginning in the mid to late 1960s. The flow recurrence index was then intersected with the eight soil drainage classes (Table 1) of soil units in the digital USDA-NRCS Soil Survey Geographic (SSURGO) database (Soil Survey Staff, 2012) to create a 72-class index of modeled flow-recurrence and soil drainage potential.

Table 1. Soil drainage class descriptions from the *Soil Survey Handbook* (Soil Survey Staff, 1993).

Soil Drainage Class	Description
Very poorly drained	Water is at or near the soil surface during much of the growing season. Internal free-water is very shallow and persistent or permanent. Unless the soil is artificially drained, most mesophytic crops cannot be grown. Commonly, the soil occupies a depression or is level. If rainfall is persistent or high, the soil can be sloping.
Poorly drained	The soil is wet at shallow depths periodically during the growing season or remains wet for long periods. Internal free-water is shallow or very shallow and common or persistent. Unless the soil is artificially drained, most mesophytic crops cannot be grown. The soil, however, is not continuously wet directly below plow depth. The water table is commonly the result of low or very low saturated hydraulic conductivity class or persistent rainfall, or a combination of both factors.
Somewhat poorly drained	The soil is wet at a shallow depth for significant periods during the growing season. Internal free-water is commonly shallow to moderately deep and transitory to permanent. Unless the soil is artificially drained, the growth of most mesophytic plants is markedly restricted. The soil commonly has a low or very low saturated hydraulic conductivity class, or a high water table, or receives water from lateral flow, or persistent rainfall, or some combination of these factors.
Moderately well drained	Water is removed from the soil somewhat slowly during some periods of the year. Internal free water commonly is moderately deep and may be transitory or permanent. The soil is wet for only a short time within the rooting depth during the growing season, but long enough that most mesophytic crops are affected. The soil commonly has a moderately low, or lower, saturated hydraulic conductivity class within 1 meter of the surface, or periodically receives high rainfall, or both.
Well drained	Water is removed from the soil readily, but not rapidly. Internal free-water commonly is deep or very deep; annual duration is not specified. Water is available to plants in humid regions during much of the growing season. Wetness does not inhibit growth of roots for significant periods during most growing seasons.
Somewhat excessively drained	Water is removed from the soil rapidly. Internal free water commonly is very rare or very deep. The soils are commonly coarse-textured, and have high saturated hydraulic conductivity, or are very shallow.
Excessively drained	Water is removed from the soil very rapidly. Internal free water commonly is very rare or very deep. The soils are commonly coarse-textured, and have very high saturated hydraulic conductivity class or are very shallow.
No data	These soils have no drainage class information recorded, often these areas are underwater or urban areas.

The first part of this thesis is a literature review exploring the theory behind the LCPI and examining how the abiotic environmental factors captured within LCPI classes are expected to influence vegetation. Specific relationships explored include the effect of elevation on the frequency, duration, and kinetic energy of surface water inundation, how depth to groundwater (also a function of elevation) affects the hydroperiod in both protected and connected floodplains, and how soil drainage class can influence hydroperiod by affecting the flow of both surface and groundwater. The potential effects of these

relationships on vegetation are examined within the context of past and current land use, stochastic events, and succession.

Following the literature review, there are four analytical research elements to this thesis:

1. the current distribution of LCPI classes
2. variation in groundwater response to changes in river stage by LCPI soil drainage classes
3. relationships between LCPI classes and naturally occurring vegetation in a post-agricultural setting
4. potential future distribution of LCPI classes given changes in stream discharge due to global climate change.

If relationships between LCPI class and vegetation are to serve as the basis for resource management within the floodplain, an understanding of broad patterns of LCPI class distribution is necessary to assess the potential of the landscape to support desirable communities and species in the patterns deemed appropriate to achieve regional planning goals. For example, management for moist soil communities in river stretches with few representations of the wetter LCPI classes may require a different approach than management for those community types where wet LCPI classes are abundant. In the former case, special effort may be required to acquire and manage for lands capable of supporting wet community types. Community types that require frequent short-term inundation may require a particular suite of management actions within river sections where altered river hydrology makes overland flow less likely. And susceptibility of LCPI classes to non-native species invasion depends upon the interactions between individual species' traits and the availability of suitable habitat for their initial establishment, long term survival, and reproduction. As is shown in the literature review that follows, these factors are determined by, among other things, flood patterns and soil conditions modeled by the LCPI.

In the first research element, the relative abundances of LCPI classes in the Lower Missouri River floodplain are quantified based on ecological context, including ecological province, geomorphologically distinct river segments, proximity to major tributaries, and trends associated with tributaries draining various ecological regions. Land-use affects stream hydrologic and sediment characteristics (Malanson, 1993), and ecoregional differences in land-use have been used to classify streams (Rohm et al., 1987). The above factors are assumed to determine both the potential for inundation (through their influence on stream hydrology) and the physical properties of floodplain soils (through their influence on the total load and

particle-size distribution of suspended sediment that forms soil parent material). The objective within this section is to describe the relationships between broad ecological context and LCPI class abundance to alert regional and local planners to the issues that affect LCPI class distribution, and thus the potential for floodplain lands to support desired plant communities at multiple scales. Although no specific hypotheses are tested, a few questions are addressed:

1. Are there differences in the abundance of LCPI classes between ecological Provinces?
2. Are there differences in the abundance of LCPI classes between hydrogeomorphic sections?
3. Are tributaries associated with shifts in LCPI class abundance?
4. Are there trends in changing LCPI class abundance associated with tributaries draining different ecological regions (do tributaries from a given region share a hydrogeomorphic signature?)

To address the second research element, groundwater hydrologic parameters are quantified in relations to LCPI soil drainage classes using newly collected groundwater elevation data from wells on two floodplains within Missouri. The goal is to quantify how soil drainage class is related to both site-level (river reach) and local (soil mapping unit) groundwater response to changes in river stage. Specific questions explored include whether qualitative soil drainage classes predict the relative magnitude, speed, and duration of the groundwater response to flood peaks at the local and site-level scales, comparing observed groundwater response to flow changes to that predicted by the Groundwater Response Factor (GWRF) (Kelly, 2000).

The primary purpose of the research presented here is to quantify relationships between LCPI classes and the distribution and abundance of plant species and communities. The LCPI incorporates many of the abiotic factors known to influence species distribution on floodplains and in other wetland systems (see literature review that follows). Therefore, it is reasonable to expect LCPI classes to relate to the abundance of individual plant species and vegetation communities. However, the ability of the LCPI to predict species abundance at any given location on the floodplain may be hindered by the influence of site-specific past land use, land use in the adjacent landscape, stochastic events, and processes of competitive exclusion that preclude a response by species or communities to the abiotic factors for which the LCPI is a surrogate.

In the research presented here, relationships are described between vegetation and LCPI classes amidst the noise caused by other environmental factors, focusing on minimally managed areas in a post-agricultural setting. Specific null hypotheses examined in this section include:

1. The likelihood of occurrence for species does not vary between LCPI flow-return intervals or soil drainage classes.
2. Mean percent foliar cover for species does not vary between LCPI flow-return intervals or soil drainage classes.
3. The likelihood of a species becoming abundant does not vary between LCPI flow-return intervals or soil drainage classes
4. The likelihood of occurrence for communities does not vary between LCPI flow-return intervals or soil drainage classes.
5. Mean area occupied by communities does not vary between LCPI flow-return intervals or soil drainage classes.

Though not designed to test the efficacy of management actions for particular species or communities, it is assumed that the analyses presented here can inform decision making to increase resource management efficiency in more intensively managed area.

In the final research element, the likely future distribution of LCPI classes is examined in the context of changes in discharge predicted by analyses of climate change on the water budget for the Missouri River basin, with a complementary assessment of the potential impact on management for or against particular plant communities and species. Projected changes in discharge are related to historical flow regimes to anticipate future flow-return intervals based on current relationships between land-surface and water-surface elevations. As with the LCPI itself, this exercise is not intended to predict future flooding, but to provide a relative wetness index relevant to floodplain habitat management.

Theory behind LCPI: a comprehensive literature review

Scope and terms

Before delving into the theory behind the LCPI, it is necessary to establish its physical scope, define some commonly used terms, and explain the use of interrelated concepts. The geographic scope of the LCPI is the floodplain of the Lower Missouri River from the Gavins Point Dam to the confluence with the Mississippi River near St. Louis, Missouri. The model includes land surfaces between the bluff lines

that define the river valley and can extend up the mouths of major tributaries many miles. The model includes the conceptual floodplain of Ward et al. (2002) and Bren (1993), as well as the active channel of Osterkamp and Hupp (1984). Ephemeral features in the active channel are included to the extent that land surface elevation was measured on them during the Upper Mississippi River System Flow Frequency Study (U.S. Army Corps of Engineers, 2004), from which the land-surface elevation data used to develop the LCPI was taken. The LCPI also includes high ancient or recent fluvial terraces that may experience infrequent or no flooding because of their high elevation relative to the stream channel.

This review omits one third of Soil-Plant-Atmospheric Continuum (Philip, 1966). For the purposes of this discussion, water is assumed to reach the riparian system, from which it either flows outward as the Missouri River or recharges groundwater and soil moisture, where it is used by plants or lost from the system. Little or no attention is given to the manner in which water is delivered from, cycled within, or returned to the atmosphere. Soils are explored to the extent that soil attributes are reflective of and can be predicted by modeled LCPI classes and the degree to which those attributes are related to plant species and community distributions. Although vegetation is known to influence the hydrology and soil development of sites, it is examined primarily as a function of soil and hydrologic conditions.

The key modeled elements of the LCPI are 9 flow-return intervals (0–2, 2–5, 5–10, 10–20, 20–50, 50–100, 100–200, 200–500, and greater than 500 years) and 8 soil drainage classes (Table 1) (Chojnacki et al., 2012). Flow-return interval is the mean number of years that pass between river stages high enough to inundate a given location, based on flow patterns during the period of reservoir management. The modeled flow-return interval in the LCPI is derived from the intersection of land-surface elevation with water-surface elevation as modeled for various discharges. The LCPI assumes connectivity to the river and an absence of flow impeding structures, and it does not account for topographic effects on water surface elevation other than those explicitly included in the stage-discharge relationships used to derive water surface elevations associated with each river mile (U.S. Army Corps of Engineers, 2004; Chojnacki et al., 2012). Because of the direct link between flow-return interval and elevation, much of this review focuses on the relationship between those two parameters and vegetation distribution.

The LCPI flow-return intervals also provide an index for wetness relating to hydrologic parameters not specifically included in the model, including flow depth, duration, and energy. Given that

LCPI flow-return interval represents the intersection of land surface with a level modeled water surface, for any given floodplain location, it is inversely related to the depth and duration of a particular flood event. Low areas with shorter flow-return intervals are flooded first, are the last areas exposed as floods recede, and experience deeper flooding than higher elevation sites with longer flow-return intervals. Additionally, given the greater depth experienced at more frequently flooded sites, these areas also are exposed to more flow energy (although velocity is also influenced by local land shape and roughness, factors not modeled by the LCPI). Also, to the extent that groundwater elevation depends on river stage, longer flow-return intervals are associated with greater depth to groundwater and diminishing contribution of groundwater to surface inundation. Finally, it is worth noting that flow-return interval is inversely proportional to flood frequency and flow probability; locations with longer modeled flow-return intervals experience overland flow less frequently and have a lower flow probability (Poff et al., 1997). Within this review, in order to adhere to the language of the specific studies cited, flow-return interval, flow (or flood) frequency, and flow probability are used interchangeably. (“Flow-return interval” is used exclusively when discussing the LCPI model in the analytical section, because the LCPI is not a model of flood risk.) The influence of variation in flow frequency, depth, duration, and energy are explored in the sections that follow.

Soil drainage classes in the LCPI are taken directly from the SSURGO database (Soil Survey Staff, 2012), within which they are defined by the observed or inferred presence of internal free water in the soil profile for varying periods during the year (Soil Survey Staff, 1993). Where free water is not directly observed, its periodic presence is inferred from the size, shape, and color of redoximorphic features and gleying of the soil that indicate oxygen depletion due to the presence of water (Schoeneberger et al., 2012). All else being equal, coarser soils with higher hydraulic conductivity are more likely to be classified as well-drained than are fine-textured soils (Soil Survey Staff, 1993); however, soil drainage is not solely a matter of soil texture and hydraulic conductivity. Other conditions or processes that can maintain water within the soil profile include persistent water input due to precipitation or overland flow, a perched water table due to bedrock control or a significant shift in soil texture (for example a subsurface clay lens), or a water table close to the soil surface (Soil Survey Staff, 1993).

Sections of the review that follows focus on particular species or species groups that are important to resource managers along the Lower Missouri River. Early-successional species given much attention

include eastern cottonwood (*Populus deltoides*) and other members of the *Populus* genus, and a variety of willows (*Salix* spp.), including sandbar willow (*S. interior*), peachleaf willow (*S. amygdaloides*), black willow (*S. nigra*), and Missouri River willow (*S. eriocephala*). Frequently mentioned mid-successional woody species include box elder (*Acer negundo*), silver maple (*A. saccharinum*), ash (primarily *Fraxinus pennsylvanica*), elm (*Ulmus* spp.), hackberry (*Celtis occidentalis*), and sugarberry (*C. laevigata*). The most frequently mentioned late-successional species are bottomland oaks (*Quercus* spp.), black walnut (*Juglans nigra*), sugar maple (*Acer saccharum*), pecan (*Carya illinoensis*), and other hickories (*Carya* spp.). Among herbaceous species, the most frequently studied groups of species are non-native species (Federal Interagency Committee for the Management of Noxious and Exotic Weeds, 2003) and those that identify various wetland types, including cattails (*Typha* spp.), sedges (particularly *Carex* spp. and *Cyperus* spp.), smartweeds (*Polygonum* spp.), and prairie cordgrass (*Spartina pectinata*). Within this review, the response of a particular species to environmental conditions is often less important than the fact that species respond differently in a manner that affects their distribution on the floodplain. Unless there is specific evidence to the contrary, the relationships between environmental parameters and a particular member of a species group or genus are assumed relevant to other members of that group within the Missouri River corridor. Plant nomenclature follows the Integrated Taxonomic Information System (2014).

The abiotic template

The earliest attempts to link ecological processes to the distributions of communities along major rivers in the United States emphasized successional processes. These works reflect the influence of Cowles (1899; 1911) and Clements (1909; 1916), and frequently present a progression from pioneer communities to a variable climax community. On the Missouri and Mississippi Rivers, this paradigm is exemplified by the works of Johnson (1949) and Shelford (1954), respectively. Both authors describe a progression from willow, through increasingly older black willow and cottonwood communities, then ash and box elder dominated communities, and finally bottomland hardwoods communities with more oak and elm along an increasing elevation gradient. The influence of hydrology is addressed by way of the lateral migration of the river that allowed the initial deposition of sandbars, as well as periodic flooding and deposition of sediment, nutrients, and organic matter that advance successional processes. Johnson and Shelford recognize that those successional processes are accompanied by changes in the soil texture observable

along an elevation gradient, but largely leave unexplored the influence of soil and other abiotic factors on community development. Both authors describe community distributions that reflect meander processes that had functioned prior to channelization of both streams; their findings may have limited applicability to the distribution of communities on currently constrained portions of the Lower Missouri River.

By the end of the 1950s, researchers had begun to examine the relationships between elevation, soil attributes, and vegetation. Wistendahl (1958) describes the distribution of soils and vegetation along the related gradients of elevation and distance from the Raritan River [New Jersey], identifying flood frequency as the dominant factor controlling those distributions. Although Wistendahl (1958) examines communities according to their perceived successional stage, more emphasis is given to abiotic controls on community development than in Johnson (1949) and Shelford (1954). Weaver (1960) describes the distribution of communities on the Missouri River along an elevation gradient with corresponding descriptions of the dominant soil types associated with each community. Although the distributions of communities are described as a function of their historic development and the vegetation patterns are similar those of Johnson (1949), succession is not emphasized. Instead, Weaver relates the distribution of species to the drainage capabilities of the soils on which they occur. Cottonwoods and willows are found mostly on low floodplains closer to the river on well-drained, coarse soils associated with deposition in areas of higher stream velocity; marshes and swamps are found mostly on poorly drained, finer textured soils in low topographic positions; moderately drained sites are dominated by prairie cordgrass; and prairies are found in the highest locations on a variety of soil types where available water for growth is limited.

Vannote et al. (1980)

Approximately two decades later, Vannote et al. (1980) introduced the river continuum concept, in which the physical structure and hydrology of stream systems combine to form a template for the biological responses of species, resulting in predictable patterns of community structure and function. This concept asserts that species respond to gradients in order to maximize the efficiency with which they can exploit their environment, resulting in longitudinal patterns in riverine systems that are optimized to consume and dissipate the kinetic energy of the system. The authors explicitly abandon the concept of succession to focus on the response of individuals to energy gradients, a paradigm shift enabled by the increasing acceptance of the theory of individualistic response of plants to the environment (Gleason, 1926) and the

development of direct gradient analyses (Whittaker, 1967) as a means of study them. The applicability of these methods to large river floodplains had recently been demonstrated by Robertson et al. (1978), for whom the distribution of species along the Mississippi River reflected a response to an inundation gradient driven by elevation and a soil aeration gradient driven by soil texture and elevation. At the same time, the concept of a template of abiotic factors was being applied by the National Wetland Technical Council to identify and classify zones of vegetation in bottomland hardwoods of the southeastern United States (Clark and Benforado, 1981).

Wharton et al. (1982)

The river continuum concept was advanced further by Wharton et al. (1982), who considered plant species and communities as buffers to the physical energy of the riparian systems and assigned less importance to successional processes. Based on their understanding of bottomland swamps along streams in the southeastern United States, they identify flooding, soils, and slight elevation changes as the key variables establishing the environmental parameters affecting species distribution. Similar relationships had been described along the Missouri River (Keammerer et al., 1975). Among those parameters, they identify anoxic conditions as the primary factor determining the distribution of species on floodplains, and define flood tolerance almost exclusively by the ability to withstand such conditions. Other plant adaptations to the riverine environment, including the ability to withstand physical flood damage, to propagate and rapidly occupy newly exposed soils, to withstand periods of low water availability, or to compete well against other species are viewed as far less relevant to species distributions than tolerance of anoxic conditions. Elevation is the key determinant of flood depth and duration, which has direct effects on oxygen exchange between plants, soil, and the air. These factors combine with soil attributes (also a function of elevation) to establish the anoxic regime of sites, and the variable tolerances of plant species to anoxic conditions determines their distribution along the resulting oxygen-availability gradient. Elevation also is a key factor affecting the quantity and quality of organic matter and nutrients, and their subsequent fate within the system, as determined by soils, hydroperiod, and oxygen availability.

Brinson (1990)

The interrelationships between fluvial process, floodplain features, soils, and vegetation on large river systems are integrated into a description of an idealized floodplain in Brinson's (1990) review of the subject. In that work, the progression from a high naturally occurring levee with coarse substrate, across a topographically variable, lower floodplain, to swales with extended hydroperiods is accompanied by predictable shifts in plant communities. Throughout, variations in elevation and soil drainage of the type captured by LCPI classes play a prominent role in determining the hydrological conditions to which species must be adapted in order to germinate, become established, and survive.

Brinson describes a spectrum of flood types between those that are high in total power and occur infrequently, and those that are low in power and occur frequently, sometimes more than once per year. He ascribes to the former the ability to generate geomorphic patterns that last hundreds or thousands of years, and to the latter the ability to determine short-term effects such as seedling germination and early plant survival. The LCPI specifically models potential inundation frequency, but it is unable to serve as a useful model of flood power in terms of kinetic energy at any given location because it in no way addresses the local topography that will influence the velocity and turbulence of currents across the floodplain; however, the LCPI may serve as a useful surrogate for other measures of flood intensity that are determined by elevation, including flood depth and duration. In order for this to be true, we must assume Brinson's idealized floodplain "where complex topographic features are lacking and the floodplain slopes gently from the river channel to uplands", and within which "flooding frequency and depth are inversely proportional to floodplain elevation." Brinson notes the work of Franz and Bazzaz (1977), whose work shows that most floodplain species are normally distributed around a mean elevation, in accordance with the gradient response concepts of Gleason (1926) and Whittaker (1967). In his warning that vegetation responds to factors other than elevation, Brinson (1990) specifically mentions the other element modeled by the LCPI—soil drainage—as well as two factors closely linked to drainage, soil texture and aeration (Brady and Weil, 2008).

Brinson spends only a little time discussing groundwater, but he relates groundwater processes to the environmental variables modeled by the LCPI. When he connects groundwater processes to stream stage, the duration of flood pulses, and to potential hydroperiod on the floodplain itself, he is clear that

elevation determines the depth to groundwater and the potential contribution of groundwater to inundation in the absence of overland flow. Within the context of the LCPI, areas with longer flow-return intervals represent higher elevations, and generally have greater depth to groundwater and less frequent contributions from groundwater to surface pooling, all else being equal. Brinson cites the work of Grannemann and Sharp (1979) to note that the nature of the substrate also influences groundwater processes: “Thick clay strata and clay plugs reduce transmissivity and create longer time lags in the response of groundwater level to river stage than do sand or silt.” The soil drainage classes incorporated into the LCPI reflect the combined effects of flooding and soil hydraulic conductivity (transmissivity) as determined both by the texture of individual soil strata and their arrangement, with sharp transitions in soil texture impeding water flow (Soil Survey Staff, 1993).

In his discussion of vegetation, Brinson frequently attributes commonly observed patterns on floodplains to those environmental variables modeled by the LCPI. He notes that, “The pattern of vegetation most often observed in riverine forests is that species composition changes along a gradient of flooding frequency”. He cites research relating site tree richness to hydroperiod and flood frequency, and notes differential germination and survival depending on substrate. He is also careful to reiterate the findings of Hupp and Osterkamp (1985), that the adaptations of species must be considered in conjunction with hydrology in order to have a hope of predicting the distribution of plant species and communities. Brinson describes a floodplain system in which individual species respond to a moisture gradient (Gleason, 1926), with saturated, potentially anaerobic conditions at one end and low water potential at the other.

Brinson recognizes that ecoregional variation affects the relationships between vegetation and floodplain features. Hydroperiod is determined by local site factors such as elevation and soil, but also by location within a stream system and the local and basin-wide rainfall patterns. Climate obviously influences rainfall patterns, but also determines temperature regimes that define the potential ranges of species. Biogeographic location influences the geology, soils, and land-use patterns that determine the hydrologic and sediment regimes. It also defines the potential suite of species able to contribute seed to floodplain seedbanks. This latter effect accounts for the broad range of species used by Brinson to describe regional vegetation patterns on floodplains (the area modeled by the LCPI being entirely within his Central Forest

Region). Despite regional differences in species composition, the broad patterns relating floodplain features to hydrology and vegetation are consistent throughout all the regions Brinson examines.

Although Brinson recognizes the relationships between vegetation, soils, and hydrology, he would later develop a wetland classification systems based solely on the abiotic factors of geomorphic setting, water sources, and hydrodynamics (Brinson, 1993). He recognizes that “vegetation often provides important clues of the hydrodynamics at work”, but he wanted a classification system that was “relatively independent of the biogeographic distribution of species”. The Missouri River clearly occupies the riverine type identified in that system, with surface (flooding) and near-surface (groundwater response to flood pulses) flow dominating the hydrologic function to a much greater extent than either direct precipitation or groundwater inputs. Within that wetland type, the relations between elevation, hydroperiod, hydrologic energy, soils, and vegetation described in his earlier work become more important. Not coincidentally, wetland management techniques simultaneously were being developed based on control of the timing, frequency, depth and duration of flooding (Fredrickson and Batema, 1991).

Malanson (1993)

Malanson (1993) approaches the fluvial systems from a landscape ecology perspective, with the specific goal of understanding how patterns of riparian tesserae (landscape elements) and vegetation arise from and influence fluvial processes. He defines riparian to include not just areas within the bank full zone (Hupp, 1988), but also floodplains and terraces where energy and matter fluxes are dominated by fluvial processes, including flooding and groundwater responses to river fluctuations. His chapter on species dynamics focuses on concepts of landscape ecology— edge, connectivity and fragmentation, barriers and corridors—that affect species movement and determine where propagules of plant species may be deposited. These concepts generally are not addressed in this review because they are beyond the scope of the LCPI. Regarding connectivity, however, it is important to note that the LCPI model assumes connectivity to the river and does not take into account whether or not water has an overland flow path to all areas in the valley bottom at or below the modeled water-surface elevation.

Landscape structure

Malanson's concept of "landscape structure" informs how the distribution of LCPI classes changes with ecological context. He defines landscape structure as "the spatial pattern of the riparian zone within its region, including the major gradient from the source to the mouth of the river and its width." This gradient is analogous to that identified in the river-continuum concept (Vannote et al., 1980). Much as Brinson (1990) did for species composition, Malanson views landscape structure as a function of longitudinal changes in stream hydrology as a river system grows and passes through different ecological settings. Malanson specifically notes the influence of dams and tributary streams on hydrologic and sediment regimes.

Ecoregions are defined by the climate, soils, topography, and vegetation (Bailey, 1976), factors that determine the hydrologic and sediment inputs into the fluvial systems. Malanson advances his own classification of river types, with the Missouri River exemplifying rivers within his forest-grassland transition and grassland landscape types. Furthermore, Malanson points out that land-use affects stream hydrologic and sediment characteristics, and that ecoregional differences in land-use (Omernik, 1987) have been used to classify streams (Rohm et al., 1987). Ecoregional variation relevant to the Missouri River include variations in sediment quantity and quality from tributary streams, land-use changes between the Prairie Parkland (Temperate) Province and the Central Interior Broadleaf Forest Province, and a constriction of the valley below the transition between those two regions (Nigh and Schroeder, 2002).

Internal Structure

Malanson notes that landscape-scale processes help determine site-scale fluvial actions, thus shaping what he terms the "internal structure" of floodplains, defined as the arrangement of tesserae and associated vegetation on a transverse or local portion of a riparian zone. Central to this concept is the heterogeneous distribution of disturbance and resources that determine the germination success and long-term survival of individual plant species. Thus, Malanson introduces two of three paradigms he views as fundamental to riparian ecology: the individualistic response of species to environmental gradients (Gleason, 1926), and the intermediate disturbance hypothesis (Connell, 1978). The third paradigm is competition (Keddy, 1989), which Malanson views as a limit on each species' ability to respond to environmental gradients. Malanson describes riparian habitats as a "classic example of clear environmental

gradient” from upland terrestrial to aquatic conditions, with the availability of water at its core. Though water availability is central, its distribution is closely tied to a variety of other environmental gradients, including soil texture, nutrients, and coarse and dissolved organic matter. About disturbance he is more equivocal, mentioning briefly relationships between flood frequency and diversity, but focusing more on flooding attributes as environmental gradients to which individual species respond. He notes that riparian landforms shape the disturbance regime, and relates the probability of fluvial disturbance to zonation of vegetation across the valley bottom: “The specific spatial pattern of riparian vegetation is seen as a result of, and a control on, the ecological, geomorphological, and hydrological processes that operate along rivers.” In a broad sense, the LCPI is a model of the internal structure of two of Malanson’s three paradigms—potential disturbance and environmental gradients.

Direct effects of flooding

According to Malanson, direct actions by which flooding can affect plants are limited to mechanical damage (ranging from scarring to complete removal of plants), suffocation due to submersion and anoxic soil conditions, damage to or stimulation of propagules, and the distribution of those propagules to new sites. The degree to which flooding affects extant vegetation is determined by local flood frequency and intensity (defined to include depth, duration, and velocity). Malanson concedes that local topography and hydrology are important determinants of these factors, but concludes that elevation itself is often most closely associated with vegetation patterns.

Elevation is a key factor in determining plant dispersal and establishment patterns as well. Regarding propagule movement during floods, the concepts of landscape ecology upon which Malanson focuses are useful when we consider the role of elevation. It is the relationship between water elevation and land elevation that determines the degree to which low areas serve as conduits for and high areas serve as barriers against propagule flow. This dynamic interaction is beyond the scope of the LCPI, which assumes connectivity at sites under particular water-surface elevations. Nevertheless, in Malanson’s view, the duration of inundation is a function of elevation and determines the viability of propagules wherever they may be deposited; the seeds or vegetative propagules of some species survive direct contact with water for longer periods than others. Furthermore, Malanson points out that elevation determines the timing of flooding at any particular site and creates the necessary synchrony between the recession of flood waters,

the availability of viable propagules to be deposited (also determined by species' life-history traits), and soil conditions necessary to support establishment on new sites. Elevation also creates environmental gradients (for example, soil texture, nutrient content, and water holding capacity) in the sediment and debris with which propagules are deposited. Malanson correctly identifies these interactions as indirect effects on species establishment and survival, and they are addressed in the next section.

Indirect effects of flooding

According to Malanson, indirect mechanisms by which fluvial forces affect plant distributions are through the generation of resource patches upon which different species depend. Chief among those resources is water, which Malanson identifies as both an enabling resource (for those species that require an abundance of water), and a stressor (for those plant species that do not possess characteristics that enable survival in the anoxic conditions associated with prolonged flooding). Many of the studies cited by Malanson were conducted along the Missouri River and its tributaries (Weaver, 1960; Johnson et al., 1976). According to Malanson, during flood events, the abundance (or overabundance) of water depends primarily on elevation. Malanson also notes that, in the absence of flooding, topography, soil characteristics, and depth to groundwater determine water availability. The latter relationships are particularly germane to the application of the LCPI to vegetation management on protected floodplains where flooding is less likely than on similarly situated floodplains without protective levees.

According to Malanson, other than water, the primary resources required by plants are those that are obtainable from soil, including nutrients and the textural and structural properties that enable establishment and long-term survival. At the most basic level, the soil provides the physical medium for growth. Because fluvial systems are dominated by Entisols, and soils with physical properties that prevent the long-term survival of plants (for example clay pans that are impenetrable to roots) are generally rare (Brady and Weil, 2008), and virtually absent from the area modeled by the LCPI (Soil Survey Staff, 2012). The ability of soils to support trees as opposed to herbaceous communities in the face of flood waters and wind (especially when soils are saturated) depends on soil physical properties such as shear strength. Within the area modeled by the LCPI, these properties of soils are largely a function of soil texture and the pattern in which soil has been deposited over time (Brady and Weil, 2008). Research by Alexander and

Prior (1971) demonstrates that the spatial and temporal patterns of sediment deposition are a function of topography, especially elevation.

Like Brinson (1990) before him, Malanson describes a pattern in which coarse soils are deposited on higher sites and fine soils are deposited in low landscape positions, noting that local topographic features may disrupt this general pattern. Malanson's chapter of cascades of material and energy stresses that along with that mineral soil, contaminants, nutrients, and coarse and dissolved organic matter are being distributed in a heterogeneous manner that determines vegetation patterns. These also are deposited in predictable patterns, with coarse woody debris accumulating in high water channels, finer organic matter distributed to sites with slower moving water, and nutrients accumulating in low lying areas (where they are often chemically transformed during extended inundation). Additionally, soil texture and chemistry affect the availability of these constituents once they are delivered to a site (Brady and Weil, 2008). Many of these interactions are mediated by water itself, with the amount of nutrient or contaminant delivered to a site dependent on surface or groundwater flux as determined by elevation, local topography, and soil characteristics. As noted above, Malanson relates the abundance of oxygen as a subcomponent of water availability; but it could just as easily be treated as a separate resource that is dependent on above and below groundwater flux. Throughout Malanson's review, soil texture, nutrients, and other resources are deeply intertwined, and he is not concerned with suggesting which is most important. Perhaps that is because he sees them as so much less important than flood disturbance and the availability of water, upon which they are so dependent.

Parker and Bendix (1996)

Parker and Bendix (1996) also make a distinction between the direct and indirect mechanisms by which geomorphic processes influence the distribution of plant species. Indirect mechanisms include shaping the landscape in ways that affect microclimate and hydrologic processes. They conclude that one of the most important effects of geomorphic processes is on the distribution of sediments. They note that, because of variations in flow velocity and turbulence, that distribution of sediments is always heterogeneous in depth and properties. And it is the soil properties at a particular site that determine the soil aeration (Johnson et al., 1976), water availability (Malanson, 1993), and nutrient and contaminant availability (Viereck, 1970) that enhance or inhibit germination and survival of plant species. Parker and

Bendix note that sediment distribution also influences competitive interactions among different species. I note here that sediment movement and deposition can both mitigate the effect of human actions (for example, by depositing fresh, loose sediment on top of compacted agricultural sites or by removing contaminated soils) and exacerbate them (for example, by depositing contaminated sediment into particular areas). In a highly disturbed setting such as the Missouri River, the interaction between past land-use on the one hand, and erosion and sediment deposition patterns on the other, may be particularly important in determining the distribution of plant species.

Direct mechanisms by which fluvial processes influence vegetation noted by Parker and Bendix include those fluvial processes, most notably flooding, that change the vegetation itself. The effects include removal of vegetation and transport of seed to sites favorable to germination, establishment, and reproductive success. They cite numerous studies (Wistendahl, 1958; Hosner and Minckler, 1963; Robertson et al., 1978; Yanosky, 1982; Hupp and Osterkamp, 1985) that relate floodplain vegetation to the likelihood of disturbance and colonization due to flooding, two factors that are determined by topographic position within a floodplain. Critical to the concept of the LCPI and its potential to predict the distribution of plants species are their conclusions relating the likelihood of vegetation altering disturbances and the distribution of soils to elevation.

Finally, Parker and Bendix address the notion of longitudinal variation in stream hydrology as determined by landscape characteristics that are independent of but have effects on fluvial processes. These include simple hydrologic realities of generally increasing stream size and the diminishing influence of reservoirs on hydrographs and sediment load as one progresses downstream (the latter being particularly relevant to the Missouri River). It also includes geologic factors that affect the same attributes. All of these are mediated by ecoregional differences in precipitation, soil types, and land use patterns (Bailey, 1976) that affect hydrology and sediment quality and quantity through the soil-plant-atmospheric continuum (Philip, 1966).

Hupp and Osterkamp (1996)

In their review, Hupp and Osterkamp (1996) identify two factors that determine the ability of individual species to persistently occupy a site: 1) site suitability for germination and establishment, and 2) conditions that permit long-term survival until reproductive age. In their exploration of the relations

between floodplain landform and vegetation, they conclude that “in most fluvial settings across the United States, hydrogeomorphic processes have the most proximal influence on bottomland-species distribution.” Their emphasis on the disturbance gradient of fluvial processes reflects their focus on active channels and low floodplains that are flooded every one to three years. They recognize the interactions between the life-history traits of floodplain species and the magnitude, frequency, and duration of flood events, and place flood disturbance at one end of a stress-equilibrium gradient, with competition from other species at the other. Hupp and Osterkamp identify many factors that determine a site’s ability to facilitate germination and long-term survival; those particularly relevant to the LCPI are 1) the frequency of flooding and other elements controlled by elevation, and 2) soil characteristics, particularly particle size, as determined by the sediment regime and depositional patterns. Other factors identified by Hupp and Osterkamp that are particularly relevant to post-agricultural settings on the Missouri River flood plain include successional processes and the age of the bottomland surface.

Hughes (1997)

Hughes (1997) asserts that hydroperiod—defined to include the duration, frequency, depth, and seasonality of flooding (after Lugo et al., 1990)—links vegetation distribution, topography, and geomorphic landform. She places the elements of the LCPI, flood frequency and soil drainage, at the forefront of factors determining the distribution of plants on floodplains when she identifies a combined soil moisture and oxygen gradient to which species respond. On the one hand, she relates flood frequency to parameters such as flood depth and duration, noting that during floods, oxygen availability becomes a limiting factor for plant survival. On the other hand, she focuses on groundwater processes and non-flooding surface flow when she relates soil moisture to water table depth—determined in part by elevation—and to the hydraulic conductivity of soils. These latter elements are particularly important in floodplains that are protected by levees and that experience only the most infrequent flooding. In such sites, the LCPI model overestimates flood frequency, but the flood-return classes may represent well the relative depth to groundwater and the likelihood of surface flow from the uplands or from local precipitation (the LCPI does not account for levees and other structures that both impede flow to and serve as retention features that facilitate pooling at low sites).

Hughes places less emphasis on the direct effects of disturbance (for example, vegetation removal), but acknowledges its importance in determining the distribution of plant species on floodplains. Disturbance is examined through the prism of successional processes, with large floods that remove vegetation and soil viewed as mechanisms that reset succession, and small floods that provide inputs of water and sediments generally viewed as advancing succession by building up the floodplain and allowing maturation of the vegetation. In so doing, Hughes describes a system in which disturbance becomes increasingly less important as competitive processes begin to exert more influence on the distribution of species. Within this framework, it is important to note the observation of Parker and Bendix (1996) that sediment distribution influences competitive interactions, thus enabling hydrology to continue to exert an influence on plant community development.

Hughes devotes a section of her review to examining how the traits of species combine with hydrologic parameters to determine plant establishment and survival across a heterogeneous floodplain. Regeneration success is a function of synchrony between the release of viable seed and flood events that expose suitable germination sites, the timing of which is determined by elevation. Hughes also explores regeneration by means of vegetative propagule release, noting that large floods that damage vegetation and break off vegetation and an absence of flooding (which limits seed dispersal) both tend to increase the importance of this mode of reproduction relative to sexual reproduction. Again, both the occurrence and intensity of flow at a given location is dependent on elevation and the local shape of the flooded area. Hughes also notes that rapidly changing hydrologic regimes as a result of human activities, including dam construction, can adversely affect the regeneration success of many species, notably poplars (*Populus* spp.). This point is particularly germane to the Lower Missouri River, where reservoir management has reduced the sediment load below the Gavins Point Dam, leading to channel incision, less frequent flooding for hundreds of kilometers downstream, and regeneration failure for one of the key floodplain species, eastern cottonwood (Missouri River Recovery Program, 2008).

Hupp (2000)

Hupp (2000) acknowledges the interaction between vegetation (specifically forests) and fluvial processes such that “each is at least partly the result of the other”, but gives primacy to the latter in concluding that they control the landform development, sediment deposition, and vegetation distribution.

Hupp notes the conclusions of Mitsch and Gosselink (1993) that changes in elevation of only a few centimeters can profoundly influence hydroperiod, and by extension plant community composition. The purported mechanism is by means of anaerobic conditions associated with flooding (Wharton et al., 1982); however, hydroperiod also relates to the timing of flood recession relative to seed dispersion as determined by elevation. Hupp references the widespread use of zonal vegetation classification systems based largely on hydroperiod (Clark and Benforado, 1981), and describes a range of communities associated with particular locations in the floodplain defined by their elevation. Hupp suggests that the distribution of a plant species reflects its tolerance of specific stress regimes and more diffuse interactions such as competition, which together represent a stress-equilibrium gradient.

The abiotic template described above forms the basis for the presumed relationships between LCPI classes and vegetation distribution. The two most important gradients affecting the distribution of species on floodplains are 1) exposure to fluvial processes (Vannote et al., 1980; Malanson, 1993; Hupp and Osterkamp, 1996; Parker and Bendix, 1996; Hupp, 2000), and 2) soil moisture (Wharton et al., 1982; Brinson, 1990; Malanson, 1993; Hughes, 1997). Soil drainage classes of the LCPI describe soil moisture conditions, particularly anoxic conditions resulting from an abundance of water. Flow-return intervals describe the relative potential exposure of sites to fluvial processes, and, because of relationships between elevation and soil water availability, contribute to our understanding of the soil moisture gradient.

These relationships and their effects on species' distributions are explored in the sections that follow. Throughout, elevation is used as a surrogate for exposure to hydrologic processes, as well as the abiotic gradients that result from them. As is shown below, there is firm reason to believe that the LCPI captures the "fundamental abiotic factors that determine long-term suitability of land for...vegetation communities and their associated values" (Chojnacki et al., 2012). Another portion of this thesis examines the degree to which the LCPI anticipates the distribution of plant species and communities. Future studies that incorporate experimental manipulation are needed to assess the degree to which it can be used to aid management of terrestrial communities along the Missouri River.

Flow-return interval

That the frequency of flooding can influence the distribution of species has been demonstrated in field descriptions of community patterns on floodplains, manipulative experiments showing a response to

variation in flood frequency, field studies relating communities to past or current flood frequencies, and models that can effectively estimate the historic and current distribution of species. It is now widely accepted that flood frequency is a defining element of stream and wetland hydrology. At the most basic level, flooding is only one of many potential disturbances that introduce stress into a system (Grime, 1973), with concomitant effects on community development. Flood frequency represents a single environmental parameter that can be viewed as a gradient to which species respond (Gleason, 1926; Whittaker, 1967). Wetland classification systems often use flood frequency to divide wetland types (Brinson, 1993; Klimas et al., 2005). Reviews of literature consistently place flood frequency among the key variables influencing community composition, noting the changing response of individual species to variations in flood frequency (Malanson, 1993; Hupp and Osterkamp, 1996; Parker and Bendix, 1996; Hughes, 1997; Bendix and Hupp, 2000; Gurnell et al., 2000; Hupp, 2000; Ward et al., 2002; Osterkamp and Hupp, 2010). Models of floodplain species distributions routinely incorporate flood frequency as an independent variable (He et al., 2007; Thogmartin et al., 2009), and wetland management often includes flood frequency, elevation, or both as controlled parameters (Fredrickson and Batema, 1991). This section explores research demonstrating the relationships between flood frequency and the distribution of broad species groups: herbaceous species, woody species (with particular emphasis on cottonwoods and willows), and exotic species. Then it examines community-level effects of variation in flood frequency.

Herbaceous species

Research spanning many decades and many geographic regions has demonstrated that flood frequency is one of critical determinants of the distribution of herbaceous species on floodplains. In Europe, the influence of flood frequency on herbaceous species has been demonstrated on systems as varied as the Ain River (Piégay et al., 2000), and the freshwater delta ecosystem of the Rhine and Meuse Rivers, for which the hydrologic system has been significantly altered (van de Rijt et al., 1996; Lenssen et al., 1998). On a stream in England, it has been shown that herbaceous species respond differently to experimental transplanting to either wetter or drier sites, and that flooding acts as a filter on communities by excluding long-lived perennials that would be competitive in the absence of disturbance (Toogood et al., 2008). Within North America, the effects of flood frequency on herbaceous species' distributions has been demonstrated along the eastern seaboard, (Wistendahl, 1958; Sigafos, 1976), the west coast (Teversham

and Slaymaker, 1976) and within the Great Plains, (Stanley et al., 1973; Stanley and Hoffman, 1975). On other streams in the central United States, the distribution of herbaceous species is influenced by variation in flood frequency below two years, and flood frequency (determined by microtopographic variation) is positively related to species richness (Heimann and Mettler-Cherry, 2004). Finally, moist-soil management techniques to favor short-term seed production for wildlife rely on the varying responses of herbaceous species to flood frequency and duration (Fredrickson and Taylor, 1982).

Woody species

The distribution of woody species is also a function of flood frequency, as has been shown by research throughout the world, including many of the studies above. On the Raritan River [New Jersey], woody species sort along a flood frequency gradient determined by elevation (Wistendahl, 1958). A similar progression of species has been documented on streams in southern Illinois (Bell, 1974; Bell and del Moral, 1977), Missouri (Heimann and Mettler-Cherry, 2004), and Wisconsin (Turner et al., 2004). These studies show that black willow (*Salix nigra*), river birch (*Betula nigra*), silver maple (*Acer saccharinum*), and sycamore (*Platanus occidentalis*) occupy frequently flooded low elevations, but oaks (*Quercus* spp.) and hickories (*Carya* spp.) occupy higher elevations. Of the 32 species analyzed on the Lillooet River [British Columbia], one-quarter, including black cottonwood (*Populus trichocarpa*), show clear responses to a flood frequency gradient; some species demonstrate a normal distribution about intermediate flood frequencies and others were more abundant at extreme flood frequencies (Teversham and Slaymaker, 1976).

The distribution of overstory species often is recapitulated in that of seedlings. The distribution of eastern sycamore (*Platanus occidentalis*) seedlings and the broader pattern of vegetation banding of which it was a part are determined by the flood frequency to which sites are exposed along the Potomac River [Virginia] (Sigafos, 1976). In forests surrounding Horseshoe Lake [Illinois], the seedlings of bottomland hardwoods species (*Quercus* and *Carya* spp.) are more abundant on less-frequently flooded sites (Robertson et al., 1978). Given the affinity of overstory trees to sites of various flood frequencies, it is possible that seedling distributions may reflect proximity to seed sources; however flood frequency is the critical variable determining seedling abundance in the above studies.

The links between flood frequency and plant species distributions on three Virginia streams are sufficiently strong to allow estimation of flow frequency of various landscape positions from the species and communities present (Osterkamp and Hupp, 1984; Hupp and Osterkamp, 1985). On the Murray River [Australia], temporal shifts in woody species abundance and woody species invasions reflect alteration of the flow-regime, including flood frequency; however varying degrees of physiological adaptation to flooded conditions mediate the relationship between flood frequency and resulting species distributions (Bren, 1993).

Along the Missouri River and its tributaries, similar relationships between flood frequency and woody species distributions have been identified. Johnson (1949) and Johnson et al. (1976) showed strong relationships between elevation, stand age, and the structure and composition of the forest overstory. On the Platte River [Nebraska], late-seral forests are found on infrequently flooded higher elevations, mature cottonwood forests on low level sites exposed to moderately frequent inundation, and cottonwood-willow thickets along frequently flooded channels (Becker, 1980). Presumably, low flood frequency on higher sites fosters community stability, enabling occupancy by species associated with later successional stages (Tardif and Bergeron, 1999). Models developed by He et al. (2007) successfully estimate the historic probability of occurrence for species on the Lower Missouri River; oaks are more probable at higher elevations, and early-successional species and seral communities are more likely to occur at low elevations. This is consistent with field observations and management experience showing that oak seedlings are less abundant (Robertson et al., 1978) and survival is lower (Kabrick et al., 2005) on frequently flooded locations.

Cottonwood and willow

Across a broad geographical range, flood frequency has been identified as a primary determinant of the distribution of members of the cottonwood (*Populus*) and willow (*Salix*) genera. Smith (1957) was among the first to relate flood frequency to maintenance of *Populus* species, when he noted that without recurring floods along the Fraser River and other streams in British Columbia, bare soil sites suitable for black cottonwood (*Populus trichocarpa*) seedling establishment would not be created. Similar relationships have been described along the Lillooet River [British Columbia] (Teversham and Slaymaker, 1976). On the Platte River [Nebraska], the distribution of cottonwood communities follows an elevation gradient, with

cottonwood-willow thickets developing along frequently flooded, low channel margins, and mature cottonwood forests developing on low, level sites with moderate flood frequencies (Becker, 1980). Based on research from western prairie streams, Mahoney and Rood (1998) described an elevation-dependent regeneration envelope for cottonwoods that provides the following: 1) synchrony between flooding and germination to provide requisite substrate to enable germination, 2) subsequent water availability sufficient to ensure short-term survival, 3) proximity to the water table to promote survival through the summer, and 4) protection from subsequent floods that might damage, remove, or bury new seedlings. Research on the Animas River [Colorado] (Baker and Walford, 1995) and on streams in Japan (Nakamura and Shin, 2001) suggest that these parameters apply to other members of the *Populus* genus. The latter study (Nakamura and Shin, 2001) and a review by Karrenberg et al. (2002) identified a similar balance between germination potential and protection from subsequent flooding that determines the distribution of willows. The abundance of willows is related to elevation (Malanson and Butler, 1991), and growth rate (indicated by tree ring width) of willows is positively correlated to elevation (1993).

Much research on factors affecting the distribution of eastern cottonwood (*Populus deltoides*) and willows (*Salix* spp.) has occurred on the Missouri River itself. Although flood frequency is not described as a driver of species distributions by Johnson (1949), protection from damaging floods is a necessary component for the development of mature cottonwood forests and later successional seres at higher elevations. Weaver (1960) makes a more direct link between the frequency of flooding and the distribution of cottonwoods and willows on the Missouri River. An affinity for bare substrates that are more abundant in frequently flooded locations is among the many adaptations of eastern cottonwood that enabled its historic domination of the Missouri River floodplain (Johnson et al., 1982). The cottonwood regeneration box model of Mahoney and Rood (1998) was confirmed on the Missouri River by Auble and Scott (1998), and subsequent research in Montana has indicated that a flood recurrence interval of greater than nine years facilitates recruitment of cottonwood into maturity (Scott et al., 1997). More recent research by Heitmeyer (2008) and by He et al. (2007) links the historic distribution of cottonwood and willow forests along the Missouri River to the frequency of flooding.

Given the well-established link between cottonwood distribution and flood frequency, it is not surprising that alteration of the hydrologic regime along the Missouri River has been identified as a

contributing factor in the failure of cottonwood forests to regenerate and develop into mature stands (Johnson et al., 1976; Johnson et al., 1982; Johnson, 1992, 1997, 1999; National Research Council, 2002; Dixon et al., 2012a; Johnson et al., 2012). Dam construction, river channelization, and modification of the flow regime have altered the hydrologic regime of the Missouri River (Jacobson et al., 2009). In the upper portion of the river, flood peaks have been severely attenuated; the lower portion of the river is channelized and is characterized by alternating stretches of degrading and aggrading stream bed that have altered connectivity with the floodplain. Two decades ago, it was recognized that the current hydrologic regime rarely provides the flood events necessary to create newly exposed substrate (especially in the context of channelization); as a result, cottonwood forests were predicted to disappear from remnant floodplains of the Missouri (Johnson, 1992). Despite the abundance of new cottonwood forests that developed following the great flood of 1993, research in the intervening years has confirmed the dire situation for cottonwood communities on the Missouri (Dixon et al., 2010; Dixon et al., 2012a). These studies informed the development of the Cottonwood Management Plan for the Missouri River (U.S. Army Corps of Engineers, 2011), which acknowledges that channel degradation and flow regulation have combined to disconnect the river from its floodplain, reducing cottonwood regeneration on the river since the closure of the dam system. Plans to manage the river to raise the channel bed relative to the floodplain—or “lower the bench”—and thereby increase flow frequency are intended to reverse this trend. The plan specifically applies the LCPI for assessing potential flow frequency.

Exotic species

Flood frequency may be particularly important in determining the abundance of non-native species on the Missouri River. In general, flooding can be viewed as one of a spectrum of disturbance types that shares relationships to exotic species distributions common to all disturbances. Many exotic species are “competitive ruderals” that are well adapted to disturbance process, such that they increase in response to disturbance (Tickner et al., 2001). Henderson et al. (2006) identify water bodies as being particularly susceptible to invasion, due to “constant, wide-ranging propagule dispersal, continuing opportunity for disturbance during flooding events and occasional flushes of excess nutrient”. Changes in hydrology that affect flood duration can facilitate alien species invasion by creating new conditions favorable to a specific, non-native plant, or by having a negative impact of native flora; more frequent floods simply increase the

opportunities for invasion by non-native species (Richardson et al., 2007). The frequency of disturbance combines with proximity to propagule sources and the dispersal capabilities of species to define the propagule pressure on a site, with more frequently disturbed sites having greater pressure (Rejmánek et al., 2013). These studies suggest an invasion susceptibility model for floodplains in which more frequent flooding facilitates non-native species invasions by 1) changing environmental conditions (providing openings in communities, exposing substrate for colonization, and redistributing resources); and 2) mobilizing propagules and depositing them in new locations. However, this model has recently been challenged by the work of Dixon et al. (2010), who documented a higher abundance of non-native species on less frequently flooded sites on the Lower Missouri River.

The relationships between exotic species abundance and disturbance frequency are not absolute. A review by Richardson et al. (2007) suggests that the frequency of disturbance is positively, but not necessarily linearly related to the abundance of non-native species. Often, it is the mere presence or absence of disturbance, rather than the frequency, that determines the abundance of exotic species, with disturbed sites usually having more non-native species than undisturbed sites (Hansen and Clevenger, 2005). This suggests that, within the context of the LCPI, the differences in exotic species abundance between LCPI flow-return intervals may be difficult to detect among the more frequently flooded classes; however, locations with longer flow-return intervals may function like the undisturbed sites of Hansen and Clevenger (2005) and have lower exotic species abundances.

Communities

Given that the distribution and abundance of the broad species groups discussed above is a function of flood frequency, it follows that vegetation community distributions reflect variation in flood frequency as well. Many of the studies above are comprehensive enough to support this claim (Wistendahl, 1958; Teversham and Slaymaker, 1976; Piégay et al., 2000; Heimann and Mettler-Cherry, 2004). Research in the southeastern United States (Hupp and Osterkamp, 1985; Hupp, 1988, 1992; Hupp and Osterkamp, 1996; Parker and Bendix, 1996; Bendix and Hupp, 2000; Hupp, 2000) identifies flood frequency—reflected in broadly-defined floodplain landforms—as the primary determinant of community distributions in riparian systems; similar relationships were later described in Italy (Hupp and Rinaldi, 2007). On the Coosawhatchie River [South Carolina], flood frequency is one of the primary site variables determining the

distribution of tupelo (*Nyssa* spp.) and oak (*Quercus* spp.) communities (Burke et al., 2003). Several distinct communities divided by elevation were identified along an Alaska stream, and species richness was positively related to flood frequency as determined by microtopographic variation (Pollock et al., 1998). Along the Platte River [Nebraska], prairie communities are limited to higher locations subject to less frequent flooding, as are subclimax forest communities; silver maple forests and marsh communities occupy frequently flooded depressions on the floodplain (Becker, 1980).

Community distribution has been related to flood frequency on the Missouri River as well. Early works by Johnson (1949) and Weaver (1960) describe a successional gradient of communities that corresponds with increases in elevation and flow-return interval. Flood frequency is one of three components (along with soil type and geomorphic structure) that shaped the historic distribution of vegetation community types on the Middle Missouri River (Heitmeyer, 2008). That historic distribution was successfully modeled based on elevation and soil variables using data similar to the LCPI (He et al., 2007). Another study showed that the most parsimonious model to explain the current distribution of cottonwood forests and wet prairies includes flood frequency and elevation (Thogmartin et al., 2009). In addition to examining the effects of flow frequency on eastern cottonwood, Dixon et al. (2010) documented greater abundance of disturbance-tolerant shrub and herbaceous species in the more frequently flooded portions of their study area, and a shift toward late-successional communities on less frequently flooded sites.

Flow-return interval conclusion

The evidence linking flow-return interval to the distribution of species and communities is sufficiently well established that recent reviews of the topic have treated the relationships as more or less beyond dispute (Smith et al., 2008; Osterkamp and Hupp, 2010). Nevertheless, the ability of a simple, two parameter model like the LCPI to anticipate the distribution of species and communities has not yet been established. While the response of individual species to variation in flood frequency may be easily detected, zonation leading to clearly defined communities may be more elusive (Bell, 1974). The flow-return interval gradient competes for expression with other gradients, as demonstrated in the models of Bell and del Moral (1977), which show that time since disturbance and successional processes may be equally or more important than flow-return interval in determining species distributions. This may explain why potential

flood frequency, although a necessary parameter of the most parsimonious model explaining the distribution of cottonwood forests on the Missouri River, shows only weak relationships with community distribution (Thogmartin et al., 2009). Nevertheless, it is reasonable to assume that LCPI flow-return interval possess some power to predict species distributions and aid in resource management.

It should be understood that the direct causative links between flow-return interval and vegetation distribution are largely conjectural. The works of Stanley et al. (1973) and Toogood et al. (2008) are notable for their experimental approach, but even these failed to tease apart flood frequency from other hydrologic parameters that may have been affecting the response of species to flood regime. Most studies have assumed that the current distribution of species reflects past and continuing hydrologic conditions, and flood-frequency is often the only available historical data type that can be derived for any given study area. Application of such data to a specific site requires a series of assumptions about stage-discharge relationships, local relief, and water surface elevation. Additionally, there is an underlying assumption in such studies that floods are merely one of any number of potential disturbances at a site that can disrupt succession, in which case the potential time between flood events become particularly important. However, as pointed out by Brinson (1990) and Opperman et al. (2010), floods of different magnitudes serve different functions (the latter work classified them as “activation”, “maintenance”, and “resetting” flood types). As such, for any given location, the frequency of flooding may be less important than the frequency of floods of particular magnitude and disturbance potential. Nevertheless, due to its relationship to elevation, potential flood frequency is closely linked to a variety of other hydrologic conditions that have also been linked to the distribution of floodplain plant species. These hydrologic parameters are explored in the sections that follow.

Flow-return interval as a surrogate for other hydrologic variables

As described earlier, given the derivation of the LCPI model, flow-return intervals possess unequivocal relationships with other hydrologic parameters known to influence the distribution of plant species and communities. Floodplain locations with shorter flow-return intervals are necessarily lower in the landscape and therefore experience greater flooding depth and duration during a particular flood event; they also experience a longer hydroperiod in any given year. Less frequently flooded sites are inundated only during floods of greater magnitude. Additionally, because flood power increases with depth, flood

power at infrequently inundated sites is less than at lower elevations with shorter flow-return intervals. Depth to groundwater at higher, infrequently flooded sites generally is greater than in low areas with short flow-return intervals. Finally, low sites are more likely to receive water from the surrounding landscape during precipitation events. The combination of these relationships implies that low lying areas occupy the wet end of the water availability spectrum and higher elevation sites occupy the dry end; however local hydraulics and soil characteristics may disrupt these relationships.

Flow Duration

Aside from flood frequency, the flooding attribute that has been linked most closely to the distribution of plant species and communities is flood duration. An early review by Hupp (1988) includes duration of flooding as one of two primary drivers (the other being flood frequency) of plant species distribution; a second review two decades later did little to alter that author's mind (Osterkamp and Hupp, 2010). Both reviews conclude that even small variations in elevation can lead to important changes in flood duration and vegetation communities. Duration is one of the criteria used to define the three types of floods (activation, maintenance, and resetting) identified by Opperman et al. (2010); in their conceptualization of floodplains ecosystems, the duration of flooding determines the potential impact on vegetation, particularly in locations where the flow energy is insufficient to mechanically alter the vegetation. Poff et al. (1997) include duration as one of the four flow parameters driving ecological systems within the "natural flow regime". Flood duration is a critical component of wetland classification systems (Klimas et al., 2005), and it can be used to assess the suitability of sites for restoration to various wetland types (Duranel et al., 2007). Finally, the ability of species to survive varying durations of flooding is a key tenet of wetland management (Cowardin et al., 1979), and flood duration is one of the most important controlled variables in managed wetlands (Fredrickson and Batema, 1991).

In the context of the LCPI model, flood duration is directly related to flow-return interval in that lower, more frequently flooded sites necessarily experience a longer hydroperiod. Not only do lower elevation sites flood more frequently during the year, but they are the first sites inundated and the last sites exposed during individual flood events. Work by Vervuren et al. (2003) makes it clear that complex relationships between discharge and flood duration are determined by local topography. At lower elevations, flood duration is more variable and is dependent on the shape of the hydrograph associated with

a particular flood; at higher elevations, the relationship is more linear. Despite this complexity, annual flow duration data has been related to individual species and community distributions (Burke et al., 2003), and the Cottonwood Management Plan for the Missouri River specifically identifies the LCPI model (which also uses annual flow data) as a useful surrogate for flow duration capable of informing habitat management decisions on the floodplain (U.S. Army Corps of Engineers, 2011).

Numerous investigators have examined the relationship between flood duration and vegetation distribution without specifically examining the underlying causal links. Flood duration is one of four critical variables in a conceptual model describing the distribution of floodplain vegetation on the Ottawa River [Canada] (Day et al., 1988). The distribution of species along an elevation gradient at Bayou Sauvage Ridge [Louisiana] reflects their tolerance for varying flood durations (Wall and Darwin, 1999). The variable responses of 17 species in an experimental inundation study along the Rhine River [the Netherlands] reflects the elevations at which they are naturally distributed; species that possessed attributes that facilitated recovery from prolonged inundation were more likely to be found at lower elevations than species that lacked those attributes (Van Eck et al., 2004). In Japan, willow dominance increases in secondary channels with longer flood durations (Shin and Nakamura, 2005); by contrast, mortality of non-native black willow (*Salix nigra*) in Australia is higher at low elevations where flood duration is longer and anoxia greater (Stokes, 2008).

Within the Midwest, Shelford (1954) was among the first to relate the distribution of vegetation communities to the duration of inundation and associated variability in soil texture along the Mississippi River [Tennessee]. Early studies along the margins of Lake Sakakawea and Lake Oahe [North Dakota] on the then recently-impounded Missouri River relate the observed zonation of vegetation to flood duration and show varying degrees of tolerance to inundation duration for the species within the study area (Stanley et al., 1973; Stanley and Hoffman, 1975). Similarly, studies in southern Illinois identify flood duration as a controlling factor in community distribution (Bell, 1974; Bell and del Moral, 1977; Robertson et al., 1978). A study on the Platte River [Nebraska] floodplain demonstrated that silver maple (*Acer saccharinum*) forests occurred in areas with longer flood duration; prolonged inundation in the year prior to field work had induced mortality among recently established cottonwood seedling (Becker, 1980). The distribution of herbaceous and woody species on smaller streams in central Missouri is correlated with the duration of

inundation (Heimann and Mettler-Cherry, 2004). Synthesis works by Ward et al. (2002) and Smith et al. (2008) treat the relationship between hydroperiod and vegetation distribution as beyond dispute. Heitmeyer (2008) bases many of his recommendations for floodplain vegetation habitat restoration on the Middle Mississippi River on the duration of inundation. Finally, long-term declines in cottonwood forests above impoundments along the Missouri River have been attributed to chronic inundation (among other causes) resulting from dam construction (Dixon et al., 2012a).

One mechanism by which prolonged inundation affects species and community distributions is through anoxia-induced mortality. This idea was first comprehensively addressed in the Volume I of a series of publications examining the effects of changing water level on woody and riparian species (Teskey and Hinckley, 1977). The idea is supported by subsequent research along the Raritan River [New Jersey] relating differences in community types to variation in aerobic conditions (Frye and Quinn, 1979). One model of plant strategies for adaptation to fluvial systems places tolerance of anoxic conditions at the forefront of attributes determining floodplain vegetation patterns (Bornette et al., 2008).

According to Auble et al. (1994), flood duration may be an optimal predictor of vegetation because it is correlated to a variety of interrelated abiotic components, including soil oxygen concentration. For the Gunnison River example they use, vegetative response to flow duration is evident even without changes in mean annual flow, findings relevant to river systems like the Missouri River for which management is constrained by mandates regulating annual flow. The authors are careful to point out that factors other than flow duration may dominate vegetation distribution patterns in other river systems. On the Missouri River, anoxia resulting from prolonged flooding has been identified as one factor contributing to mortality of early cottonwood seedlings (Dixon, 2003). The relationship between soil anoxia and vegetation distribution is explored further in the sections relating soil drainage classes to water availability.

In addition to anoxia-induced mortality, the duration of flooding can affect species distributions through impacts on other environmental gradients and by affecting plants via mechanisms other than mortality. For example, within the riparian area immediately adjacent to the channel of the Severn River [United Kingdom], duration of inundation determines sediment quantity, with associated effects on plant distributions (Steiger et al., 2001). Other soil attributes affecting species distributions, including shear stress and soil moisture, also have been correlated with inundation duration (Auble et al., 1994). The duration of

flooding is a stronger determinant of germination success and timing for pin oak (*Quercus palustris*) and ash (*Fraxinus pennsylvanica*) than is flow periodicity (Walls et al., 2005). Finally, Lowe et al. (2010) demonstrate contrasting responses in growth and reproductive effort for two sedge species to prolonged inundation. These studies demonstrate that oxygen availability (or lack thereof) is only one of many environmental gradients affecting species distribution that are determined by flood duration.

Reflooding

The potential for flooding two or more times in a year is known to affect species distributions and is likely to be reflected in LCPI flow-return intervals. Fredrickson and Taylor (1982) point out that reflooding within a given year can have important consequences on the composition of communities. On the one hand, it can affect the survival of those plants that have already become established; on the other hand, it can provide opportunities for new species to become established, particularly those that are propagating during subsequent floods. In an experimental study of smartweeds (*Polygonum* spp.), burial of seeds by return flooding reduced viability and germination of seeds deposited earlier in the year (Staniforth and Cavers, 1976). In wetlands in the Netherlands, return flooding limits the ability of other species to outcompete common reed (*Phragmites australis*), and is the critical factor determining the abundance of herbaceous species along an elevation gradient leading to vegetation zonation (Lenssen et al., 2000). For eastern cottonwood (*Populus deltoides*), exposure to return flooding determines the lower elevation limit of regeneration in the model developed for the active riparian zone (Mahoney and Rood, 1998). Similarly, once cottonwood seedlings become established following an appropriately timed flood, subsequent summer flooding (which erodes or buries new seedling in sediment) and winter fluvial activity determine the mortality rate of seedlings (Johnson, 2000). While the likelihood of reflooding during a given year is not specifically modeled by the LCPI, it is inversely proportional to flow-return interval.

Depth to groundwater

Although not explicitly modeled by the LCPI, depth to groundwater is an important hydrologic variable for which the LCPI flow-return intervals serve as a surrogate and which is known to affect plant distributions. The direct, though not invariable, relationship between elevation and depth to groundwater has been advanced in synthesis works (Hupp and Osterkamp, 1985; Brinson, 1990) and has been

documented on numerous fluvial systems, including the Raritan River [New Jersey] (Frye and Quinn, 1979), the Coosawhatchie River [South Carolina] (Burke et al., 2003), and on smaller streams in central Missouri (Heimann and Mettler-Cherry, 2004). Even small changes in elevation over scales of less than one hectare can influence the depth to the water table (Reynolds and Parrott, 1980). The link between land elevation and depth to groundwater also has been demonstrated on the Missouri River (Grannemann and Sharp Jr, 1979; Foreman and Sharp Jr, 1981; Kelly, 2000, 2001) and is acknowledged in the Army Corps of Engineer's conclusion that incision of the stream bed along some river stretches has raised the relative land-surface elevation and increased the depth to groundwater (U.S. Army Corps of Engineers, 2011). Given that depth to groundwater is directly related to elevation, LCPI classes with longer flow-return intervals should be associated with greater depths to groundwater.

On the Missouri River, the most important factor controlling groundwater elevation is variation in river stage (Grannemann and Sharp Jr, 1979). Because of this relationship between water-surface level elevation and depth to groundwater, the LCPI should provide a good index of the latter parameter. The conclusion that tributary streams and other valley features affect groundwater processes (Grannemann and Sharp Jr, 1979) was empirically demonstrated in a comparison of water level response of two wetlands to changes in river stage, which also showed that depth to groundwater is a function of the hydraulic conductivity of the alluvium (Kelly, 2001). However, it is important to note that within the Missouri River alluvial aquifer, precipitation and tributary recharge play relatively minor roles in groundwater processes (Foreman and Sharp Jr, 1981). Therefore, at the local scale, it may be sufficient to know that lower, more frequently flooded locations are also more likely to have a shallower depth to groundwater, which is closely tied to water-surface elevation of the main river.

In addition to determining overall soil water availability, depth to groundwater determines the relative contribution of groundwater (as opposed to surface flow and precipitation) to the maintenance of wetlands. Areas with less connectivity to groundwater are influenced more by upland water inputs and direct precipitation, with associated changes in nutrients and conductivity that affect vegetation community composition and structure (Piégay et al., 2000). Whether a wetland is maintained by precipitation or by groundwater is a principal criterion used to subdivide wetland types (Klimas et al., 1981; Brinson, 1993), and "it is widely accepted that interactions between groundwater and surface waters from flooding strongly

control the spatial pattern of habitats within alluvial riparian areas” (Baatrup-Pedersen et al., 2013).

However, given the conclusion of Forman and Sharp (1981) that surface water and tributary contributions to groundwater processes are slight on the Missouri River, it is reasonable to assume that their effect on plant species distribution is slight.

The most relevant effect of groundwater level on the distribution of species within the study area is on the soil moisture gradient of Brinson (1990), in which individual species respond to saturated, potentially anaerobic conditions at one end and low water potential at the other. At the saturated end of the spectrum, depth to groundwater affects species abundance by placing a lower limit on the potential rooting volume of plants (Burke et al., 2003). Additionally, a high water table (rather than flooding) is the primary cause of anoxic conditions in some settings (Shin and Nakamura, 2005). At the dry end of the spectrum, disconnection from the water table restricts the distribution of phreatic species such as cottonwood that require access to a water supply to survive periods of drought (Rood and Mahoney, 1990).

Variation in depth to water table has been demonstrated to have profound impacts on numerous species. For example, a water table near the surface of the Missouri River floodplain enables fast growing competitive species such as cottonwood and willow to thrive in a disturbance mediated environment (Johnson et al., 1976). In New Jersey, depth to groundwater determines vegetation patterns on the Raritan River (Frye and Quinn, 1979), and is related to the distribution of tree species in a swamp (Reynolds and Parrott, 1980). In the latter study, variable depth to water table is associated with microtopographic variation over scales less than 1 hectare. A major lowering of the water table level was one necessary component to facilitate successional progression toward an oak-hickory climax community along southern Illinois rivers (Hosner and Minckler, 1963); by contrast, a rise in groundwater level following dam construction on the Missouri River has been blamed for a sharp reduction in forest cover (Johnson et al., 2012).

In the management realm, depth to groundwater has been used to assess the suitability of sites for restoration toward particular wetland community types (Duranel et al., 2007). Successful management for wet meadows dominated by salt grass (*Distichlis spicata*) on the Bosque del Apache National Wildlife Refuge is enabled by providing the elevated water-table characteristic of the riparian system prior to alteration of the river flow (Smith et al., 2008). Finally, depth to the water table is a critical factor

determining the susceptibility of sites to invasion by exotic species (Tickner et al., 2001). Even those researchers who have shown only weak or no relationships between species distributions and depth to groundwater (Osterkamp and Hupp, 1984; Hupp and Osterkamp, 1985), or who have concluded that such relationships are complex and determined by factors operating at multiple scales (Bendix, 1999), acknowledge that depth to groundwater affects plant species distributions and that it is directly related to elevation.

Given the status of cottonwoods and willows as phreatophytes, it is not surprising that numerous studies and synthesis works have attributed variation in their abundances to groundwater depth. Although willow and cottonwood germination is associated with a receding waterline following floods, early survival of seedlings requires continuing access to a phreatic water supply (McBride and Strahan, 1984; Rood and Mahoney; Pezeshki and Shields, 2006; Pezeshki et al., 2007). Others have documented more complex relationships driven not by mean depth to water table, but rather by the ability of root growth to keep up with the rate of water table decline, with higher elevation sites experiencing faster drawdown rates that reduce herbaceous cover and preclude establishment of cottonwood and willow (Shafroth et al., 1998). (The falling limb of a hydrograph is characterized by rapid rates of decline when water levels are high and lower rates of decline as discharge approaches base flow). On the Lower Missouri River, greater depth to groundwater (because of channel incision and a resulting increase in floodplain elevation relative to water surface) has been cited as one cause of regeneration failure of cottonwoods (U.S. Army Corps of Engineers, 2011). Numerous studies on the river have concluded that a higher water table in the channelized portion of the study area could facilitate cottonwood recruitment (Thogmartin et al., 2009; Dixon et al., 2010; Jacobson et al., 2011; Dixon et al., 2012a; Dixon et al., 2012b). The Cottonwood Management Plan for the Lower Missouri River (U.S. Army Corps of Engineers, 2011) specifically applies the LCPI as an indicator of depth to groundwater, among other hydrologic variables.

There are other mechanisms by which depth to groundwater may affect species distributions. Along the Chena River in Alaska the effect of a rising water table was expressed in the soil thermal regime; greater soil moisture provided greater soil heat capacity, which moderated fluctuations in soil temperature (Viereck, 1970). Though Viereck was focused on the presence or absence of permafrost as an abiotic factor affecting species distributions, the findings are relevant to the communities on the Missouri River in that

variation in soil temperature can affect the phenology of plants, disrupting synchrony between flooding and seed release that determines seedling distribution (Niiyama, 1990), and water and soil temperatures during germination can influence the initial seedling composition of wetlands (Seabloom et al., 1998).

Additionally, depth to groundwater can affect competitive interactions and the relative abundance of species (Fraser and Miletti, 2008). Although these interactions are likely relevant to the distribution of species on the Missouri River floodplain, it is probable that the most important effect of variation in depth to groundwater is the water availability stress gradient described by Brinson (1990).

Surface water depth

Water depth, whether a result of flooding, of groundwater seepage, or of overland flow to low landscape positions, is known to affect the distribution of plants species and communities. Observational studies in the mid-20th century linked the distribution of plant communities to the depth of flooding (Wistendahl, 1958; Weaver, 1960), and the link between water depth and species distributions has been documented in numerous subsequent studies (Day et al., 1988; Seabloom et al., 2001; Van Eck et al., 2004; Fernández-Aláez et al., 2005; Toogood et al., 2008). Variation in the depth of potential flooding has been linked to changes in herbaceous cover (Shafroth et al., 1998); alteration of age structure and dominant reproductive mode of woody species such as black ash (*Fraxinus nigra*) (Tardif and Bergeron, 1999); and changes in species' germination patterns (Willis and Mitsch, 1995; Seabloom et al., 1998). The depth of potential flooding also has been linked to the abundance of exotic species (Lenssen et al., 2000; Stokes, 2008). From a management perspective, mean water depth is a key criterion used to identify different wetland types (Brinson, 1993; Klimas et al., 2005), and control of flooding depth is used to promote desirable species (Fredrickson and Batema, 1991) and to limit the abundance of non-native invasive species (Euliss et al., 2008). Much of Heitmeyer's (2008) analysis of vegetation restoration potential for the Middle Mississippi River relies on the mean flooding depths at various periods during the year.

Variation in flood depth can affect species distribution through various mechanisms. At one end of the life cycle, flood depth can determine patterns of species establishment by altering the dominant reproductive mode (Tardif and Bergeron, 1999; Barsoum, 2001) and germination success (Willis and Mitsch, 1995; Seabloom et al., 1998) of species. At the other end of the life cycle, mortality may be determined by the depth of flooding (Van Eck et al., 2004; Stokes, 2008). Because oxygen diffusion

decreases with water depth, deeper flooding inhibits gas exchange in stems and leaves, leading to greater mortality (Wharton et al., 1982). Additionally, increasing attenuation of light with greater water depth inhibits photosynthesis, inducing greater mortality during deep floods that carry more light blocking sediment than in shallow floods (Vervuren et al., 2003).

Elevation and flow energy

Flow energy determines the ability of flowing water to physically alter the floodplain and the biotic communities on it. The synthesis works of Vannote et al. (1980), Wharton et al. (1982), and Brinson (1990) accept as fact that the physical components of the floodplain are a function of hydraulic energy. The river continuum concept of Vannote et al. (1980) asserts that plant species and communities themselves respond to the kinetic energy of the riverine system, resulting in patterns of distribution that optimally dissipate that energy. Similarly, Wharton et al. (1982) concludes that the riverine plant communities serve as buffers to the energy of the system. The wetland classification scheme of Brinson (1993) acknowledges that variation in hydrologic energy influences the distribution of species and communities. Alteration of flow energy is one of the ecological parameters to which species adjust following disruption of natural flow regimes; some species are negatively affected by such changes, while others (often exotic species) tend to be favored (Poff et al., 1997).

The distribution of each floodplain plant species is a function of the degree of alignment between its morphological and reproductive characteristics and the flow energy to which it is exposed. Zimmermann and Thom (1982) warn that analyses of plant distributions against static growth conditions are frustrated by the fact that distributions of species are often limited by low-frequency, extreme events. Within the context of the LCPI, that a site is at an elevation subject to annual flooding may be less important to determining the species that occur there than the fact that it also is occasionally subject to higher energy flow with greater influence on the entire landform (such as the 100-year “resetting” floods of (Opperman et al., 2010).

Flow energy should not be confused with flood magnitude. The latter is a systemic attribute quantified as discharge, but the former is a measure of the mass, velocity, and turbulence of water moving past a particular point at any given time. The two terms are related in that the water elevation determined by a particular flood magnitude combines with local topography and vegetative cover to determine flow energy at a particular point on the floodplain. Though attenuation of peak flow (magnitude) has been linked

to changes in sediment deposition, reduced substrate heterogeneity, a loss of suitable regeneration habitat for many riparian species, and decreased floodplain species diversity (Pearlstone et al., 1985; Nilsson et al., 1989; Nakamura and Shin, 2001; National Research Council, 2002), it cannot be modeled by the LCPI. However, within the context of the LCPI, variation in flood magnitude exposes sites with short flow-return intervals to a broad flow-energy spectrum; by contrast, infrequently flooded sites are inundated only during high magnitude events. Furthermore, during any given flood event, shallower (and usually lower velocity) flooding on infrequently flooded sites causes them to experience lower flow energy than frequently flooded locations. This section examines how species distributions are determined by biotic and abiotic effects of variation in flow energy.

Damage and mortality

One of the most obvious forms of flood damage is alteration in the growth or survival of established vegetation. Once species have become established on a site, their ability to continue occupying that site depends on interactions between their life history traits and the flow energy to which they are exposed. Working on streams in the southeastern United States, Hupp (1988) and Bendix (1999) concluded that species are distributed along a flood power gradient, with the life history traits of each species determining its ability to survive the flood events to which it is exposed. The seedling stage is particularly vulnerable to damage from high-energy flow, which has been shown to affect species recruitment and survival of black ash (*Fraxinus nigra*) along the shores of Lake Duparquet [Quebec] (Tardif and Bergeron, 1999), mule-fat (*Baccharis salicifolia*) and salt cedar (*Tamarix ramosissima*) on the Bill Williams River [Arizona] (Shafroth et al., 1998), and numerous species on the Raritan River [New Jersey] (Frye and Quinn, 1979). Flow velocity explains much of the variation in basal area and tree growth along the Potomac River [Virginia] (Yanosky, 1982). On the Missouri River, the presence of certain species such as pawpaw (*Asimina triloba*) indicates forest maturity enabled by protection of sites from high energy flow events (Bragg and Tatschl, 1977).

The distributions of cottonwoods (*Populus* spp.) and willows (*Salix* spp.) are similarly affected by the intensity of flooding to which they are exposed. On the one hand, potential exposure to floods is expressed in morphological adaptations of the genera that enable them to withstand high energy flooding. Martens (1993) relates variations in the growth form of willows to the intensity of flooding to which they

are exposed. Stem flexibility has been identified as one trait of willows that enable them to become more abundant in areas with moderately high energy flows (Karrenberg et al., 2002). Variable allocation of energy to roots or shoots in both willows and cottonwoods allows them to survive floods of varying flow energy (Lytle and Poff, 2004).

On the other hand, exposure to high energy floods is expressed in the distribution of the *Populus* and *Salix* genera within the riparian system. Exposure of new seedlings to flow events with sufficient energy to scour is a critical factor limiting cottonwood regeneration in Colorado (Friedman et al., 1995). Locations with a flow recurrence interval greater than 9 years are associated with higher regeneration and long-term survival of cottonwoods; floods that reach these locations possess hydrologic characteristics that created bare soil necessary for germination in locations where seedlings are protected from later flooding (Scott et al., 1997); mature cottonwood trees are found only above higher discharge levels (Auble and Scott, 1998). Similarly, the lower elevation limits of cottonwood and willow are determined by exposure to late-season floods (Rood and Mahoney, 1990; Shafroth et al., 1998). This information has been incorporated into a cottonwood “regeneration box” model (Mahoney and Rood, 1998), in which protection from high intensity flooding is a key factor enabling long-term survival. One positive effect of dam closure in the upper reaches of the Missouri River was to reduce peak flows, thereby providing stability that enabled contemporary (1930s-1960s) cohorts of newly established cottonwoods to survive to maturity; however continuing attenuation of flow magnitude has eliminated the high magnitude flooding necessary for new recruitment on higher elevation sites (Dixon et al., 2012a).

Propagule deposition

The intensity of flooding has also been linked to the type and quantity of propagules that get delivered to a site, with implications for subsequent community composition and development. Elevation determines the number of seeds and vegetative propagules deposited on a site (Becker, 1980; Nilsson and Grelsson, 1990) and the composition and viability of deposited propagules (Goodson et al., 2003). The latter study showed that differences in propagule composition between sites diminish with elevation (i.e. seed in deposited sediment became more similar between sites on lower elevations with more frequent flooding), suggesting that in higher energy, less-frequently flooded locations, the local seed source exerts a greater influence on the seed bank. Deposition of seedlings with sediment tends to favor recruitment of

disturbance-tolerant opportunistic species and is unlikely to be a natural source of recruitment for species that are generally less tolerant of flooding (Baattrup-Pedersen et al., 2013).

Successful establishment of many species in riparian systems requires an alignment of flood parameters, including intensity, with the particular habitat needs of the species (Richardson et al., 2007). This conclusion has been incorporated into a model of plants strategies for fluvial systems (Bornette et al., 2008), in which the propagation and dispersal strategies of species are the primary determinants of their distributions and are related to the intensity and frequency of flooding. In the case of cottonwood and willow, variation in the number of seeds deposited has little effect of regeneration rates unless accompanied by exposure of bare mineral soil associated with flooding above a certain energy threshold (Friedman et al., 1995). Nevertheless, diminished seed and sediment deposition associated with flood peak attenuation has been cited as one factor limiting the regeneration of cottonwoods on the Missouri River (Dixon et al., 2010).

Opportunities for establishment and growth

Once propagules have been delivered to a site, the conditions that they encounter determine germination success and subsequent survival. The link between disturbance intensity and opportunities for new species has been demonstrated across a variety of ecological systems and disturbance types. Fire and grazing disturbances in prairies that do not completely remove dominants have different effects than those that facilitate primary succession on new or fully exposed substrate; additionally, disturbance can shift relative abundance of annuals and perennials (Collins, 1987). Manipulative experiments have demonstrated that removal of established dominant vegetation serves as a release for otherwise less-dominant species, and that disruption of vegetation during the early stages of growth alters the competitive dynamics of communities and alters future dominance patterns (Carson and Pickett, 1990). Finally, the degree to which communities shift from dominance by perennials to dominance by annuals is positively related to disturbance intensity, because higher intensity disturbance makes sites more suitable for annual germination and increases mortality of perennials (Wilson and Tilman, 1991).

In riparian systems, flow energy determines the quantity and quality of existing vegetation destroyed or damaged, and therefore the amount of substrate available for germination and available light and nutrients required for subsequent growth of new plant species. Cottonwood (*Populus deltoides*), willow

(*Salix* spp.), and sycamore (*Platanus occidentalis*) regeneration is negatively related to vegetative cover; that of mid- and late-successional hardwood species is normally distributed about intermediate vegetation cover values (Hosner and Minckler, 1960). Sycamore germination in both forested and herbaceous communities requires bare substrate provided by flood removal of vegetation (Sigafos, 1976). On the Raritan River [New Jersey], physical damage to vegetation is the primary mechanism by which flooding affects vegetation, particularly through its effects on recently established seedlings (Frye and Quinn, 1979).

Lack of floods of sufficient power to remove existing vegetation is one factor blamed for the regeneration failure of cottonwood and willow forests on the Missouri River (Johnson et al., 1976; Johnson et al., 1982; Johnson, 1997, 1999, 2000; Johnson et al., 2012). Richardson et al. (2007) identified the removal of vegetation as an opportunity for invasion by non-native species. In studies such as those above, flow energy establishes an upper boundary on the potential amount of vegetation removed and the resulting opportunities for colonization by new propagules.

Similar to the removal of standing vegetation, the removal (or deposition) of litter also is a function of flow energy and affects species distributions. The patterns of regeneration in relation to vegetative cover documented by Hosner and Minckler (1960) and Sigafos (1976) are echoed in the relationships between litter cover and regeneration, with litter cover positively related to elevation. Additionally, heavy litter encountered on infrequently flooded sites is associated with reduced recruitment of nearly all species examined (Hosner and Minckler, 1960). Similar patterns have been documented on the Vindel River [Sweden], where leaf litter mass is distributed along an elevation-driven flow-energy gradient, is negatively related to vegetative cover, species richness, and diversity, and is positively related to the total number of seeds deposited; extreme leaf litter mass values are also associated with a greater abundance of taller growing species (Nilsson and Grelsson, 1990). In wetlands in the Netherlands, litter cover is positively related to elevation and negatively related to the abundance of *Phragmites australis* (a non-native species within the U.S.); within communities dominated by *Phragmites*, litter cover is the only factor significantly related to community composition (Lenssen et al., 2000).

The converse of litter removal, deposition of organic debris, has also been related to the distribution of species on floodplains (Steiger et al., 2001; Goodson et al., 2003). The two studies identify

complex relationships between elevation and organic matter deposition dependent on site-specific flow energy and the size, shape, and buoyancy of the litter being transport during any particular flood event.

Other studies have not specifically examined the relationships between elevation and litter cover, but have examined the effects of variable litter cover on species. For riverine marshes along the Ottawa River, the quantity of litter flushed from the system during spring flooding is the primary determinant of community composition (Day et al., 1988). For gravel bars along a small Montana stream, the abundance of black cottonwood (*Populus trichocarpa*) and willows (*Salix* spp.) is weakly related to woody debris deposited upstream (Malanson and Butler, 1991). These field studies are supported by manipulative experiments. Removal and addition of litter in an experimental marsh complex increased and decreased, respectively, the germination of seeds from the seed bank (Van der Valk, 1986). Similarly, removal of litter promoted germination, particularly for three species associated with wet habitats and having small seeds similar to cottonwood and willow (Seiwa and Kikuzawa, 1996).

As shown by the previously cited study (Seiwa and Kikuzawa, 1996), one important mechanism by which removal of litter and vegetation affects species distributions is the exposure of bare mineral soils, a prerequisite for the germination of many species. Consistent with that research, silver maple (*Acer saccharinum*) seedling establishment requires bare mineral soil produced by more frequent and higher energy flooding, which clears the litter from the flood plain and deposits additional layers of alluvium (Bell, 1974). Becker (1980) concluded that higher energy flooding is better able to create new surfaces for plant colonization than is low energy flooding and warned that attenuation of peak flows along the Platte River [Nebraska] would cause decreases in species richness. Lower elevation sites generally receive more soil deposition than higher sites, providing fresh bare substrate necessary for germination of many species (Goodson et al., 2003). In addition to the presence of bare soil, the timing of its exposure following floods (as determined by elevation) relative to the peak dispersal of propagules is a critical determinant of initial species composition (Dixon, 2003). An examination of the historical distribution of vegetation on the Missouri River attributed the greater abundance of early-successional communities in frequently flooded areas to the erosional and depositional processes that generated the bare soils needed for the establishment and survival of early-successional species (He et al., 2007). Finally, well-timed exposure of bare mineral

soils to encourage germination of desired species has been a hallmark of wetland management for more than three decades (Fredrickson and Taylor, 1982; Fredrickson and Batema, 1991).

Perhaps no riparian taxa have been more closely linked to the need for bare mineral soil for germination than have willows (*Salix* spp.) and cottonwoods (*Populus* spp.). Smith (1957) was among the first to assert that black cottonwood (*Populus trichocarpa*) required bare mineral soil to germinate. Shortly thereafter, Hosner and Minckler (1960) related flow energy to the percent cover of bare soil and the germination success of eastern cottonwood (*Populus deltoides*), willow, and sycamore (*Platanus occidentalis*). That research has been supported by more recent research relating successful germination of willows to the availability of moist, bare mineral soils (Karrenberg et al., 2002).

Research on numerous streams in western North America (Rood and Mahoney, 1990; Friedman et al., 1995) and Japan (Nakamura and Shin, 2001) have implicated attenuation of peak flows below dams as a contributing factor in the regeneration failure of cottonwoods and willows; such attenuation reduces flow energy or completely eliminates the flooding necessary to remove litter from potential germination sites. On the Missouri River too, reduction in bare mineral soil sites resulting from changes to stream hydrology has been blamed for the regeneration failure of cottonwoods and willows (Johnson et al., 1976; Johnson et al., 1982; Johnson, 1992, 1997, 1999; National Research Council, 2002; Dixon et al., 2012a; Johnson et al., 2012). In all of these scenarios, reduced peak flood magnitude has eliminated flows with energy sufficient to generate new surfaces via point bar deposition, removal of existing vegetation, and delivery of sediment to the floodplain.

Soil deposition and sedimentation

Another mechanism by which substrate is made available for colonization is through the deposition of sediment that creates new soil surfaces. In a broad review of the relationships between geomorphic processes and ecological patterns, Swanson et al. (1988) identified depositional events that create new soil surfaces in fluvial systems as the most obvious example of how geomorphic processes control the distribution of substrates upon which vegetation communities depend. Steiger et al. (2005) place sedimentation processes at the forefront of factors controlling the development of floodplains and associated vegetation communities. Previous studies on Severn River [United Kingdom] (Steiger and others, 2001) and the Garonne River [France] (Steiger and Gurnell, 2002) had shown that locations with

high energy during a flood of a particular magnitude receive more sediment dominated by coarse materials; lower energy locations during the same flood receive less and finer-textured sediment. However, flow energy is a function of hydrologic and hydraulic parameters determined by local topography and flood magnitude (Steiger and Gurnell, 2002), suggesting that patterns of deposition affecting sediment quantity and quality have complex, non-linear relationships with elevation (Steiger et al., 2001; Steiger et al., 2005). These findings relating to texture are consistent with earlier research by Osterkamp and Hupp (1984). On Long Branch Creek [Missouri] depression features (scours, oxbows, and depressions) receive less sediment deposition than the surrounding matrix and levees (Heimann, 2001), in other settings, such sites receive greater water velocity and sediment deposition (Piégay et al., 2000). Nevertheless, studies are generally in agreement that higher elevation sites receive lower flow energy that results in deposition of finer sediment. The relationships between elevation and soil texture are explored in greater depth in the sections exploring soil drainage and vegetation.

The effects of sedimentation on previously established species are as variable as the sediment distribution patterns themselves. Those effects can be measured in degrees of altered germination, growth, and survival that return this review to the theme of opportunities provided by removal or reduction of vegetative cover. The survival of American eelgrass (*Vallisneria americana*) on the Potomac River [Maryland] is negatively related to the depth of silt deposition (Rybicki and Carter, 1986). On the Ain River [France], the variable response of plant species to different degrees of siltation is the primary determinant of their distribution on the floodplain (Piégay et al., 2000). Sediment deposition during floods can be more influential in determining successful recruitment than the physical submersion of seedlings by water; varying growth responses among ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*), and pin oak (*Quercus palustris*) seedlings are indicative of varying tolerances to sediment deposition (Walls et al., 2005). In microcosms representing three wetland types, the responses of species to sedimentation were smaller than in microcosms representing headwater floodplains, suggesting that the species chosen to represent that wetland type were more tolerant of sedimentation (Mahaney et al., 2004). In the same experiment, the exotic invasive reed canary grass (*Phalaris arundinacea*) was the only of seven species in microcosms representing riparian depressions to have any successful seedling establishment and the only species to show a positive biomass yield response to sediment loading (probably from reduced competition,

since no other species became established). In a later experiment by Lowe et al. (2010), mortality of a sedge increased with sedimentation depth, and reached 100 percent for another species as sedimentation depth increased.

Other elevation-related environmental factors

Soil organic matter

Soil organic matter content should also be reflected in the LCPI flow-return intervals in that soil organic matter content in floodplains increases with elevation (Burke et al., 2003; Turner et al., 2004; Shin and Nakamura, 2005). In attempting to explain this phenomenon on the Chena River in Alaska, Viereck (1970) identified two potential explanations: 1) the stability and less frequent exposure to scouring floods of higher landforms enables accumulation or autochthonous organic matter, and 2) higher sites generally have finer soils with greater organic content deposited in association with higher magnitude floods. Regarding the first mechanism, this is consistent with observation made on the Missouri River (Johnson et al., 1976) and the Potomac River (Sigafoos, 1976) in which successional stage was related to elevation and the abundance of litter. Regarding the latter mechanism, conflicting results presented by Goodson et al. (2003) and more complex relationships between elevation and organic matter deposition described by Wharton et al. (1982) and Steiger et al. (2001) suggest that patterns of deposition are site specific. Local topography determines flow energy, with cascading effects on the quantity and quality of organic matter deposited or scoured during floods. However, in locations that approximate an idealized floodplain “where complex topographic features are lacking and the floodplain slopes gently from the river channel to uplands” (Brinson, 1990), the absence of local features that alter flow energy and potential exposure to scouring floods results in higher elevation sites generally having greater soil organic matter content.

Many of the above studies documented relationships between plant species distributions and soil organic matter content. Along the Rhone River [France], species richness in cut-off channels is a function of elevation-driven fluvial process that remove or deposit organic matter (Bornette et al., 1998). In floodplain forests of the blackwater Coosawhatchie River [South Carolina], lower elevation sites have more soil organic content and support tupelo communities; higher elevation sites support oak communities (Burke et al., 2003). Organic matter content is negatively related to the abundance of black oak (*Quercus*

velutina var. *ellipsoides*) on the Wisconsin River (Turner et al., 2004). On the Rekifune River in Japan, aside from water availability, the most important factors affecting the distribution of many species are the development of a soil A horizon and nitrogen and organic matter content (Shin and Nakamura, 2005); both values are positively related to landscape elevation. The abundance of common reed (*Phragmites australis*) in wetlands in the Netherlands varies with soil organic matter content, which also is related to community composition (Lenssen et al., 2000). An experiment by Rebele (2008) showed that variation in the condition of deposited soils, most notably organic matter content, determined the successional trajectories of plots.

It is important to note that soil organic matter content competes with other variables for expression in plant species distributions. For example, even though experiments by Wilson and Keddy (1985) showed positive correlations between soil organic content and biomass of 11 out of 12 species grown, the frequency of these species showed a more variable response to organic matter when measured in the field. The authors concluded that competition between species was attenuating the species' responses to environmental gradients. Similarly, where hydrologic conditions are dominant (i.e. in frequently flooded areas), effects of organic matter content on vegetation communities may be muted (Stanley et al., 1973).

Despite the ambiguities surrounding organic matter in relation to elevation and plant distributions, research with specific application to the Missouri River and its dominant species has shown the effects of variation in soil organic matter on species distributions. Johnson (1949) related a lack of organic humus to proximity to the river and the frequency of flooding, and Wilson (1970) described a carbon gradient increasing with elevation and successional stage subsequent to the closing of the Gavins Point Dam. Along channelized portions of the Missouri, lower organic matter content is associated with a higher percentage of sand, though vegetation communities do not show an affinity for particular edaphic conditions (Vaubel and Hoffman, 1975). Black cottonwood (*Populus trichocarpa*) and eastern cottonwood (*P. deltoides*) abundance is negatively related to organic matter content (Keammerer, 1972; Johnson et al., 1976; Malanson and Butler, 1991); ash, elm, and box elder abundances are positively related (Keammerer, 1972; Johnson et al., 1976). In the latter studies, organic matter content also was related to the distribution of herbaceous species; however, both variables were viewed as a function of stand age.

Nutrient deposition/soil chemistry

Soil organic matter content is reflective of broader trends that relate nutrient deposition and availability to elevation and species abundance. Wharton et al. (1982) linked the chemical properties of floodplain soils to the replenishment of soil minerals and associated nutrients by flooding; the intensity of such action is a function of hydroperiod, as determined by land elevation relative to flood stage. Frequently, higher nutrient concentrations are associated with higher elevations similar to that for soil organic matter (Vioreck, 1970; Wilson, 1970; Keammerer, 1972; Vaubel and Hoffman, 1975). Fertility gradients closely linked to elevation determine the composition of wetland communities along the Ottawa River [Canada]; the highest elevations sites have the greatest nutrient concentrations and are dominated by cattails (*Typha latifolia*) (Day et al., 1988). The concentrations of sodium (Na) and Phosphorous (P) in the A and B soil horizons, respectively are related positively to elevation; additionally, aerobic conditions associated with lower landscape positions can reduce the availability of nutrients (Burke et al., 2003). On the Rekifune River [Japan], nutrients concentrations are higher in less frequently flooded high sites than in sites subjected to more frequent flooding, with corresponding shifts in communities (Shin and Nakamura, 2005). On the Garonne River [France], nutrients are positively correlated with the percentage of silt and clay, which increase in higher elevation areas of low energy deposition (Steiger and Gurnell, 2002). Without the flushing of nutrients that accompanies periodic overland flows, eutrophication can occur in wetlands due to autochthonous inputs (Euliss et al., 2008); higher sites with infrequent flooded are less likely to receive such flushing flows.

Other studies have documented a negative relationship between elevation and nutrient concentrations. Frye and Quinn (1979) documented a negative relationship between cation exchange capacity and elevation, with corresponding changes in vegetation along the Rariton River [New Jersey]. In cottonwood communities on the Snake River [Idaho], lower nutrient stocks on higher floodplain locations contribute to decreases in productivity and changes in community composition (Merigliano, 2005). On the Rhone River [France], low-lying areas subject to frequent flooding receive greater nutrient input (Bornette et al., 1998). The conflicting relationships between soil nutrient concentrations and elevation suggest that the relationship may be driven by local topography and its effects on deposition and erosion patterns for soil and organic matter.

Manipulative experiments in former agricultural fields have shown that overall biomass increases, though individual species respond variably, to nutrient additions (Carson and Pickett, 1990). Different herbaceous cover types along the streams in British Columbia indicate the nutrient content (among other soil properties) that determined the suitability of sites for black cottonwood (*Populus trichocarpa*) growth (Smith, 1957). On the Wisconsin River [Wisconsin], soil fertility is significantly related to the abundance of 4 out of 8 commonly occurring species; two species show positive relationships, and two show negative responses (Turner et al., 2004). Nutrient availability determines the distribution of species on a longitudinal gradients in the Sil River basin [Spain] (Fernández-Aláez et al., 2005) and along the Akarçay Stream [Turkey] (Serteser et al., 2008). On the Missouri River, the floristic quality of wetlands is significantly related to the concentration of multiple dissolved nutrients (Kriz et al., 2007). Within the restoration and management realm, soil nutrient content is one factor determining the suitability of sites for wetland communities (Duranel et al., 2007).

The complex relationships described above imply that soil nutrient concentrations compete with other site attributes for expression in community composition and structure. Among those factors are rules of prior-establishment that are particularly important following abandonment of agricultural land. For example, nitrogen concentration plays only a minor role in determining plant species composition compared to dispersal and colonization patterns related to time since abandonment in old-field communities (Inouye et al., 1987). Additionally, higher fertility can accelerate the dispersal rates of species in post-agricultural settings (Orczewska, 2009), thus giving a competitive advantage to species that are abundantly represented in reproductive stages at the time of abandonment. Early dominance by one or two species can limit the impacts of subsequent nutrient additions on species distributions, implying that once a community is established, competition becomes more important and disturbance is necessary to modify species abundance (Collins and Wein, 1998). Additionally, the presence of an aggressive competitor can obscure the effects of changing nutrients or water content, even when such factors are known to influence species abundance (Wetzel and van der Valk, 1998). In intact portions of the Everglades [Florida], fine scale variation in nutrient availability is related to vegetation composition and structure; however, these relationships are masked in degraded systems in which allogenic spatial and environmental factors were more important (King et al., 2004). Additionally, where hydrologic factors are dominant, effects of nutrient

variation on vegetation communities may be difficult to detect (Stanley et al., 1973). The above findings are particularly germane to the Missouri River, where restoration activities are limited to former agricultural lands, and prominent features such as levees and drainage features still exert significant influence on the hydrology of sites.

Contaminant deposition

Though there is little research to support it, contaminant levels may also be related to floodplain elevation. At extreme concentrations, nutrients themselves can be viewed as contaminants, and an absence of scouring floods can contribute to eutrophication of low lying wetlands on unconnected floodplains (Euliss et al., 2008). The presence of urban contaminants is a main factor driving species distribution on a longitudinal gradient in the Sil River basin [Spain] (Fernández-Aláez et al., 2005). Increasing concentrations of Pb and Zn on native soils in southeast Missouri were significantly related to reductions in floristic quality (Struckhoff et al., 2013). Although the latter study included landscape positions outside of the floodplain, in both that study and the Sil River basin (Fernández-Aláez et al., 2005), measured nutrients were positively related to contaminant concentrations, suggesting that nutrients and contaminants accumulate in the same positions. Therefore, to the extent that nutrient concentrations on floodplains follow an elevation gradient, so too should the concentrations of contaminants.

Soil drainage and the water availability gradient

Aside from fluvial processes, the most important gradient to which species respond is water availability (Wharton et al., 1982; Brinson, 1990; Malanson, 1993; Hughes, 1997). At one end of the spectrum, plants are limited by anoxic soil conditions resulting from too much water; at the other end of the spectrum, plants experience periods of drought from too little water. That water availability is a critical determinant of plant distributions is beyond dispute and provides the basis for widespread agricultural practices to both remove water from the landscape by means of drainage structures and to increase its abundance through irrigation. Manipulative experiments have shown that variation in irrigation of old field plots determines the relative dominance of species (Carson and Pickett, 1990), and that the response of species to changes in water availability depends upon the soil moisture regime of the habitat to which they are adapted (Toogood et al., 2008). Additionally, the distribution of species has been shown to reflect an

inverse relationship between tolerance of anoxic conditions and tolerance of drought (Silvertown et al., 1999). Within the realm of wetland management, the amount of available water has been applied as the basis for wetland classification systems (Cowardin et al., 1979; Brinson, 1993; Klimas et al., 2005), is a key factor determining the suitability of sites for restoration to various wetland types (Duranel et al., 2007), and is the critical controlled variable in wetland management (Fredrickson and Batema, 1991).

Soil drainage classes within the LCPI describe the relative ability of soils to provide water and oxygen for growth throughout the growing season, and are defined by the presence of free water in the soil profile for varying periods during the year (Soil Survey Staff, 1993; Schoeneberger et al., 2012). Water is either observed or its presence is inferred from redoximorphic features in the soil. These features provide evidence of anoxic conditions associated with abundant water during some or all of the year, but are unable to indicate whether sites experience periods of drought that also may influence species abundance. Fortunately, drainage classes also are associated with soil textural and saturated hydraulic conductivity gradients that reflect the relative potential exposure of sites to drought conditions (Table 1). Poor drainage is associated with fine textured soils that impede flow; well and excessively drained soils are usually coarse and sandy and have high conductivity (Soil Survey Staff, 1993). The latter are more susceptible to drought conditions, particularly in high landscape positions that are protected from flooding and unlikely to receive water through groundwater inputs or surface flow. Thus, although soil drainage classes are based on attributes reflecting a lack of oxygen due to abundant water, they also describe the broader pattern of water availability through their relationships to soil texture.

Within the soil survey that informs the SSURGO database, one factor that can affect soil drainage is persistent water input, from either direct precipitation, a perched water table, surface water flow from higher landscape positions, flooding, or groundwater near the surface (Soil Survey Staff, 1993). For the latter three inputs, the potential amount of water that can be delivered to a site is a function of elevation. As discussed previously, lower elevations sites with shorter flow-return intervals are more likely to be flooded, and to experience longer and deeper flooding than relatively higher landscape positions.

During non-flooding periods, both the depth to groundwater at any given location and the duration of free water availability at any particular depth is determined by elevation. Variation in depth to the water table has been blamed for shifts in composition and diversity measures between high and low elevation

sites (Frye and Quinn, 1979), alteration of successional patterns among alder communities (Fujimura et al., 2008), and variable survival of willows (Schaff et al., 2003; Shin and Nakamura, 2005). Finally, non-flooding surface flow gathers in the lowest local landscape position, where it either seeps into the soil or pools on the surface (depending on the relative rates of inflow and infiltration). This type of “topographic capture” is important in creating saturated conditions on elevated wetlands with a perched water table along the Apalachicola [Florida] floodplain (Leitman, 1978; in Wharton et al., 1982) and in determining long-term tree survival along Missouri streams (Heimann and Mettler-Cherry, 2004). Rainfall inputs may be the only means by which wetlands are maintained in high floodplains that have little interaction with groundwater or flood events (Klimas et al., 2005). Given the above effects of elevation on potential water inputs, it logically follows that poorly drained soils should be more abundant in lower elevation sites with shorter flow-return intervals. This conclusion is supported by an examination of the distribution of LCPI soil drainage classes; for most river sections, the proportion of land represented by poorly drained soil classes decreases as flow-return interval increases (Figure 1).

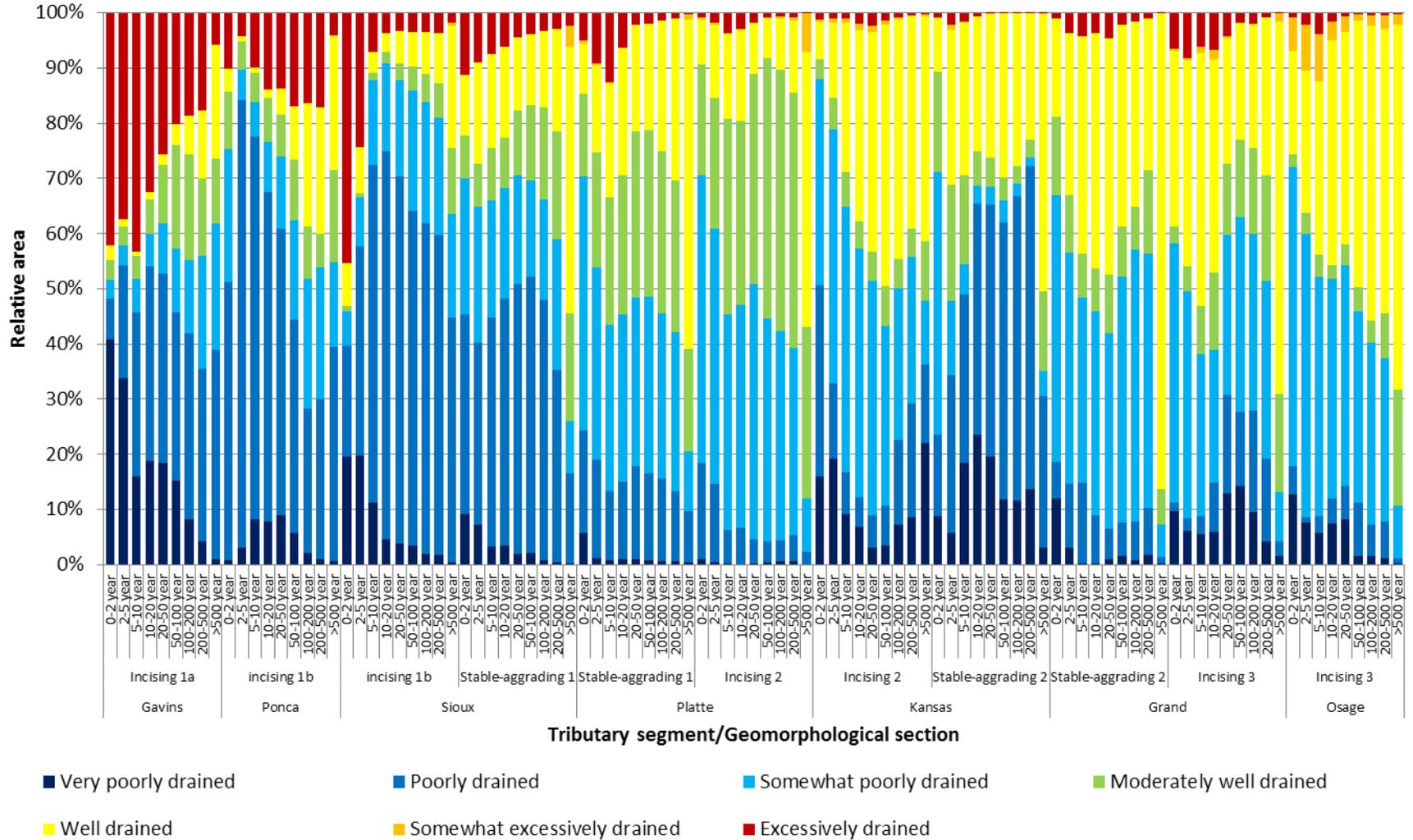


Figure 1. Bar graph of relative area of soil drainage classes for each flow-return interval by river segment showing that poorly drained soils generally represent a lower proportion of total area on higher elevation lands than on lower elevation lands.

Elevation and soil texture themselves are interrelated. During any given flow event, the horizontal distribution of sediment of varying particle sizes is determined by the flow magnitude and the flow energy to which individual sites are exposed. Hupp (2000) describes a general pattern in which rapid reductions in flow energy as water leaves the main channel cause coarse material to be deposited near the stream, forming a natural levee. This levee causes an elevation-driven velocity gradient that maintains the levee with coarse sediment deposition during over-bank events, with increasingly fine sediment deposited as one proceeds away and downward across the floodplain. Lower sites tend to have finer sediments than higher elevation sites (Hosner and Minckler, 1963; Alexander and Prior, 1971; Bragg and Tatschl, 1977; Brinson, 1990; Malanson, 1993; Goodson et al., 2003; Heimann and Mettler-Cherry, 2004; Klimas et al., 2005; Merigliano, 2005); however, this pattern of finer deposition at lower elevation does not always hold. Microtopographic variation and other floodplain features (including vegetation communities) determine local flow velocities and the texture of sediment deposited (Hupp, 2000), as does distance from the river (Steiger et al., 2001). Thus, although velocity and deposition patterns are a function of elevation, predictable relationships between elevation and soil texture are difficult to describe (Hupp, 2000; Steiger et al., 2005).

As a floodplain builds up through repeated deposition events, the vertical pattern of sediment deposition is determined by the variation in flow energy to which sites are exposed over time (Malanson, 1993). The soil profiles of low sites repeatedly exposed to high energy flows are dominated by coarse sediment; those in high sites exposed only to low-energy flows may be dominated by fine particles known to impede drainage (Steiger et al., 2001). Soil profiles in those sites exposed to variation in flow energy may exhibit dramatic vertical shifts in particle size, which are also known to impede drainage (Brady and Weil, 2008).

Within the context of the LCPI soil drainage classes, the degree to which soil texture is a function elevation is less important than the manner in which texture and elevation interact to determine soil moisture availability after deposition. For example, fine textured soils create higher capillary rise than coarse soils, reducing late-season water stress in wetland species even when the water table is well below rooting zone (Merigliano, 2005). This is one mechanism by which phreatophytes are able to persist on sites with fine-textured soils following alterations in flow regime that result in a lower water table (Nilsson and

Svedmark, 2002). To the degree that drainage classes reflect soil texture, they complement flow-return intervals as a means of describing the relative soil water availability of sites.

In the sections that follow, the relationship between water availability and the distribution of species is explored. First, plant species distributions are examined in relationship to variability in soil oxygen content, because that is the soil feature that is most directly reflected in the redoximorphic features that form the basis of the LCPI soil drainage classes. Here, the emphasis is on anoxic conditions resulting from too much water as a limiting factor to species growth and survival. The review then expands to encompass the full water-availability spectrum, examining the ways in which elevation, soil texture, or both affect species distribution through their influence on soil water availability. Throughout, high water availability is assumed to represent the dominant conditions of poorly drained soils, and low water availability those of excessively drained soils.

Soil oxygen availability

Variation in oxygen availability along an elevation gradient has been identified as a factor affecting the distribution of floodplain species for many decades. Smith (1957) related the suitability of sites for black cottonwood (*Populus trichocarpa*) to soil oxygen availability and asserted that sites with appropriately aerated soils along the streams in British Columbia could be identified by the distribution of herbaceous species. Similarly, soil aeration is a dominant factor affecting the distribution of species across the Missouri River floodplain and is a function of water availability as determined by elevation and soil texture (Weaver, 1960). Multiple experimental studies by Hosner (Hosner, 1958, 1960; Hosner and Boyce, 1962) assessed the flood tolerance of species by their ability to tolerate anoxic conditions. Along the margins of two impoundments of the Missouri River, the presumed effect of anoxic conditions on the distribution of species was confirmed by inundation experiments (Stanley and Hoffman, 1975). Robertson et al. (1978) identify clear relationships between bottomland tree abundance and the presence of redoximorphic features in the soil; these are the same types of features used to determine soil drainage within the SSURGO dataset (Schoeneberger et al., 2012).

The link between oxygen availability and vegetation distribution gained prominence with the publication of a comprehensive government document (the first of a series) examining the effects of changing water level on woody and riparian species (Teskey and Hinckley, 1977). The idea was supported

by subsequent research along the Raritan River [New Jersey] relating differences in community types to variation in soil aerobic condition (Frye and Quinn, 1979). Numerous synthesis works in subsequent years expanded upon the work of Teskey and Hinkley. For Wharton et al. (1982), anoxia is the dominant parameter controlling the distribution of species, and flood tolerance was defined almost exclusively by the ability to withstand anoxic conditions. By contrast, Brinson (1990), Malanson (1993), and Hughes (1997) conceive of a more balanced influence between anoxia at one end of stress gradient and low water potential at the other end. Nevertheless, at the time of these reviews, it had already been widely accepted that control of the oxygen content of soils through variation in hydroperiod could be used to influence the distribution of wetland species (Fredrickson and Batema, 1991).

Subsequent work has confirmed that soil oxygen availability can affect species distributions, often linking the aerobic state of sites to elevation, soil texture, or both. In floodplain meadows in the United Kingdom, species separate along an oxygen availability gradient determined by elevation (Silvertown et al., 1999). On the Coosawhatchie River [South Carolina], soil aeration (as reflected in the chroma values of various soil strata) is negatively related to an elevation gradient that defines plant community distributions (Burke et al., 2003). In that study, the oxygen content of soils was a function of soil drainage and the nature of inundation (high-oxygen through-flow as opposed to low-oxygen back-flow), and anaerobic conditions reduced the availability of nutrients. Along the Missouri River, low oxygen during summer floods contributes to reduced dominance by species that become established during spring floods of the same year (Dixon, 2003). Along the Osage River [Missouri], variation in wetland communities is a function of available soil oxygen as determined by elevation, with less available oxygen in low-lying areas where “topographic capture” enables prolonged ponding on fine-textured, poorly drained soils (Heimann and Mettler-Cherry, 2004). In Japan, anoxic conditions created by a high water table push succession toward alder communities in lower lying areas in the Kushiro Mire (Fujimura et al., 2008). Greater dominance by willow species in secondary channels of the Rekifune River [Japan] reflects their greater tolerance for anoxic conditions created by a water table near the surface (Shin and Nakamura, 2005), and research examining survival of black willow cuttings planted on a creek in Mississippi showed no effect of soil aerobic condition on growth and survival of willows (Schaff et al., 2003). The latter two studies suggest

that soil oxygenation may be less important than overall water availability in determining willow growth and survival.

Elevation and water availability

Research relating available water in the soils to elevation and species distributions has been conducted in many systems throughout the world. Anoxic conditions associated with abundant water are considered part of the broader spectrum of elevation-driven water availability determining community composition and woody species' abundance values on the Raritan River [New Jersey] (Frye and Quinn, 1979). Along the Platte River [Nebraska], communities are distributed along an elevation gradient that determines the likelihood of flooding that would recharge soil moisture (Becker, 1980). Similar relationships between the zonation of vegetation and an elevation-driven soil moisture gradient have been documented along free-flowing rivers in Norway (Nilsson and Svedmark, 2002) and along streams in Italy (Hupp and Rinaldi, 2007). In a recent study of the distribution of communities on the floodplain of the Missouri River, wet soils in low landscape positions were occupied almost exclusively by prairie communities; higher sites with lower water availability were also more likely to have prairie communities (Thogmartin et al., 2009).

At the dry end of the water-availability spectrum, research in the Great Plains has shown that drought induced reductions in growth and vigor for wetland species not adapted to dry conditions in the low-lying areas where they are usually found; these effects were reversed following a large flood that replenished soil moisture (Becker, 1980). Along the Bill Williams River [Arizona], higher elevation sites have less herbaceous cover and are more likely to experience drought-induced mortality of woody seedlings resulting from lack of access to the water table (Shafroth et al., 1998). In a reciprocal transplant experiment between wet and dry communities on an English floodplain, depth to water table (or inundation) drove shifts in species abundance (Toogood et al., 2008). Although a response to transplanting was evident in both communities, the effect of recovery and then drought following a large flood appeared to be the dominant factor influencing species abundance.

Other studies have examined the relationships between elevation, water availability, and species distributions in a resource management context. Long-term vegetation change following a lake drawdown in Norway demonstrated that in the absence of disturbance, a water-availability gradient determined by

elevation became the dominant driving force of community composition (Odland and del Moral, 2002). Susceptibility of sites to invasion by non-native invasive species has also been related to the soil water availability gradient determined by depth to the water-table and substrate composition (Tickner et al., 2001); the relationships they describe apply to all but the most specialized species. Euliss et al. (2008) point out that more prolonged and more extensive flooding can attenuate the spatial and temporal differences in moisture availability that serves to limit some species while favoring others. They focus almost exclusively on the elevation-water depth-vegetation relationship, because water depth is of one of the few things within the control of wetland managers.

Soil texture and water availability

In addition to being a function of elevation, soil water availability is a function of soil texture (Brady and Weil, 2008) and interactions between the two variables. The relationships between soil texture, soil available water capacity (or actual soil moisture content), and species distributions has been demonstrated in studies throughout the world. In the Kushiro Mire [Japan], shifts toward better drained soils of coarse texture drives successional changes away from alder communities (Fujimura et al., 2008). On the Sorachi River [Japan], soil water availability as determined by elevation and soil texture is the primary determinant of regeneration niches for six co-occurring willow (*Salix*) species (Niiyama, 1990). Maximum species richness along two Swedish streams occurs at locations with intermediate soil coarseness and soil water-holding capacity; reductions in textural heterogeneity due to modification of the flow regime is blamed for a reduction in overall floodplain diversity (Nilsson et al., 1989). This study suggests that the extremes of soil texture establish water availability conditions that filter out species that are not adapted to them. Vegetation communities in a freshwater tidal estuary in the Netherlands are arranged along a soil moisture gradient correlated with texture and bulk density, though the relationships with individual species and communities is generally weak (van de Rijt et al., 1996). On streams in Italy, the distribution of communities reflects soil moisture availability on landforms defined by their elevation and soil textures (coarse soils dominate lower landforms) (Hupp and Rinaldi, 2007). The authors suggest that the moisture availability may be less important in humid areas, but could be relevant in the semiarid Great Plains (within the area modeled by the LCPI, mean annual precipitation ranges approximately from 500 mm near the Gavins Point Dam to 1100 mm in eastern Missouri). Though Piégay et al. (2000) focus on the fluvial

processes that determine soil texture at various sites in France, they also document relationships between texture, water storage capacity, and the vegetation communities identified. Soil moisture is specifically identified as both a function of texture and one of the most important gradients to which species respond along streams in temperate Europe (Steiger et al., 2005).

In the United States, the relationships between texture, soil water availability, and the distribution of vegetation has been demonstrated across a variety of ecological settings. An early model for streams on the Atlantic Coastal Plain relates the occurrence of species and communities to the perceived drainage characteristics of soils (Wistendahl, 1958). These observations were confirmed quantitatively two decades later by research showing that changes in community composition and woody species' abundance values are related to water availability along elevation and soil texture gradients (Frye and Quinn, 1979). Along streams in North Carolina, occupation of sites by river birch (*Betula nigra*) is facilitated by greater soil water capacity associated with finer soils (Wolfe and Pittillo, 1977); the overall low frequency and duration of flooding suggest that soil texture, rather than flooding, was the prime driver of soil water content. Along the Coosawhatchie River [South Carolina], the distribution of vegetation is a function of depth to the water table (elevation) and the porosity of soils as determined by texture and structure; more porous soils have greater available water capacity and reduce the potential for exposure to drought conditions (Burke et al., 2003). The hydrogeomorphic classification system for the Arkansas Coastal Plain recognizes that some wetland community types are closely associated with particular soil series with drainage characteristics determined by texture and elevation (Klimas et al., 2005).

Studies in the western United States have also contributed to the body of knowledge relating vegetation communities to soil water availability as determined by texture. On the Chena River in Alaska, soil texture becomes finer along an increasing elevation gradient, and is the dominant factor affecting soil water availability across a corresponding successional gradient (Viereck, 1970). Along Plum Creek in eastern Colorado, an absence of finer particles in lower soil layers contributed to xeric conditions that favor drought-adapted species (Friedman et al., 1996). The higher silt and clay content of some sites along the Bill Williams River [Arizona] increases water availability and the abundance of four woody species (Shafroth et al., 1998). In the La Copita Research Area of south Texas, most sites are able to support both the woody mesquite (*Prosopis glandulosa*) and the herbaceous thin paspalum (*Paspalum setaceum*);

however, during years with extreme hydrologic outcomes (drought or heavy precipitation), soil texture determines water availability, which in turn serves as a limiting factor on the distribution of each species (Fernandez-Illescas et al., 2001). The latter two studies suggest that the greater available water capacity of finer soils may be particularly important in arid climates. On floodplains of the Snake River [Idaho], fine textured soils with greater water availability tend to be found at lower surface elevations and support more understory species associated with mesic conditions (Merigliano, 2005). This work was notable because it demonstrated that finer soils created higher capillary rise than nearby coarse soils, reducing late-season water stress in wetland species found in association with these soils, even when the water table was well below rooting zone. As such, it is the only study found that explicitly examined the interaction between elevation, groundwater, and soil texture in determining available soil moisture.

Not surprisingly, the above relationships between soil texture, available water, and vegetation also are evident in the Prairie Parkland (Temperate) and Central Interior Broadleaf Forest Provinces through which the Missouri River flows (McNab et al., 2005). On streams in the Missouri River valley, the distribution of plant communities is a function of soil water availability as determined primarily by soil texture and elevation (Weaver, 1960). On streams in southern Illinois, soil available water capacity as determined by texture is positively related to the recruitment of bottomland hardwoods; well drained coarse soils are found at high floodplain elevations and poorly drained clayey soils in low-lying back water areas (Hosner and Minckler, 1960, 1963). The distributions of mature species and communities also follow a soil texture gradient. Near the confluence of the Mississippi and Ohio rivers [Illinois], the abundance of tree species is related to the abundance clay particles associated with poorly drained soils (Robertson et al., 1978). Along two streams in Missouri, clay is more abundant in lower elevations, silt in higher locations, and sand near levees (Heimann and Mettler-Cherry, 2004). That system includes a gradient from coarse, well-drained soils on high elevations near rivers to fine-textured soils in low lying areas distant from the rivers. This gradient is reflected in the relative likelihood of exposure to drought conditions throughout the growing season, with concomitant effects on the distribution of woody and herbaceous species. Among sites at similar elevations (and thus subject to approximately the same likelihood of flooding), vegetation composition is a function of the duration of ponding as determined by soil texture-driven drainage capacity (Heimann and Mettler-Cherry, 2004). From a wetland management perspective, the suitability of sites for

wetland species often depends upon the texture-driven drainage capability of the soils (Fredrickson and Batema, 1991). Heitmeyer (2008) links soil texture and drainage capacity as related factors determining the distribution of historic vegetation, and uses these links to inform recommendations for the floodplain restoration of the Middle Mississippi River.

The Missouri River itself has been the theater for exploring relationships between soil texture, water availability, and vegetation distributions. The early qualitative description (Johnson, 1949) of a soil texture gradient from sandy to loamy soils with increasing clay content between willow stands, cottonwood stands, and later successional stages along the Missouri River would be confirmed in the following decades. Wilson (1970) related differences in the abundance of multiple species to soil variables, including available water capacity. Quantitative analyses from the Oahe Reservoir [North Dakota] indicate that available water content increases from cottonwood forests on sandy soil to areas dominated by ash, elm and box elder on finer soils with silt and clay, accompanied by shifts in herbaceous species (Keammerer, 1972). Also in North Dakota, ash, elm and box elder exhibit variable responses in frequency and density to changing available water capacity (Johnson et al., 1976). Kabrick et al. (2005) identify poor soil drainage as a frequently cited reason for failure of bottomland restoration plantings. They cite numerous studies that have shown that improving soil drainage at a site can positively affect growth and survival of planted hardwoods; however, their own results on the Missouri River suggest that improving drainage may only be effective on the most poorly drained soils. Finally, the most parsimonious model developed by Thogmartin et al. (2009) to explain the current distribution of cottonwood forests and wet prairies on the Missouri River included soil drainage.

Effects of variation in soil drainage on cottonwood and willow

Because cottonwood and willow are closely associated with rivers and other aquatic systems, numerous studies have examined the effects of variable water availability on these species. The abundance of cottonwood and willow has been related to water availability and the drainage capability of soils along the Missouri, (Weaver, 1960; Keammerer, 1972; Johnson et al., 1976) and the Mississippi River (Shelford, 1954). On numerous small streams in southern Illinois, the greater abundance of cottonwoods on sites with sandy soils possessing low available water capacity is enabled by late-season access to the water table provided in lower landscape positions (Hosner and Minckler, 1960, 1963). Research on Plum Creek

[Colorado] (Friedman et al., 1996) and the Bill Williams River [Arizona] (Shafroth et al., 1998) confirms these soil water availability-elevation-vegetation relationships with respect to cottonwood and willow abundance. The latter study concludes that access to the water table as determined by elevation is the primary determinant of cottonwood and willow survival. Along the Fraser River and other streams in British Columbia, the suitability of sites for black cottonwood (*Populus trichocarpa*) is related to soil moisture conditions as indicated by shifts in herbaceous species composition (Smith, 1957). Though primarily determined by flood frequency, the abundance of black cottonwood on coarse soils of the Lillooet River [British Columbia] also reflects soil moisture conditions that preclude invasive species (Teversham and Slaymaker, 1976). Viereck (1970) relates the distribution of feltleaf willow (*Salix alaxensis*) and balsam poplar (*Populus balsamifera*) communities along the Chena River [Alaska] to soil moisture content as determined by texture and elevation.

Soils particle size is a critical factor influencing the germination and initial establishment of willow and cottonwood on an intermittent stream in California (McBride and Strahan, 1984). Along the Middle Fork of the Flathead River in Montana, the abundance of willows and cottonwoods is positively, though weakly, related to the depth of fine sediments with greater availability water capacity than coarse sediments (Malanson and Butler, 1991). The variable response of different species to water availability is demonstrated by research showing that irrigation positively influences the regeneration of cottonwood (*Populus deltoides* ssp. *monilifera*), but has little effect of the survival of peach-leaf willow (*Salix amygdaloides*) (Friedman et al., 1995). Karrenberg et al. (2002) identify prolonged high water availability as a requisite for successful seedling establishment in willows. A study examining streambank restoration success in Mississippi, identifies restricted root growth in less permeable fine soils as the limiting factor on the survival of black willow cuttings; soil water potential is not limiting, because it tended to be higher in finer soils (Schaff et al., 2003). Willow survival and water availability are both lower on elevated sites. Later studies in the same area show that mortality on coarse soils is caused by soil moisture deficits; that on fine textured soils is due to poor drainage (Pezeshki and Shields, 2006; Pezeshki et al., 2007). In Japan, the abundance of willows and other species on gravel bars and low floodplains reflects the ability of these species to withstand low available water conditions (Shin and Nakamura, 2005). On the Missouri River, Thogmartin et al. (2009) documented that cottonwood and willow forests were almost entirely absent from

the wettest soils, which were instead occupied by prairie communities; cottonwood forests were also less abundant on the high elevation sites which had low soil available water.

Water availability appears to exert its most profound influence on seedling survival. This is supported by much of the research cited above (Friedman et al., 1995; Friedman et al., 1996; Shafroth et al., 1998; Karrenberg et al., 2002; Shin and Nakamura, 2005). Rood and Mahoney (1990) conclude that cottonwood seedling survival is determined by water availability, and include it as one of the two parameters (the other being susceptibility to flood damage) defining their “regeneration box” model for cottonwoods (Mahoney and Rood, 1998). Within that model, water availability is determined by tight relationships between the maximum root growth rate of cottonwood seedlings, depth to the water table as related to elevation above annual low flow, and the height of the capillary fringe as determined by soil texture. Water availability as determined by elevation and soil texture is also critical in determining the timing of seedling release and germination, and deposition of seedlings onto locations that have adequate water after germination (Niiyama, 1990). After seedling release, wet soils are more likely to trap windblown seeds of willow species than dry soils (Seiwa et al., 2008); thus, wet soil surfaces increase not just germinations success, but the likelihood that propagules are deposited on soils that have sufficient available water for short-term seedling survival.

On the Missouri River, low water availability following alteration of the hydrologic regime has been blamed for regeneration failure of cottonwoods. Rood and Mahoney (1990) attribute this decline to a lower water table resulting from channel incision, which reduces the ability of river rise to recharge soil water sufficient to reduce drought effects. Others have suggested that the absence of overbank flooding resulting from flow regulation has disconnected the river from its floodplain, reducing available water for growth (National Research Council, 2002). The reduced frequency of flow events that recharge soil moisture has specifically been blamed for reduced regeneration of cottonwoods on the Lower Missouri River (National Research Council, 2002; U.S. Army Corps of Engineers, 2011; Dixon et al., 2012a).

Soil drainage classification reflects past conditions

Within the SSURGO soil classification, the “natural drainage class refers to the frequency and duration of wet periods under conditions similar to those under which the soil developed. Alteration of the water regime by humans, either through drainage or irrigation, is not a consideration unless the alterations

have significantly changed the morphology of the soil” (Soil Survey Staff, 1993). To the extent that the conditions under which the soils developed persist to the present, the soil drainage attributes of the LCPI classes will accurately reflect the current hydrologic regime of the site (assuming sites are classified correctly). However, the hydrology of the Missouri River has been drastically altered in many ways. Management of the river has attenuated peak flows, such that many locations that would have received moderately frequent flooding are now flooded infrequently or not at all; by contrast, hydroperiods at lower elevations may be extended by prolonged maintenance of higher discharge throughout the year (Jacobson et al., 2009). These effects of dam construction and flow management are particularly acute closer to the Gavins Point Dam. Associated with these changes, dam construction and river management have modified the sediment load of the river, leading to degradation of the river channel in many locations and raising of the channel in others (Jacobson et al., 2009). These changes in the relative height of the floodplain to the channel have altered the peak flow required to inundate sites along the river (Jacobson et al., 2009). Given the tight relationship between groundwater elevation and river stage on the Missouri River (Grannemann and Sharp Jr, 1979; Foreman and Sharp Jr, 1981), these changes also have altered the likelihood and duration that groundwater will be at or near the surface for any given point of the floodplain.

Hydrology has been affected by agricultural practices on the floodplains as well. The most obvious floodplain features affecting floodplain hydrology are levees and other structures designed to limit flooding. On the one hand, these features exacerbate the disconnection between the river and the floodplain by restricting overland flow to only the highest magnitude events. On the other hand, this effect is offset where levees constrict flow, reducing the ability of the stream to disperse on the floodplain, thereby increasing river stage and groundwater elevation for a particular discharge. Given the tight relationship between groundwater elevation and river stage on the Missouri River (Grannemann and Sharp Jr, 1979; Foreman and Sharp Jr, 1981), the practices and structures described above will affect broad areas, such that the drainage capabilities of sites on a floodplain will not change relative to one another. By contrast, where levees and other features (for example, roads) serve to impound water and prolong flood exposure, effects may be localized. Similarly, features such as drainage ditches and pumping systems facilitate rapid removal of surface water from the floodplain, reducing flood duration, soil water residence time, and groundwater

elevation. While such features affect the groundwater level across an entire floodplain, the impact increases with proximity to the activity in question.

Agricultural practices may also affect soil drainage independent of the link between river stage, land-surface elevation, and groundwater levels. On the one hand, plowing can break up restrictive soil layers and increase soil permeability; on the other hand, repeated plowing can lead to the development of an impermeable plow-pan (Brady and Weil, 2008). These practices may cause the current drainage to deviate from historic conditions or from conditions at the time of the soil mapping that forms the basis for the drainage classification with the SSUGO database (Soil Survey Staff, 2012). Because the effects are local, they have the potential to change the relative wetness of a site compared to nearby locations, in addition to altering the drainage compared to what it was during soil mapping. Where species have not had sufficient time to adjust to new hydrologic conditions, links between LCPI classes and vegetation distributions may be difficult to detect and describe.

Environmental parameters not addressed by the LCPI

Flow timing

One of the critical environmental parameters not reflected in the LCPI flow-return intervals is flow timing. Successful establishment of many species in riparian systems requires an alignment of flood parameters, including timing, with the particular habitat needs of the species (Richardson et al., 2007). Lytle and Poff (2004) conclude that many of the adaptations of plant species to flow regimes relate to the timing of floods, rather than magnitude, frequency, or duration. Plants distributions at smaller scales (for example, across a given floodplain) are determined by the coincidence of physiographic processes and phenological events, particularly those related to reproduction (Zimmermann and Thom, 1982; Baattrup-Pedersen et al., 2013). In managed wetlands, the timing of flooding can be more important than the depth or duration in determining which species dominate a site (Fredrickson and Taylor, 1982; Fredrickson and Batema, 1991). Effects of variation in flow timing on floodplain vegetation can include reduction or elimination of riparian plant recruitment, reduced plant growth rates (Poff et al., 1997), and invasion by exotic riparian species (Poff et al., 1997; Tickner et al., 2001).

Among the most critical and most scientifically investigated elements of flood timing is its effect on propagule dispersal and deposition patterns. The importance of flood timing in relation to propagule dispersion is an offshoot of the flood-pulse concept advanced by Junk et al. (1989); propagules are one of the many types of matter and energy that are deposited during floods. Many riparian species possess phenological characteristics to ensure synchrony between periods of high flow that increase dispersal capabilities (Dixon, 2003; Baattrup-Pedersen et al., 2013). For example, synchrony between spring floods and seed release is a critical component of cottonwood and willow regeneration (Smith and Richards, 2008); autumn flood timing is more critical for the dispersal, deposition, and successful germination of smartweeds (*Polygonum* spp.) (Staniforth and Cavers, 1976). Synchrony between maximum fruiting and various stages of inundation sorts the propagules of various species based on coincident water level (Kubitzki and Ziburski, 1994). Variation in both the number and composition of viable seeds has been related to elevation, because the timing of site exposure following floods influences the potential seed bank (Goodson et al., 2003).

In addition to affecting propagule dispersion and deposition, flow timing shapes the environment in ways that interact with later developmental stages to determine recruitment success and long-term survival. Flood timing determines not just when and how much seed of a given species is deposited, but also soil particle size of the substrate, which can influence germination success (McBride and Strahan, 1984). Late-season floods can reduce the dominance of species that managed to occupy sites following early-season floods (Dixon, 2003; Baattrup-Pedersen et al., 2013). Alteration of flow regimes has affected the tree growth patterns of a variety of species in many river systems (Reily and Johnson, 1982; Bren, 1993; Dudek et al., 1998). Wharton et al. (1982) identify flood timing as one of three key factors (the others being depth and duration) that limit oxygen availability at sites, and thus the distribution of plant species; seasonality of flooding determines the temperature of flood waters, which governs the rate of biotic activity that consumes and generates oxygen.

Flood timing is also a critical variable in the successful establishment and long-term survival of willow and cottonwood communities. For example, Johnson (2000) demonstrated on the Platte River that the timing of floods is a more important determinant of cottonwood regeneration success than flow frequency. For cottonwoods and willows on the Great Plains, consistent timing of cottonwood seed

maturation has been attributed to the long-term, fairly predictable nature of snow-melt driven flooding (Lytle and Poff, 2004). Synchrony between seedling release and the exposure of suitable locations for seedling establishment and survival is a key component of the “regeneration box” model for cottonwood developed (Mahoney and Rood, 1998). In some settings, the proper timing of seedling release allows windblown seeds to adhere to wet soil surfaces (Seiwa et al., 2008) that are likely to have sufficient soil moisture for germination and establishment (Niiyama, 1990; Mahoney and Rood, 1998). The collapse of cottonwood communities along western prairie streams (Rood and Mahoney, 1990; Johnson, 2000) and the Missouri River (Johnson, 1992) has been attributed to asynchrony between flooding and seedling germination caused by dam construction and flow modification. Following a flow pulse, a rapid decline in groundwater surface elevation can outpace root growth, inducing mortality in newly established seedlings or vegetative propagules (Stokes, 2008). Regardless of the mechanism of its effects, flow timing is now widely accepted as a critical variable affecting the distribution of species (Smith et al., 2008) that the LCPI is unable to address.

Variation in flow-return interval

Because the LCPI incorporates data relating only to mean flow-return interval, it is unable to address variation in flow frequency. Low-frequency extreme events may be more critical to plant distributions than frequent events (Zimmermann and Thom, 1982). Within the context of the LCPI, that a site is subject to annual flooding may be less important to determining the species that occur there than the fact that it is also subject to 100-year “resetting” floods with greater influence on the entire landform (Brinson, 1990; Opperman et al., 2010). Many forest types require both periods of frequent flooding for maintenance and periods in which flooding does not occur to enable regeneration (Bren, 1993). This is supported for cottonwood forests on the Platt River [Nebraska] (Johnson, 2000) and the Missouri River (Scott et al., 1997; Auble and Scott, 1998). Additionally, variable hydrologic processes within a river stretch limit the extent to which elevation is related to successful cottonwood establishment (Scott et al., 1997). For example, the establishment processes first described by Johnson (1949) requires a meandering stream in which established seedlings on newly created point bars are protected from future flooding by the lateral migrations of the river that are not reflected in LCPI classes. That the LCPI is unable to address the

variety of flow-events and hydrologic processes to which sites are exposed may limit its ability to anticipate the distribution of species.

Spatial configuration

Another variable affecting the distributions of species and communities not addressed by the LCPI is the spatial configuration of the various wetness classes and the communities that form on them. It is widely held that connectivity, patch size, and the presence or absence of dispersal corridors contributes to the ability of species to occupy sites (Malanson, 1993). A river can serve as both a barrier to and facilitator of plant propagule dispersion; during floods, submerged lands play a similar roles (Malanson, 1993). Models that incorporate only niche characteristics are not as accurate in predicting species abundance in fluctuating environments as are spatially explicit models (Seabloom et al., 2001). Spatial configuration can be as important as environmental factors in determining forest species composition, and these effects are not evenly expressed in each vegetative stratum (Gonzalez et al., 2009). The ability of some species to become established on former agricultural sites depends on the proximity of a nearby seed source (Thomson, 1943). Distance from areas of disturbance can affect the abundance of non-native species, and the degree to which such species can penetrate communities depends on the type of community that already exists on a site (Hansen and Clevenger, 2005). Fragmentation of successional advanced communities facilitates invasion by non-native species (Rejmánek et al., 2013). On the other hand, flooding is a sufficiently dynamic process to override spatial dependencies related to the slow dispersal patterns of species in post-agricultural settings (Orczewska, 2009).

To take one example from recent literature, distance from the river has been shown to be an important determinant of tree species and forest community distribution along both the Wisconsin River (Turner et al., 2004) and the Missouri River (Thogmartin et al., 2009). This makes intuitive sense, since the river is the primary conduit of energy and matter within the system, and less of that energy (e.g., velocity) and matter (e.g., sediment) is delivered to points farther from the stream (Vannote et al., 1980; Wharton et al., 1982; Malanson, 1993). However, in highly modified riparian systems like the Missouri River, the current distribution of species may be a function of past land use as much as of the flow regime. For example, the abundance of some species is dependent on the proximity of a nearby seed source (Thomson, 1943), and the tendency of cottonwood to be more abundant close to the Missouri River (Thogmartin et al.,

2009) may reflect agricultural practices that have left most of the mature cottonwoods capable of providing seed along floodplain margins outside of protected levees (Struckhoff et al., 2011; Struckhoff, 2013). Additionally, because the Missouri River floodplain has been so thoroughly disconnected from fluvial processes (National Research Council, 2002; U.S. Army Corps of Engineers, 2011; Dixon et al., 2012a), there is reason to suspect that distance from the river relates to vegetation distribution only by means of other environmental variables for which it now acts as a surrogate (for example, depth to the water table or soil drainage). At present, the river may serve less as a part of the floodplain system than as a boundary to it, serving primarily to delineate the limits of human activity, with perhaps some ancillary effect on vegetation distribution.

Perhaps more important than the metrics of spatial configuration are the flow processes to which sites and species are exposed because of their location within the landscape. Urban and Daniels (Urban and Daniels, 2006) warn of the disconnect between landforms and the processes generating them, an issue that becomes even more significant as spatial scale increases. Within any riparian setting, the most obvious processes are hydrologic, and the LCPI is unable to address many of these. For example, ponding of surface waters can be a critical means of soil moisture maintenance that enables the long-term survival of tree species in elevated landscape positions (Heimann and Mettler-Cherry, 2004); although the LCPI flow-return intervals identify lower elevation sites where ponding is more likely to occur following rain or after floods recede, they provide no indication that the local landscape makes such ponding a reality.

Additionally, topographic form confounds soil and site variables such that elevation alone may be a poor predictor of species abundance (Robertson et al., 1978). Along the Missouri River and Potomac River, low landscape positions (for example, the downstream ends of islands) provide protection from flooding and long-term survival of cottonwoods similar to high elevation sites that are only rarely flooded (Yanosky, 1982; Scott et al., 1997). The position of sites relative to hydrologic features such as convex banks, locations with spatially variable flow, water inlet, and water outlets affects the type and quantity of sediment delivered to a site (Steiger et al., 2001; Steiger and Gurnell, 2002). On the Missouri River, this phenomenon is illustrated by the proximity of sand splays to levee breaches resulting from floods in 2011 (unpublished data). The nature of the inundation (backflow or throughflow) can be as important as the frequency of inundation in determining silting dynamics and vegetation patterns (Piégay et al., 2000).

Similarly, whether a wetland is impounded (naturally or otherwise) is a critical criterion used to define wetland function (Cowardin et al., 1979; Brinson, 1993; Klimas et al., 2005). In addition to these abiotic considerations, local vegetation and the spatial pattern of vegetation across broader areas affect the surface hydraulics of sites (Tabacchi et al., 2000; Steiger et al., 2005; Bornette et al., 2008). And beneath these surface processes, the response of groundwater to changes in river stage is a function of distance from the river (Kelly, 2000). The features and processes described above are not elevation dependent and compete with elevation-driven processes captured in the LCPI for expression in the distribution of species.

Terrestrial and hydrologic modification

Past land use and hydrologic changes may exert long-term influence on sites and either make the LCPI classes incorrect for a particular site, or mask the relationships between vegetation and the environmental variables modeled in the LCPI. In degraded portions of the Everglades, for example, spatial dependency and allogenic environmental factors masked the relationships between fine-scale environmental variables and vegetation structure and composition in degraded areas; these effects were not evident in locations least affected by hydrologic changes (King et al., 2004). One obvious example of land-use change that would be inaccurately reflected in the LCPI would be soil drainage alterations that have occurred since soil mapping. The effect of a particular practice designed to affect drainage would likely be local, but such practices are widespread.

Systemic changes that may make LCPI classes incorrect include hydrologic changes associated with dam construction and flow management. Such changes affect the flow energy, to which the physical and biotic components of riparian systems adjust over time; however, during periods of adjustment, the relationships between species and physical gradients that had formed to maximize efficient use of energy within the system may no longer exist or may be obscured (Vannote et al., 1980). Within the area modeled by the LCPI, recently produced maps of vegetation on Big Muddy National Fish and Wildlife Refuge [Missouri] indicate that in many areas abandoned subsequent to flooding in 1993, past land use and priority establishment rules determine the vegetation patterns observed (Struckhoff et al., 2011; Struckhoff, 2013). Although species appear to be sorting along hydrologic gradients, there are areas where it is evident that the presence of particular communities is a function of past agricultural practice. For example, most mature forests are located outside of protected levees where they were either allowed to remain as sites were

cleared for agriculture or developed after levee construction; box-elder forests are more abundant on agricultural sites that were abandoned prior to flooding (Struckhoff et al., 2011; Struckhoff, 2013). As a result, distance to the river becomes a predictive variable for cottonwood abundance (Thogmartin et al., 2009), but it is not necessarily reflective of the hydrologic processes to which species and communities are currently exposed.

Competition

Competition among species can mask the influence of environmental parameters on species distributions, but is more important in some settings than in others. According to Grime (1973), species exist along a stress-competition gradient in which, as the intensity of stress decreases, the importance of individual species' adaptation to that stress becomes less important relative to their ability to compete for resources. The negative relationship between stress and competition was incorporated in a model for large rivers, with a gradient from physical to biological influence as one moves away from the river (Johnson et al., 1995). It was later applied as a general model for streams of all sizes in which flood disturbance is placed at one end of the stress-equilibrium gradient and competition from other species at the other end (Hupp and Osterkamp, 1996). As disturbance stress decreases, increasing competition inhibits the ability of individual species to respond to environmental gradients (Keddy, 1989; Malanson, 1993).

The tension between competition and environmental gradients has been shown in numerous studies. The work of Wilson and Keddy (1985) documents positive correlations between soil organic content and biomass of 11 out of 12 species grown in experiments; however, in their field experiments, many species exhibit a normal distribution around a mean value, suggesting that competition attenuate the species' responses to environmental gradients. Similar effects of have been documented in two English meadows, where competition shapes the biomass production response curves of multiple species to a gradient defined by depth to water table (Silvertown et al., 1999). Research examining the effects of fire and grazing in prairies has shown that disturbance intensity determines the extent to which dominant species are removed, shaping future community development (Collins, 1987). In controlled experiments using eight species common to Ohio wetlands, flood-induced stress reduced the ability of 4 species to suppress their neighbors (Fraser and Miletti, 2008). Species distribution models that include the presence of competitive ruderal competitive species in the seed bank are more accurate than a simple niche-based

model (Seabloom et al., 2001), suggesting that environmental gradients vie with competition resulting from historical establishment events in determining the distribution of species. To put this in the context of the LCPI flow-return intervals, priority establishment effects on the Missouri River can be virtually eliminated by repeated flood disturbances, especially those that affect predominately the first established species (Dixon, 2003). This suggests that competition is less critical in areas with short flow-return intervals, but on infrequently flooded sites or where river management has reduced the likelihood of repeated disturbances, priority establishment effects may be both stronger and longer lasting.

The effects of competition in riparian systems were discussed previously in the context of opportunities for colonization provided by flood-induced removal of existing vegetation. In that context, flow energy determines the intensity of disturbance (as measured in damage to existing vegetation, for example) and thus the competition to which colonizing species would be exposed once flood waters recede. This was shown to affect the distribution of cottonwood and willow (Hosner and Minckler, 1960; Johnson et al., 1976; Johnson et al., 1982; Johnson, 1997, 1999, 2000; Johnson et al., 2012), sycamore (Hosner and Minckler, 1960; Sigafos, 1976), and non-native invasive species (Richardson et al., 2007). Regeneration of early-successional species is related negatively to the cover of existing vegetation, but regeneration of late-successional species in areas less prone to flooding is normally distributed around an intermediate level of vegetative cover (Hosner and Minckler, 1960; Wilson and Keddy, 1985). However, opportunities for colonization may not be disturbance-dependent. Specialists adapted to extremely wet or dry conditions thrive in environmental conditions beyond the suitable range for other species; alternatively, species that exhibit limited responsiveness to environmental gradients may reach their maximum development on sites occupy sites at the margins or outside of the suitable range of species that are responsive to those gradients. For example, the inability of cottonwood or willow to occupy infrequently flooded sites with low available water capacity provides a potential niche to be occupied by later successional species such as ash and box elder.

One environmental variable affected by removal of vegetation is light availability for germination and growth. Removal of existing vegetation increases light to support sycamore (*Platanus occidentalis*) germination on the Potomac River (Sigafos, 1976). Similarly, on the Bill Williams River [Arizona], four species (*Populus fremontii*, *Salix gooddingii*, *Tamarix ramosissima*, and *Baccharis salicifolia*) are less

likely to become established on sites with high basal area and low light, two environmental variables correlated negatively with each other (Shafroth et al., 1998). Experimental forest canopy removal has shown that light availability determines the recruitment success of riparian species with small seedlings similar to willow and cottonwood (Seiwa and Kikuzawa, 1996). In a broadleaf forest in Denmark, the variable most associated with understory species composition is available light as determined by canopy density, with some understory species indicative of higher light availability (Thomsen et al., 2005). Similarly, light availability is a controlling variable of understory composition along the Snake River [Idaho](Merigliano, 2005). In managed wetlands, controlled flooding is the dominant process for the generation of canopy openings in which new species have an opportunity to become established (Fredrickson and Batema, 1991).

Much of the research on relationships between competition and disturbance has been conducted in systems dominated by one or two species. In an experimental marsh complex in Canada, removal of standing litter of 2 dominant exotic species to simulate late-season floods increased seedling richness and germination rate of seeds in the seedbank of an exposed wetland mudflat; removal of an abundant annual species increased germination and accelerated the flowering phenology of grasses (Van der Valk, 1986). In old fields in Poland, the presence of a dominant species in the understory limits the dispersal of other species, slowing forest expansion; however flooding is a sufficiently dynamic process to override this limitation (Orczewska, 2009). A study of succession following a flood thirty years earlier, documented that a muted response to environmental gradients by native species in old fields dominated by a non-native grass planted prior to the flood compared to fields where the grass had not been planted (Friedman et al., 1996). The presence of an aggressive competitor can obscure the effects of changing nutrients or water content, even when such factors are known to influence species abundance (Wetzel and van der Valk). Nearly complete dominance by a single species masks the effects of heterogeneous resource distribution during the early stages of community development and inhibits the establishment of less-dominant species (Collins and Wein, 1998). In the Netherlands, species composition of wetlands is determined in part by the abundance of common reed (*Phragmites australis*), a non-native species in the United States (Lensen et al., 2000). Accuracy in predicting the distribution of wetland species can be improved by incorporating establishment constraints compared to niche models incorporating a single environmental gradient ; this

may be particularly true in the presence of highly competitive exotic species, which can delay by decades the observed convergence observed between niche models and spatially explicit models incorporating establishment constraints (Seabloom et al., 2001). Where a single species has become dominant, it can suspend succession such that other species' potential response to environmental gradients is masked (del Moral et al., 2009). In a flooding-stress context, these studies imply competition is more important in areas that experience lower intensity floods that do not completely remove dominant species and their propagules.

The stability that accompanies protection from flood stress may also affect competition. The relative importance of competition changes over time, with allogenic processes dominant early, and competition becoming more important with time (Bornette et al., 2008). For example, the development of forests on abandoned agricultural fields has been linked to a decreasing abundance and richness of exotic species (Meiners et al., 2002). Non-native species are generally less abundant in communities dominated by long-lived species, which occupy available space and compete for resources with potential invaders (Rejmánek et al., 2013); however, there are exceptions to this rule. For example, within the study area of this project, the exotic garlic mustard (*Alliaria petiolata*) thrives in the shade provided by a dense canopy of mature forests (Yatskievych, 2006; Struckhoff et al., 2011). Areas protected from high-intensity disturbances (for example, LCPI classes with long flow-return intervals) possess the stability necessary for progression toward later successional stages in which autogenic processes become more important.

Although the LCPI does not address competition directly, its flood frequency classes should serve as a proxy for the relative importance of flood-stress and competition in determining the abundance of species. Flood adapted species should be more abundant in frequently flooded areas, and those with the competitive traits described by Grime (1973) should be more abundant in higher landscape positions. Certain species may be both flood tolerant and competitive, such that their distribution is less affected by temporal progression along this gradient.

Non-equilibrium/Succession

From the above discussion of competition, it is evident that successional processes may also influence species assemblage patterns, making it more difficult to detect relationships between LCPI classes and the distribution of species and communities. The primacy given to successional processes in

determining species distribution in much of the early research along streams demonstrates an adherence to the concepts of Clements (1916). In riparian settings, this conceptual framework is exemplified by work on streams of the southeastern coastal plain (Wells, 1928), the Raritan River (Wistendahl, 1958), Midwestern streams (Hosner and Minckler, 1960, 1963), streams in British Columbia (Smith, 1957), and the Missouri River itself (Johnson, 1949; Wilson, 1970). Although many of these studies described the environmental parameters of elevation, hydrologic processes, and soil texture associated with the successional stages they identified, the influence of those parameters on the distributions of species mostly was left unexplored; succession was believed to be far more important.

Broader acceptance of the theory that species respond individually to their environment (Gleason, 1926) and analytical means to test that theory (Whittaker, 1967) allowed researchers to explore the relative effects of succession and environmental variables on species distributions. On the Chena River (Viereck, 1970) and the Potomac River (Sigafos, 1976), the distribution of species was examined in the context of succession, but each successional stage was associated with a set of environmental conditions (soil texture, elevation, flow frequency, depth to groundwater) also related to the distribution of species. In a floodplain forest in Illinois, that soil and hydrologic variables were less related to species distributions in a secondary-growth forest than in an old-growth forest was attributed to the increasing influence of succession as stands aged (Robertson et al., 1978). It was suggested that the distribution of species in the second-growth forest was an expression of “physiological range”; the old-growth distributions reflected the “ecological range” of species, in which competition from other species limits the response to environmental variables. Additional research in Illinois showed that a successional gradient is equally as important as flood frequency in determining the distribution of species; time since disturbance is one of many environmental gradients to which species respond (Bell and del Moral, 1977). Within that framework, successional stage is merely competition expressed in the structure and composition of community types, and the stress-competition gradient of Grime (1973) becomes more relevant.

Many studies have addressed the relative contributions of successional processes compared to environmental gradients. Malanson (1993) is often cited in manuscripts relating local environmental parameters to the distribution of species, but was himself aware that stochastic establishment events and subsequent successional processes help determine the distribution of species (Malanson and Butler, 1991).

Bendix (1999) suggests that time since disturbance and successional processes can mask the influence of environmental gradients that may be at play. The pattern of herbaceous, willow, and cottonwood communities along Plum Creek in eastern Colorado is explained by a successional model in which the initial establishment of species facilitates deposition and a gradual building-up of sandbars and the floodplain; that build-up is accompanied by changes in soil particle size and water availability that further affect the composition of communities (Friedman et al., 1996). Successional processes were one of two factors (the other being elevation) that determined species composition following drawdown of a reservoir in Norway (Odland and del Moral, 2002).

These patterns have been incorporated into conceptual models of floodplain development by Hughes et al. (1997) and Bornette et al. (2008). The former posit a gradual build up floodplain surface accompanied by transitions from pioneer to shade tolerant individuals, reflecting a transition from dominance by allogenic disturbance factors (specifically, floods and sedimentation) to dominance by autogenic disturbance (Hughes, 1997). The latter conceived a model of plant strategies in fluvial systems in which the influence of flood frequency is inversely proportional to the influence of autogenic processes of succession and competition (Bornette et al., 2008). Osterkamp and Hupp (2010) emphasized successional processes in suggesting that the community occupying a given site indicates its stage of recovery; succession becomes more important in those sites that are stable enough to allow it to occur. Such stable sites tend to be at higher elevations (as reflected in LCPI flow-return intervals) or at protected locations, such as the downstream ends of river bends and islands (Sigafos, 1976). In managed systems, as time since conversion to managed wetland increases, the successional processes become less important compared to hydrology in determining species distributions (Fredrickson and Taylor, 1982).

Specific mechanisms of successional processes have been explored. First, even among those authors that give primacy to fluvial processes as a driver of floodplain development, it is widely recognized that vegetation helps to shape the physical environment by affecting hydraulics during periods of flow, with cascading impacts on sediment deposition and vegetation (Malanson, 1993; Hupp, 2000; Tabacchi et al., 2000; Steiger et al., 2005; Bornette et al., 2008). Such processes have been described along the Missouri River (Johnson, 1949; Johnson et al., 1976), the Potomac (Sigafos, 1976), the Raritan River (Wistendahl, 1958; Frye and Quinn, 1979), a small stream in the western Great Plains (Friedman et al., 1996), and for

multiple streams in the southeastern United States (Hupp, 2000). Another mechanism by which succession affects species distribution is by altering available light. Many studies have shown that cottonwoods cannot reproduce under an established canopy (Smith, 1957; Wilson, 1970; Bazzaz, 1975); so too for sycamore (Sigafos, 1976) and a variety of mid-successional species (Weaver, 1960). The inclusion of shade tolerance in a table of species characteristics for restoration of bottomland hardwood habitat is a tacit acknowledgement of the influence of preexisting vegetation on the ability of new species to become established and thrive (Haynes et al., 1988).

The relationship between light availability as a function of successional stage and the distribution of species may be particularly important in determining the abundance of non-native species. Exotic species abundance and richness in former agricultural fields has been shown to decrease with time since abandonment, with particularly large changes associated with successional conversion to forested conditions with lower light availability in the understory (Meiners et al., 2002). Similarly, the abundance of non-native species in grasslands adjacent to frequently disturbed transportation corridors is higher than in forests adjacent to those corridors (Hansen and Cleverger, 2005). These results are consistent with broader patterns in which advanced successional stages are less susceptible to invasion by non-native species (Rejmánek et al., 2013). However, this is not true of all species; as was noted earlier, garlic mustard (*Alliaria petiolata*) responds favorably to increased shade associated with advanced successional stage. In many ways, the inability of exotic species to invade developed communities is an expression of competition for limited resources.

Literature review summary

The Land Capability Potential Index provides a wetness index for floodplain landforms based on potential flow-recurrence interval and soil drainage. Sites in low landscape positions and those with poorly-drained, fine textured soils occupy one end of the wetness spectrum; those in high landscape positions and with excessively-drained, coarse soils occupy the other. Additionally, though the LCPI is not meant to provide a model of flood probability (its assumption of connectivity is violated on most of the Lower Missouri River floodplain), it does provide an index of the relative susceptibility of sites to flood-induced disturbance, which is more probable at lower sites with short flow-return intervals. That disturbance comes

in the form of reshaping floodplain landforms, physical damage to plants, and plant mortality from physical damage and anoxic soil conditions resulting from prolonged flooding.

Soil drainage and flow-return interval are related, in that poorly drained soils are more abundant in low landscape positions. This reflects the susceptibility of lower sites to prolonged water inputs, (either because the water table is closer to the surface or because water pools in such locations following rain or floods) and the tendency of finer soils to accumulate in lower landscape positions on a floodplain. In locations where soil drainage class is a function of prolonged water input due to elevation, it will likely mirror flow-return interval class for a given site. Where soil drainage class is a function of soil texture, it will reflect flow-return interval only to the extent that elevation and soil texture are related. The distribution of each species will be affected uniquely by the disturbance and water-availability gradients determined by these two factors, and the LCPI provides an index of each.

Because flow-return interval in the LCPI is derived from water- and land-surface elevation models, it is directly related to numerous other elevation-driven variables that are known to affect species distributions. Chief among these are the hydrologic variables of flow-duration, depth of flooding, and the probability of multiple floods within a particular year (which are negatively related to flow-return interval), and depth to groundwater (which is positively related to flow-return interval). Flow duration, surface water depth, and reflooding determine the intensity of disturbance to which sites are exposed, both through physical impacts on the soil and plants and through their influence on soil aeration that affects plant survival. Reflooding, flow duration, and depth to groundwater influence the broad water-availability spectrum to which species respond throughout their lifespans.

Flow energy is also a function of elevation and determines the potential disturbance intensity to which sites are exposed. In general, high elevation sites are exposed only to shallower, lower energy floods, while lower landscape positions are exposed to a broader spectrum of flow energy. Additionally, during any particular flood event, low sites generally experience higher flow-energy than high elevation locations. Thus, lower elevation sites are more likely to experience floods of sufficient energy to damage or remove existing vegetation and provide opportunities for establishment of new species and communities. Species adapted to take advantage of those conditions are likely to be more abundant in lower landscape positions.

Additionally, the flow energy to which sites are exposed affects non-hydrologic abiotic factors such as the distribution of sediment, organic matter, nutrients, and contaminants. In general, across a floodplain, mean particle size of sediment decreases with elevation and flow energy. Conversely, soil nutrients and organic matter tend to be greater in higher landscape positions where stability allows for prolonged community development and autochthonous inputs without scouring floods to remove them. Exceptions to these rules may occur in association with microtopographic features that disrupt relationships between elevation and flow energy. For example, floodplain depressions that impound water and sites that experience backflow inundation may experience prolonged, low-energy flooding that contributes to deep deposition of fine sediment, nutrients, and contaminants. Additionally, flow energy is strongly dependent on the spatial relationship to hydrologic features, including proximity to water inlets and outlets where energy gradients are higher, and proximity to and positioning relative to the channel (for example, inside bends as opposed to outside bends, or head of a floodplain as opposed to the downstream end). Because the LCPI is unable to provide information about where such local features may occur, it may be difficult to detect relationships between LCPI classes and the distribution of plant species.

Soil drainage classes in the LCPI reflect actual conditions during soil development. Therefore, the specific processes that create soil conditions and the relationship to elevation is less important than the fact that those classes reflect the potential soil moisture at any given site. At one end of the spectrum are anoxic conditions associated with an overabundance of water during floods or due to other persistent water inputs and soils with low hydraulic conductivity. Within the soil survey on which LCPI soil drainage classes was constructed, such conditions have been inferred from the redoximorphic features present in the soil. The flood tolerances of many species are defined by their ability to withstand diminished soil oxygen, while other species have no such ability. The soil texture associated with LCPI drainage class provides insights into water availability where redoximorphic features are absent. Coarse, well drained soils are more prone to drought conditions than are fine-textured, poorly drained soils. The former soils are more commonly be associated with the dry extreme of the water-availability gradient, particularly in high elevation sites not susceptible to flooding or water inputs from higher landscape positions.

The Land Capability Potential Index explicitly models flow-return interval and soil drainage and serves as a surrogate for numerous abiotic variables that are linked to floodplain elevation. This review has

examined the relationships between those variables and the distribution of floodplain species. Previous reviews on the subject laid the groundwork for understanding the abiotic template to which species must respond. Research from around the globe has been used to explore those relationships in greater detail, with particular emphasis on the Missouri River system and the dominant species within it. As in all ecological systems, the relationships between the environmental variables of interest (in this case, flow-return interval and soil drainage) and the distribution of species are obscured by the numerous unexplored variables to which species are exposed. The ability of a simple, two parameter model like the LCPI to anticipate the distribution of species and communities has not yet been established. Nevertheless, the evidence suggests that the LCPI classes address the “fundamental abiotic factors that determine long-term suitability of land...for vegetation communities and their associated values” (Chojnacki et al., 2012). Another portion of this thesis explores the degree to which this is true.

Chapter II:

Methods and Materials

The methods used to develop the LCPI are provided in the U.S. Geological Survey Data Series report that accompanies the latest version of the model (Chojnacki et al., 2012). In brief, a 5 m digital elevation model for the floodplain was derived from photogrammetrically generated point data from the Upper Mississippi River System Flood Frequency Study (UMRSFFS) (U.S. Army Corps of Engineers, 2004). In the same study water surface elevations associated with 8 estimated flows for each mile along the river were modeled, accounting for the effects of levees on local stage and using flow data from the period of reservoir management. For the LCPI, water-surface elevations representing flow-return intervals were assigned to points representing each river mile and points along the left and right valley walls based on their proximity as nearest neighbors to the river point miles. These points were then used to generate 5 m water surface elevation models corresponding to 8 stream discharges. The area inundated during flows representing each recurrence interval was identified by subtracting the land surface elevation grid from the water surface elevation grids, with positive values indicating inundated lands for a given water elevation. Within a geographical information system, a conditional function was used to classify cells of the land-surface elevation model into the appropriate flow-recurrence interval (0–2, 2–5, 5–10, 10–20, 20–50, 50–100, 100–200, 200–500, and greater than 500 years). The 5 m flow recurrence grid was then intersected with the eight soil drainage classes (Table 1) of soil units mapped at 1:24,000 in the digital USDA-NRCS Soil Survey Geographic (SSURGO) database (Soil Survey Staff, 2012) to create a 72-class index of flow-recurrence and soil drainage potential.

From among the dozens of other soil attributes in the SSURGO, available water capacity (AWC) to 25, 50, 100, and 150 cm for each soil map unit was also included in the LCPI model. This attribute was included because AWC determines the amount of water potentially available to plants and can have a strong influence on species distributions (Schoeneberger et al., 2012; Soil Survey Staff, 2012). The primary determinants of AWC are soil texture and structure, and the presence of soil layers such as clay pans or perched water tables that limit the effective root zone of plants. All else being equal, sandy soils have low

AWC values and intermediate soil textures have the highest AWC values (Brady and Weil, 2008; Schoeneberger et al., 2012; Soil Survey Staff, 2012). In locations where soil drainage class is a function of texture, better-drained sandy soils will be associated with low AWC; however, where landscape position or other soil factors determine drainage or limit rooting depth, this relationship may be disrupted.

Current distribution of LCPI Classes

This research element quantifies differences in LCPI class abundance based on a variety of ecological parameters acting at multiple scales. At the coarsest scale, LCPI class abundance is examined in terms of ecological provinces (Bailey, 1976). At this scale, possible factors affecting the hydrology and soil characteristics of the floodplain include climate, soil parent material, stream hydrology, and patterns of land use both in the floodplain and in the uplands. Analysis is limited to exploration of maps of soil drainage and flow-return interval, corroborated by representations of the longitudinal variation in the relative abundance of LCPI classes from the Gavins Point Dam to the mouth. The goal is to describe broad patterns, with subsequent analyses to explore how these relate to hydrologic and other features.

At intermediate spatial scales, LCPI class abundance is examined in relation to river segments defined by hydrologic zones (Jacobson et al., 2009) and by major tributaries (the Big Sioux, Platte, Kansas, Grand, and Osage Rivers) believed to affect the hydrologic and sediment regimes of the Missouri River (Chojnacki et al., 2012). Presumably, hydrologic shifts associated with these zones and tributaries can alter LCPI class abundance through their influence on both soil characteristics (by changing the total load and particle-size distribution of suspended sediment that forms the parent material of fluvial soils) and the potential for flood events (through stream bed aggradation or degradation and structures such as levees that constrain water movement). At the smallest scale, the abundance of LCPI classes are examined in relation to tributaries to the Missouri River, with the intent of detecting alterations in potential flow-return interval and drainage classes that may inform management planning at smaller scales of tens of miles.

The goal of this section is to provide insights into the environmental factors related to the distribution of LCPI classes at local and regional scales. To do so, the LCPI model is utilized as it might be by regional planners and resource managers to identify areas with more or less wetness potential, with the

assumption that this determines the ability of such lands to support desired communities and species based on their ecological needs. Although no specific hypotheses are tested, a few questions are addressed:

1. Are there differences in the abundance of LCPI classes between ecological Provinces?
2. Are there differences in the abundance of LCPI classes between hydrogeomorphic sections?
3. Are tributaries associated with shifts in LCPI class abundance?
4. Are there trends in changing LCPI class abundance associated with tributaries draining different ecological regions (do tributaries from a given region share a hydrogeomorphic signature?)

In answering these questions, the analyses provide examples of the types of information that can be gleaned from the LCPI model to identify the factors associated with changes in the distribution of LCPI classes. Such information can help regional planners and resource managers use the LCPI to support decision making in the management of floodplain habitat.

Subdivision by ecological province

The largest scale of analysis is the Ecological Province level defined by Bailey (1976), updated by Cleland et al. (2007), and described by McNab et al. (2005) (Figure 2). The upper portion of area modeled by the LCPI is in the Prairie Parkland (Temperate) Province; the lower portion lies along the northern edge of the Central Interior Broadleaf Forest Province (Cleland et al., 2007). The dividing line between these provinces occurs approximately at river mile 220 (just below the mouth of the Little Chariton River), where the floodplain of the Missouri River constricts to generally less than 3 miles wide (Cleland et al., 2007).



Figure 2. Area modeled by the LCPI (yellow) in relation to the Prairie Parkland (Temperate) and Central Interior Broadleaf Forest ecological provinces (Cleland et al., 2007)

The Prairie Parkland (Temperate) Province is characterized by flat terrain with local elevation range rarely exceeding 50 meters (McNab and Avers, 1994). Greater relief occurs near drainages and the Missouri River (Nigh and Schroeder, 2002). Prairie was the dominant historical vegetation, with oak-hickory (*Quercus* spp.-*Carya* spp.) forests occupying slopes near drainages and riverfront forests of cottonwood (*Populus deltoides*), black willow (*Salix nigra*) and American elm (*Ulmus americana*) occupying floodplains (McNab et al., 2005). The province is characterized by deep Quaternary loess over glacial till in the uplands; Quaternary and Tertiary alluvium in the Missouri river valley; and soils dominated by Mollisols, with lesser amount of Alfisols, consistent with soil development in prairie ecosystems (McNab and Avers, 1994). Residual soils from sedimentary bedrock are more abundant in areas with dissected terrain near major rivers (Nigh and Schroeder, 2002). Today, the entire province is dominated by row crop agriculture, with lesser amounts of grazing. The province includes well developed, dendritic drainage networks significantly affected by agriculture, udic moisture regimes, and mesic temperature regimes (McNab and Avers, 1994). Mean annual rainfall ranges from 500 mm in the northwest of the modeled area to 1000 where the Missouri River exits the province (McNab and Avers, 1994).

Tributaries to the Missouri River in this region are characterized by high sediment-yield potential (Simon et al., 2004).

The lower portion of the study area passes through the very different ecological setting of the Ozark Highlands in the Central Interior Broadleaf Forest Province (McNab et al., 2005). Precipitation averages about 1,000 mm annually (primarily during the growing season), and the temperature regime is mesic (McNab and Avers, 1994). Drainage from the uplands is by way of small to medium sized streams with flashy flow patterns (McNab and Avers, 1994). Local relief is much greater than in the other province, sometimes exceeding 300 meters. Near the Missouri River, uplands are covered with a loess cap that decreases in thickness farther south, but are otherwise dominated by cherty residuum and colluvium (Nigh and Schroeder, 2002). Dominant soils are Alfisols, consistent with development of soils under deciduous forests (Brady and Weil, 2008), the dominant historic vegetation type (McNab and Avers, 1994). The soil parent material in the Missouri River valley itself is primarily Tertiary and Quaternary alluvium, as in the other province though which the river flows (McNab and Avers, 1994). Unlike the Prairie Parkland Province, current land use in the Ozark Highlands is dominated by timber production, and to a lesser extent, grazing (McNab and Avers, 1994; Nigh and Schroeder, 2002). Ozark Highlands streams carry very little suspended sediment (Nigh and Schroeder, 2002), and are characterized by extremely low sediment yield potentials (Simon et al., 2004).

It is anticipated that differences between these ecological settings would be detectable in the distribution of LCPI classes within the floodplain. Differences in land use (row crop agriculture as opposed to timber production), upland drainage (heavily altered by agriculture as opposed to flashy, higher gradient flow), moisture regimes (ranging from approximately 500 mm annually in the upper reaches of the study area to more than 1,100 mm near the mouth of the river), and soil (thick loess over till as opposed to thin loess over cherty residuum) could reasonably be expected to affect the quantity and quality of sediment and bed load being delivered to the Missouri River system from the uplands. That load historically has formed the alluvial parent material of the Missouri River floodplain, and should be reflected in fluctuations in the abundance of LCPI classes.

Subdivision by geomorphological segments and tributary-defined sections

Mid-scale analysis of LCPI class abundance was conducted using segments of the Lower Missouri River defined by the intersection between geomorphologic zones (Jacobson et al., 2009) and the locations of major tributaries believed to have a strong influence on the sediment regime (Chojnacki et al., 2012) (Figure 3) (Table 2). Jacobson et al. (2009) identified six river segments based on hydrogeomorphic considerations, including the complexity of the channel, the degree to which the historical flow regime has been altered by upstream dam management, the quantity of sediment relative to pre-dam levels, and whether the channel is currently degrading (incising) or aggrading relative to the floodplain. Of these, the last item is expected to have the greatest influence on the distribution of LCPI flow-return intervals (Jacobson et al., 2009). The quantity and quality of sediment are also important due to their contribution to floodplain soil characteristics; however, these effects of post-dam construction sediment regimes may be reflected only in soil drainage classes for lands accreted since that time, while soil drainage classes on floodplains that were formed prior to dam construction are more likely to reflect historic sediment regimes. The major tributaries that are used to subdivide the river include the Big Sioux, Platte, Kansas, Grand, and Osage Rivers (Chojnacki et al., 2012). Preliminary analysis indicated differences between river segments in the relative abundance of LCPI flow-recurrence intervals (Chojnacki et al., 2012) and that these differences are consistent with patterns of channel aggradation and degradation identified by the U.S. Army Corps of Engineers (2004).

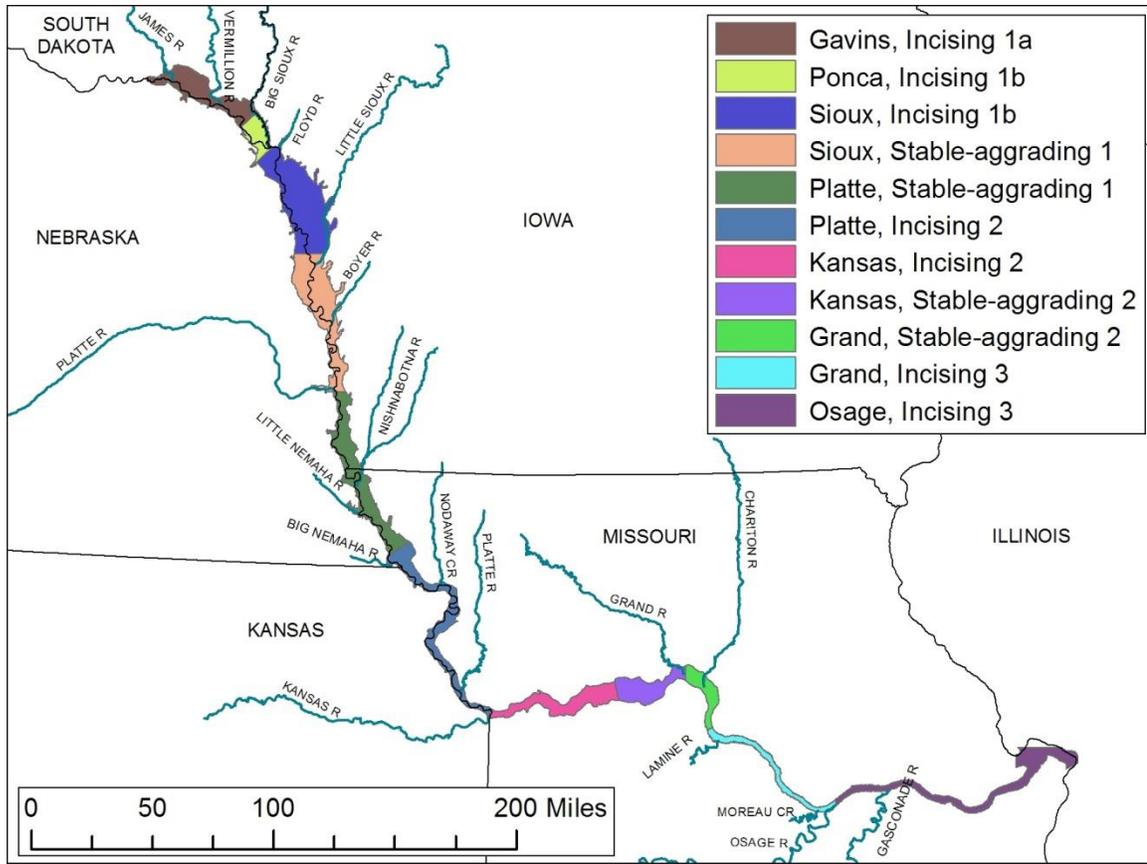


Figure 3. Sections of the Lower Missouri River based on geomorphologic criteria (Jacobson et al., 2009) and major tributaries believed to have a strong effect on the hydrologic and sediment regimes of the river (Chojnacki et al., 2012).

Table 2. Tributary-defined segments and geomorphological zones of the lower Missouri River.

Segment ¹	Geomorphological zone ²	Description ²	Upper Mile	Lower Mile	Length (miles)
Gavins	Incising 1A	Complex channel morphology Severely altered flow regime Severe sediment deficit Degraded channel	811	754	57
Ponca	Incising 1B	Simple channel morphology Severely altered flow regime Severe sediment deficit Degraded channel	753	734	18
Sioux	Incising 1B	Simple channel morphology Moderately altered flow regime Sediment surplus Aggraded channel	734	676	58
Sioux	Stable-aggrading 1	Simple channel morphology Moderately altered flow regime Sediment surplus Aggraded channel	675	594	81
Platte	Stable-aggrading 1	Simple channel morphology Moderately altered flow regime Sediment deficit Severely degraded channel	593	500	93
Platte	Incising 2	Simple channel morphology Moderately altered flow regime Sediment deficit Severely degraded channel	499	372	127
Kansas	Incising 2	Simple channel morphology Slightly altered flow regime Sediment balance	371	301	70
Kansas	Stable-aggrading 2	Simple channel morphology Slightly altered flow regime Sediment balance	300	250	50
Grand	Stable-aggrading 2	Simple channel morphology Slightly altered flow regime Sediment deficit Degraded channel	249	210	39
Grand	Incising 3	Simple channel morphology Slightly altered flow regime Sediment deficit Degraded channel	209	131	78
Osage	Incising 3	Degraded channel	130	0	130

¹Chojnacki et al. (2012)²Jacobson et al. (2009)

Effects of tributaries

The finest scale at which the abundance of LCPI class abundance is analyzed is tens of miles in association with the mouths of tributary streams, and where larger streams enter the river valley (if distinct from the tributary mouth). Analysis is initially limited to the streams defining river segments described above, and changing LCPI class abundance is explored at each individually. Later analyses examining trends incorporate additional tributaries.

Shifts in LCPI class abundance were examined by cross sections of the river valley approximately 3 km wide (Figure 4). Within a geographic information system, a line was drawn following the dominant directional trend of the river valley, with nodes at 3 km intervals. These nodes were used to generate a Thiessen polygon surface that was used to subdivide the area modeled by the LCPI into cross-sections spanning the river valley. To provide a spatial reference commonly used along the river, each segment was addressed with the middle mile value of all mile points that fell within that polygon, based on 1960 river

mile designations (U.S. Army Corps of Engineers, 1995b). Although the LCPI model often extends up the valley of major tributaries, for the purposes of analysis, these areas were manually excluded by drawing a line connecting the valley wall across the mouth of such tributaries. For each cross section, the relative abundance of each LCPI class was then derived and used as the basis for detection of longitudinal trends associated with tributaries. Trends were examined from 3 cross-sections upstream of the mouth to 3 cross-sections below the mouth.

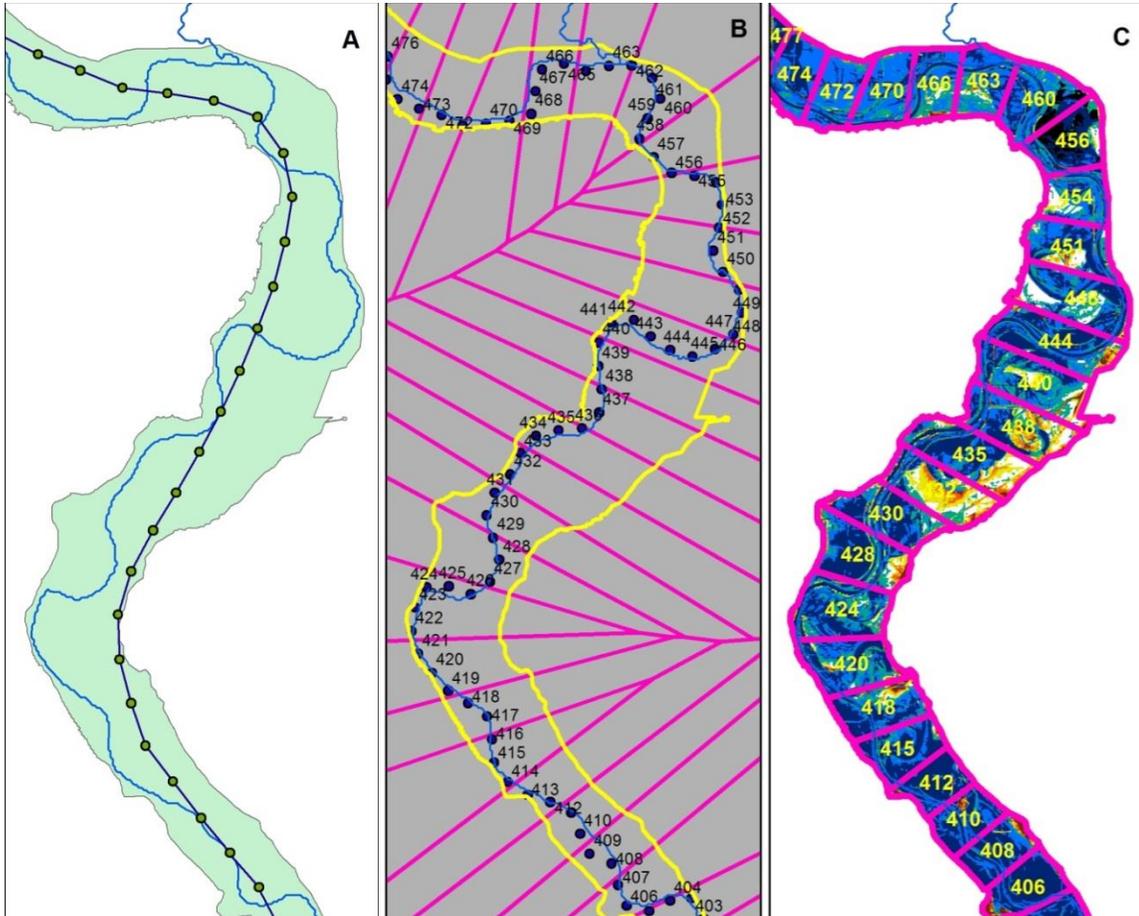


Figure 4. Process for subdividing the study area into cross-sections for analyses: A) a line approximating the directional trend of the valley was drawn with nodes at 3 km intervals, B) the nodes were used to create Thiessen polygons, which were attributed with the mean value of river mile points within the polygon, and C) the LCPI model was partitioned by intersecting it with the Thiessen polygon surface.

Additionally, the influence of provinces and smaller ecological subunits was explored by examining the effects of major tributaries draining each province or smaller ecological units using indices derived for flow-return interval and soil drainage classes. First, integer values were assigned to drainage

and flow-return intervals within valley cross sections used to explore the effects of individual tributaries (described above). Flow-return interval values start at 1 for the less than 2 year flow-return interval class and proceed to 9 for the greater than 500 year class; Soil drainage values begin at 0 for water and increase to 7 for excessively drained soils. The Soil Drainage Index and the Flow-return Interval Index for each cross-section was generated by summing the area-weighted value for all LCPI soil drainage or flow-return interval polygons within the cross section. These indices were then used to identify longitudinal trends in the abundance of LCPI classes associated with tributaries flowing from four areas (Figure 5):

1. North Central Glaciated Plains, drained by the James, Vermillion, Big Sioux, Floyd and Little Sioux Rivers
2. Western Prairies, flowing through the Nebraska Rolling Hills and drained by the Platte [Nebraska], Little Nemaha, Big Nemaha, and Kansas Rivers
3. Central Dissected Till Plains, drained by the Boyer, Nishnabotna, Nodaway, Platte [Missouri], Grand, and Chariton Rivers
4. Ozark Highlands, drained by the Lamine, Moreau, Osage, and Gasconade Rivers

The first 3 areas incorporate the major streams of the Prairie Parkland (Temperate) Province; the last, those streams from the Central Interior Broadleaf Forest Province. For each stream, indices were calculated for each cross section starting three sections above each tributary and continuing to three cross sections below. In order to allow comparisons between rivers, index values for each cross section of each tributary were adjusted to indicate value relative to the index value for the cross section at the tributary mouth.

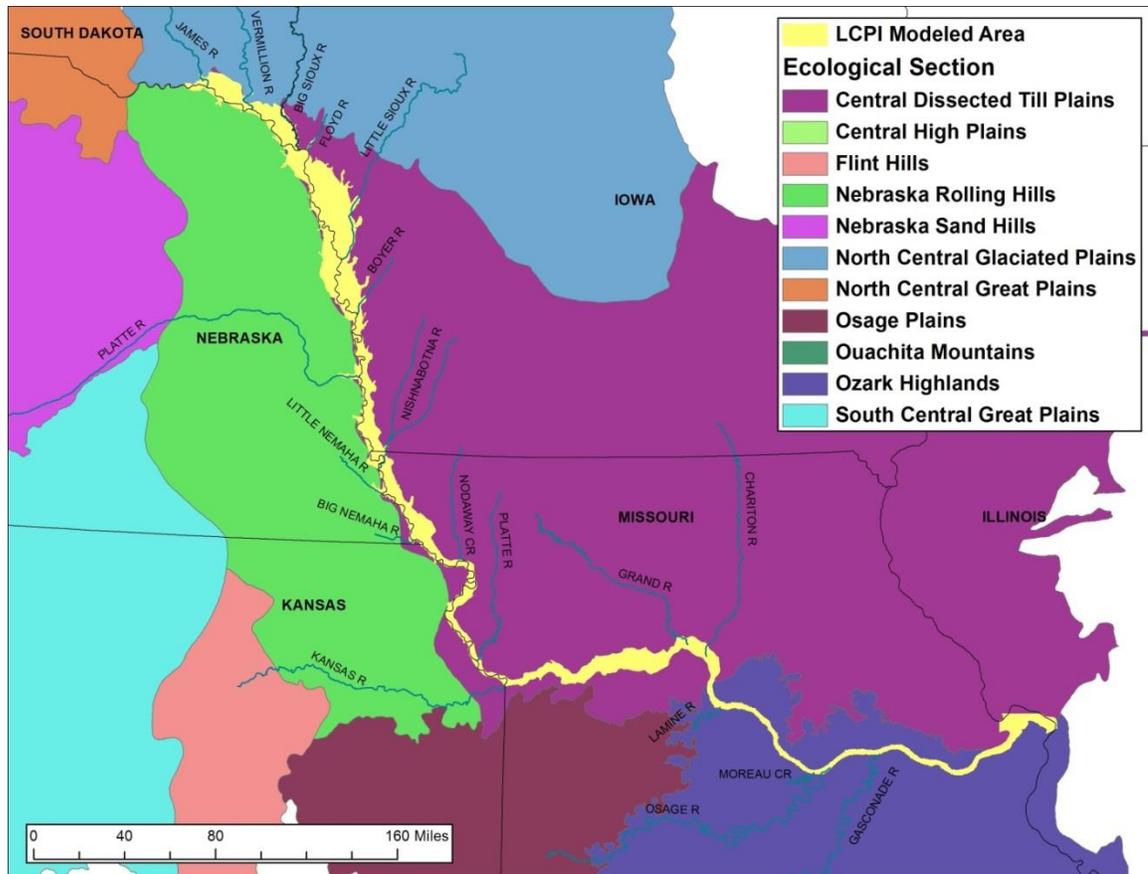


Figure 5. The area of the Lower Missouri River modeled by the Land Capability Potential Index in relation to Ecological Sections (Cleland et al., 2007).

Trends in the effects of tributaries were analyzed based upon four areas that they drain; The North Central Glaciated Plains, the Western Prairies (including the Nebraska Rolling Hills and areas westward), the Central Dissected Till Plains, and the Ozark Highlands.

Variation in groundwater processes by soil drainage classes

Background—the Groundwater Response Factor (GWRF)

The Groundwater Response Factor is defined as “the change in ground-water level at a known distance from the river divided by the magnitude of the flood pulse, at a specified time after the beginning of a flood pulse” (Kelly, 2000). The GWRF has been used to simulate the effects of various Missouri River flow management plans on groundwater processes at four sites in Missouri (Kelly, 2000), and to assess the relative contributions of river stage and precipitation inputs to groundwater processes at two wetlands (Kelly, 2001). Maximum GWRF during a flow pulse decreases with distance from the river, but the time at which maximum GWRF reaches a particular location increases with distance from the river (Kelly, 2000).

Simulations of GWRF assume uniform soil hydraulic conductivity, and observed deviations from simulated results are attributed to variations in soil hydraulic conductivity and the transmissivity of the broader Missouri River aquifer (Kelly, 2000, 2001).

The GWRF reflects the natural tendency of fluid to achieve equilibrium pressure within a system as moderated by Darcy's Law describing the flow of fluid through a porous medium. Darcy's Law is given by the following equation:

$$Q = \frac{-kA}{\mu} * \frac{(P_b - P_a)}{L},$$

where Q equals the discharge in volume per unit time, k = permeability of the medium, A is the cross-sectional area of flow, (P_a-P_b) is the difference in pressure between points a and b, (often called the hydraulic head), μ is the viscosity of the fluid, and L is the distance between those points. Conceptually, the GWRF implicitly recognizes that a flow pulse represents an increase in P at the river from a presumed state of equilibrium to which groundwater on the floodplain responds according to the formula above. If all other factors (permeability, area, viscosity, and volume) are assumed constant, the time required before a change occurs at a point increases with distance. However, points further from the river are less likely to reach equilibrium before the flow pulse ends, resulting in a partial response, the magnitude of which is determined by the flow pulse magnitude (difference in pressure), duration, and distance from the river.

In the work presented here, groundwater response at paired deep and shallow wells at two sites in Missouri are examined relative to each other and in the context of simulated GWRF results from previous work on the Missouri River floodplain (Kelly, 2000). Although no formal hypotheses are tested in this section, there are a number of specific questions to be addressed. First, does GWRF response to changes in river stage at each site follow the expected patterns based on earlier work (Kelly, 2000, 2001)? Second, does variation in SSURGO soil drainage classification reasonably explain deviations from those patterns across a site? Darcy's Law requires that, where soil drainage classification reflects the hydraulic characteristics of the soil, the magnitude and speed of GWRF will decrease with soil drainage capacity from excessively drained soils down to very poorly drained soils. Finally, does local SSURGO soil drainage classification explain differences (if any) in the speed or magnitude of response between paired deep and shallow wells? Groundwater response in deep wells is governed by the coarse fluvial aquifer of

the Missouri River in which transmissivity is likely equal to or exceeds that of the upper strata of excessively drained soils (Kelly, 2000), suggesting that differences in groundwater response between shallow and deep wells increases as SSURGO soil drainage capacity decreases.

The analyses provided assess the utility of SSURGO drainage classes in understanding groundwater processes and in aiding management of floodplain communities. As such, soil drainage classes are accepted as they were mapped. No effort is made to relate groundwater processes to any of the myriad physical characteristics described for each soil series within the SSURGO database (Soil Survey Staff, 2012). Additionally, only minimal effort is made to assess those characteristics on a well-by-well basis. The justification for this naïve approach is that the LCPI itself is intended to provide a surrogate for those characteristics and to obviate the need for a comprehensive understanding of them.

Aside from fluvial processes, the most important environmental gradient to which species on the Missouri River floodplain is water availability (Wharton et al., 1982; Brinson, 1990; Malanson, 1993; Hughes, 1997). At one end of the spectrum, plants are limited by anoxic soil conditions resulting from too much water; at the other end of the spectrum, plants experience periods of drought from too little water. That water availability is a critical determinant of plant distributions is beyond dispute and provides the basis for widespread agricultural practices to both remove water from the landscape by means of drainage structures and to increase its abundance through irrigation.

The link between oxygen availability and vegetation distribution gained prominence with the publication of a comprehensive government document (the first of a series) examining the effects of changing water level on woody and riparian species (Teskey and Hinckley, 1977). Numerous synthesis works in subsequent years would build upon that work. For Wharton et al. (1982), anoxia was the dominant controlling parameter of the distribution of species, and flood tolerance was defined almost exclusively by the ability to withstand anoxic conditions. By contrast, Brinson (1990), Malanson (1993), and Hughes (1997) conceived of a more balanced influence between anoxia at one end of stress gradient and low water potential at the other end.

The LCPI incorporates soil drainage classes directly from the SSURGO soil database (Soil Survey Staff, 2012). The primary criteria for soil drainage classification are either the presence of water itself or of redoximorphic features that indicate free water leading to soil anoxia during some part of the year (Soil

Survey Staff, 1993; Schoeneberger et al., 2012). These features indicate the relative duration and frequency of free water within the soil profile, either through flooding, groundwater at or near the soil surface, or perching of water due to restricted water flow. Flooding and groundwater elevation are driven largely by landscape characteristics, particularly elevation relative to the river; lower areas are more likely to gather surface water following precipitation events, are more susceptible to inundation during floods, and are more likely to have groundwater at or near the surface than higher elevation sites. Within the context of the LCPI, lower elevation areas with shorter flow-return intervals have a greater abundance of poorly drained soil classes than do areas with long flow-return intervals (Figure 1).

Groundwater elevation is also a function of the characteristics of the soil, as is the flow of groundwater through the system. Soil drainage is a function of the inherent characteristics of the soil, particularly hydraulic conductivity as determined by texture and structure within and between soil strata (Soil Survey Staff, 1993; Schoeneberger et al., 2012). Generally coarser soils and those for which the soil profile lacks abrupt transitions in texture are better drained due to their higher hydraulic conductivity (Brady and Weil, 2008).

The purpose of this section of the thesis is to explore groundwater response to changes in river stage across a range of SSURGO soil drainage classes, and to compare results to previous simulations of groundwater response on the Missouri River floodplain (Kelly, 2000, 2001). The primary goal is to provide an assessment of the relative potential wetness of LCPI classes as determined by fluctuations in groundwater in response to flow pulses. This wetness potential complements potential wetness as suggested by LCPI flow-return intervals. Together with relationships between vegetation and LCPI classes to be explored in the next section, the data presented here provide an assessment of the potential for floodplain land to support desired vegetation and a tool to help achieve floodplain habitat management objectives.

Sites

In order to assess the impacts of local and site-scale variations in soil drainage on the response of groundwater to flow pulses, two sites were selected for observation of groundwater response to changes in river stage. Both sites had been used in previous studies of groundwater process and the GWRF (Kelly, 2000, 2001). The first site, near Forest City, Missouri (hereafter called Forest City), stretches from river

mile 472 to river mile 467 (U.S. Army Corps of Engineers, 1995b), from 25 to 18 miles upstream of St. Joseph, Missouri (Figure 6). The site is dominated by row-crop agriculture, and most of the floodplain is protected from flooding by a 500-year levee; however, within this stretch the river curves away from the levee and there is a broad, low floodplain between them. Wells at this site had been used to compare predicted and observed changes in groundwater elevation to flood pulses (Kelly, 2000). Although it was suggested that variation in aquifer properties was responsible for deviations between predicted and observed responses, results had not been examined in relation to SSURGO soil drainage classes.

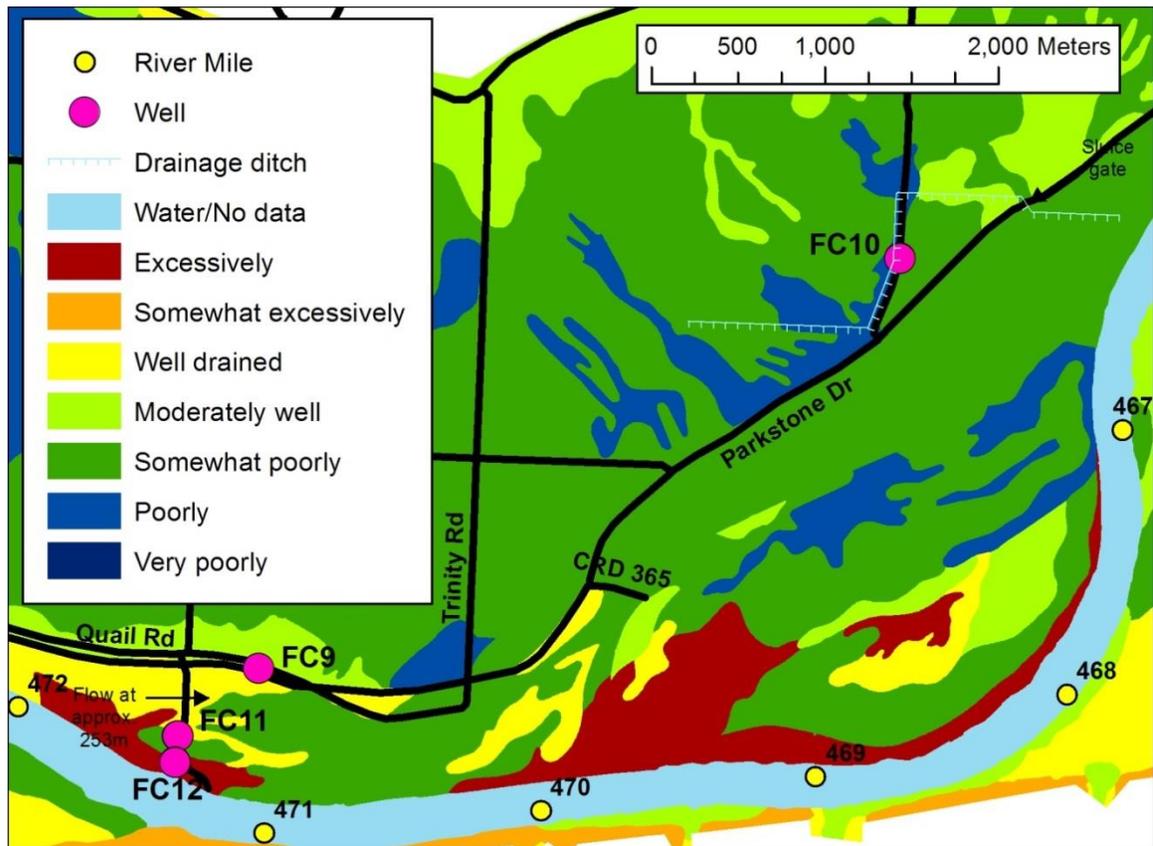


Figure 6. Location of groundwater level monitoring wells in relation to mapped SSURGO soil drainage classes (Soil Survey Staff, 2012) at the Forest City study site.

The second site is on the Overton North Management Unit (Overton North) of Big Muddy National Fish and Wildlife Refuge at Overton, Missouri, approximately 11 downstream of Booneville, Missouri (Figure 7). The focal area spans about 2.5 miles from river mile 188 to the Interstate 70 bridge across the river. The site was in agricultural production and was protected by a 100-year levee until the Great Flood of 1993. That flood breached the levee near mile 188 and deposited coarse surface soils across

the southwest section of the area (Holbrook et al., 2006). The breach was subsequently modified to allow flow across the floodplain when river stage at Booneville exceeds approximately 24 feet, corresponding to a local river elevation of approximately 176.9 m. In 2001 in an effort to create a secondary channel and island, a chute was constructed by the U.S Army Corps of Engineers along the northwest portion of the study area (Jacobson, 2006). The intended channel never fully developed, but the chute currently allows passage of water when river stage at Booneville exceeds approximately 19 feet (Watkins, 2014); this corresponds to an estimated river elevation at Overton North of 175.4 m. A second chute was constructed in 2003 to provide a permanent secondary channel and an island in the north central portion of the area (Jacobson, 2006). At a river elevation of approximately 175.4 m, water from this constructed channel begins to flow west-southwest across the floodplain (Watkins, 2014). This site had previously been used to estimate the relative contributions of groundwater and precipitation to the groundwater processes of two wetlands (Kelly, 2001).

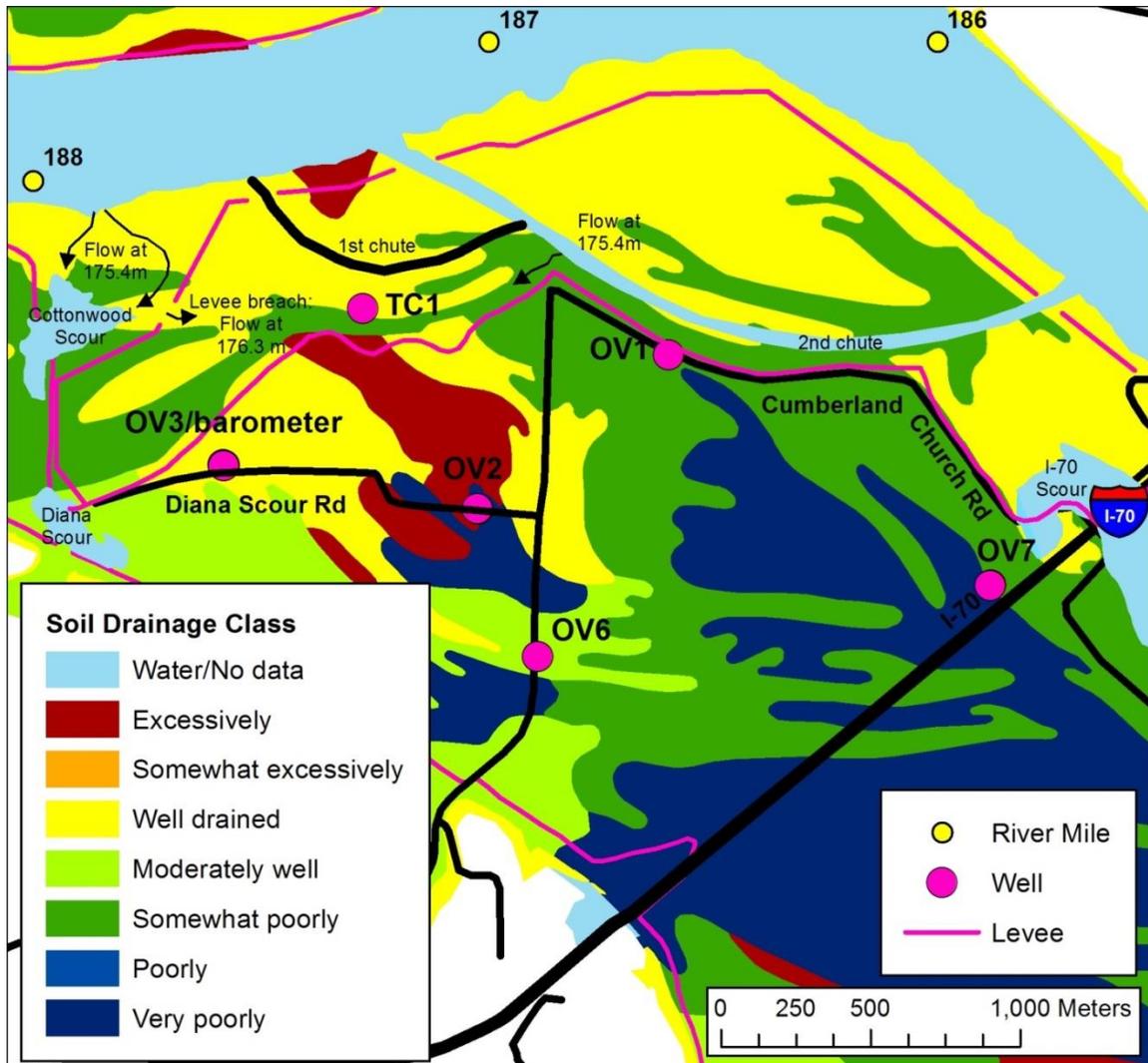


Figure 7. Location of groundwater level monitoring wells in relation to mapped SSURGO soil drainage classes (Soil Survey Staff, 2012) at the Big Muddy National Fish and Wildlife Refuge Overton North Management Unit, Missouri.

Well selection and installation

Existing deep wells (each approximately 40 ft. deep) at each site were selected to represent a range of soil drainage classes. Although these wells are deep enough to penetrate to the aquifer, the soil drainage characteristics of the entire soil profile determine the transmissivity of the floodplain and the response of groundwater to flood pulses. In order to assess the local effects of soil drainage on the movement of water through the soil, a new shallow well was installed to a depth of approximately 10 feet within a few meters of each deep well. The intent was to capture variations between deep and shallow wells in the speed and magnitude of groundwater response to flood pulses that could be attributed to variation in soil drainage. For

the purpose of analysis and to provide the best assessment of the utility of the LCPI for management purposes, drainage classes from the SSURGO database (Soil Survey Staff, 2012) are assumed to accurately reflect the drainage capacity of the soils as they are mapped. Evidence contrary to SSURGO classifications that was discovered during establishment of new wells was noted, but was not used to adjust soil drainage classification.

Installation of shallow wells followed Natural Resource Conservation Service methods (Figure 8) (Sprecher, 2008). A hole was bored to a depth of 8 to 10 feet and approximately 6 inches of sand was poured into the bottom. Then, a plastic well casing measuring 10 feet in length with a slotted lower half was installed. The hole around the casing was packed with sand to within approximately 18 inches of the surface and sealed with bentonite pellets. During installation of the new wells, the soil profile was examined in order to assess soil drainage.

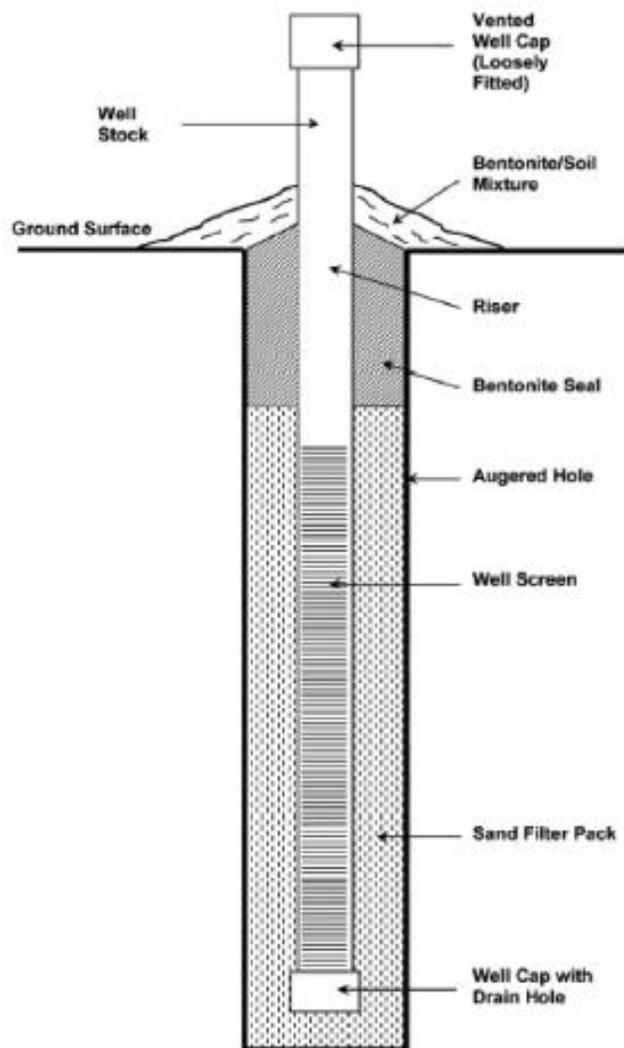


Figure 8. Schematic representation of newly installed wells at Overton and Forest City, Missouri .

At the Forest City site, existing wells FC9, FC10, FC11, and FC12 were selected to represent moderately well, poorly, somewhat poorly, and excessively drained soil types, respectively (Table 3, Figure 6). Installation notes for FC9 indicate silt loam to a depth of 7 feet, with no recorded evidence of poor drainage (Kelly, 2013). Inspection of the soil profile during installation of the new shallow well indicated sand and sandy loam to a depth of about 6 feet, at which point there was a thin clay layer with some evidence of reduced drainage capacity consistent with the classification as moderately well drained. Installation notes for FC10 indicated silt loam and silt to a depth of 8 feet, with only limited evidence of poor drainage (Kelly, 2013); this conflicts with the SSURGO classification of soils as poorly drained (Soil

Survey Staff, 2012). Installation of the new well revealed a drainage-impeding clay layer from 2 to 3 feet and few redoximorphic features, suggesting that a more appropriate classification would be somewhat poorly drained, as is mapped in the adjacent polygon a few meters away (Soil Survey Staff, 2012).

Although FC11 is within an area mapped as somewhat poorly drained by the soil survey (Soil Survey Staff, 2012), examination of the soil profile during installation of the shallow well revealed that soils were consistent with the classification of the adjacent SSURGO polygon as well drained (the well is within 20 m of the boundary between mapped polygons). Installation of the shallow well at FC12 revealed a soil profile that was medium to fine sand throughout, with a thin clay layer at approximately 10 feet. This is consistent with field notes for the installation of the deep well (Kelly, 2013), and supports the classification of excessively drained soils (Soil Survey Staff, 2012).

Wells FC11 and FC12 are on the low floodplain outside of the levee; wells FC9 and FC10 are protected by the levee and are within 20 m of roads. Across the road from well FC10 is a drainage ditch that connects to the river through a sluice gate northeast of the well. This ditch holds water after precipitation events and may provide a path for backflow from the river during elevated flow events when the sluice gate is not closed. At a river elevation of approximately 253 m, overland flow can separate wells FC11 and FC12 from the rest of the floodplain. Flooding during 2011 scoured this flow path upstream of the wells. During installation of water-level monitors in 2012, this scour was estimated to range from 1 to 2 meters below the surrounding floodplain and had standing water in it. The GWRF models predict that the maximum GWRF will decrease with distance from the river and that lag time between the initiation of flow pulses and peak water elevation within wells will increase with distance from the river. In order of increasing distance from the river, the wells are FC12, FC11, FC9 and FC10.

At Overton North, existing wells OV1, OV2, OV3, OV6, OV7, and OVTC were selected to represent somewhat poorly, very poorly, well, moderately well, very poorly, and well drained soils, respectively (Figure 7, Table 3). Detailed maps of surficial alluvium (Holbrook et al., 2006) indicate that well OV1 is located on a site with a one meter clay mud veneer over fine and loamy sands. Alternating layers of clays and sands and redoximorphic features in the upper strata encountered during installation of the new well, suggest that the SSURGO classification of somewhat poorly drained is correct (Soil Survey Staff, 2012).

Although well 2 was in a polygon mapped as poorly drained (Soil Survey Staff, 2012), it is also mapped on the edge of a sand splay capping a channel-fill allunit with clay soils to a depth of 1 meter over sandy loam (Holbrook et al., 2006). Examination of the soil profile during installation of the new shallow well revealed sandy loam soil with no redoximorphic features consistent with an excessively drained or somewhat excessively drained soil. However, this may be a poor classification because the upper soils strata are known to have been very recently deposited during the Great Flood of 1993 (Holbrook et al., 2006) such that poor drainage is not yet reflected in the young upper soils layers. Additionally, the shallow well may not have penetrated the sand splay cap that had been deposited to reveal deeper features consistent with poorer drainage.

Well 6 is also on a channel-fill allunit, but with loamy sand and silt loam to a depth of about 4 meters (Holbrook et al., 2006). Inspection during well installation revealed the soil profile to be silt-loam throughout, except for clay from 50 to 68 inches and again below 94 inches. Redoximorphic features were sparse, consistent with the SSURGO classification as moderately well drained. Well 3 is in the same allunit, but approximately 1,200 m upstream from the sample location used to describe the unit (Holbrook et al., 2006). The soil profile was sandy loam throughout, except for finer layers at 24-28 inches and at 33 to 40 inches; few if any redoximorphic features were present, confirming the classification of well drained soils. Well 7 is in the same channel-fill allunit as well 2, but approximately 1,700 m east of it. The soil profile of well 7 was silt loam to a depth of 1 foot, below which was clay to 4 feet, transitioning to sand at approximately 6 feet. Abundant reduction features suggest poorly drained soils, consistent with the SSURGO soil map (Soil Survey Staff, 2012).

Well OVTC is in a channel-fill allunit following a former meander loop. Because there was already an existing shallow well, no new well was installed; as a result no field data were available for assessing drainage. Excavation of the 2nd chute at Overton revealed sands to a depth of 1.5 m over a clay drape where this unit intersects the constructed chute at Overton North (see Figure 8 in Holbrook et al., 2006).

In order of increasing distance from the river, the wells at OV1, OVTC, OV7, OV2, OV3, and OV6. Well OVTC is the well with the lowest ground elevation at Overton North and is adjacent to the first constructed chute, which receives flow when local river elevation exceeds approximately 175.4 meters.

Well 1 is adjacent to the second constructed chute that has flow at all stages. Well OV7 is approximately 50 m from Interstate 70 and 180 m from the I-70 scour formed by the flood of 1993. Wells OV1, OV2, OV3, and OV6 are adjacent to refuge roads.

Table 3. Elevation attributes, drainage classification, and distance from the river for wells used to monitor groundwater elevation at Forest City and Overton North.

Well*	Ground elevation (m)	Sensor elevation (m)	Sensor depth (m)	Drainage class	Distance from the river (m)
Forest City (FC)					
FC09D	255.180	248.475	6.705	Moderately well	780
FC09S	255.180	253.160	2.020	drained	
FC10D	254.100	246.660	7.440	Poorly drained	1,235
FC10S	254.100	251.360	2.740		
FC11D	254.310	246.513	7.797	Somewhat	230
FC11S	254.310	251.619	2.691	poorly drained	
FC12D	255.220	247.609	7.611	Excessively	90
FC12S	255.220	252.833	2.387	drained	
Overton North Management Unit, Big Muddy National Fish and Wildlife Refuge (Missouri River Recovery Program)					
OV1D	177.066	169.604	7.462	Somewhat	100
OV1S	177.066	174.921	2.145	poorly drained	
OV2D	178.692	173.422	5.270	Very poorly	870
OV2S	178.760	176.120	2.640	drained	
OV3D	178.138	170.371	7.096	Well drained	940
OV3S	178.157	175.541	2.616		
OV6D	177.620	170.912	6.708	Moderately well	1,160
OV6S	177.620	175.776	1.844	drained	
OV7D	176.775	169.833	6.942	Very poorly	820
OV7S	176.771	175.672	1.100	drained	
OVTCD	176.524	169.447	7.077	Well drained	460
OVTCS	176.524	173.979	2.545		

* D = deep; S = Shallow

Water level data collection

Ground elevation at each well was derived from the digital elevation model (DEM) used to generate the LCPI (Chojnacki et al., 2012), data for which were originally collected for the Upper Mississippi River System Flow Frequency Study (U.S. Army Corps of Engineers, 2004). For each well, a reference point on the well head was identified and its distance to the ground was measured. Then, Solinst LevelLogger unvented pressure-sensitive water depth monitors were attached at a measured depth from the

reference point using steel cable. Water levels were measured every 15 minutes from February 2012 until October, 2013, and were adjusted for barometric pressure using simultaneously collected data from an on-site barometric data logger. At Overton North, data at wells 1 and 3 were initially collected using vented water depth monitors requiring no barometric compensation; these were replaced with unvented water depth monitors on July 23, 2012. The sensors for wells at OVTC were installed April 27, 2012.

At Forest City, river stage at river mile 471 (near well 12) was estimated using relationships developed during a previous study of groundwater at the site (Kelly, 2000). Simultaneous data were collected at the U.S. Geological Survey National Water Information Service (NWIS) gage at St. Joseph, Missouri and at a second temporary gage at Payne's Landing 6 miles upstream of well 12. These data were used to develop a model relating velocity to river stage at St. Joseph, based on lag times between peak flows between gages from 1996 to 1998:

$$Velocity (mph) = 0.0002 * stage \text{ ft}^3 - 0.0082 * stage \text{ ft}^2 + 0.1825 * stage \text{ ft} + 1.8581, R^2$$

Stage-specific velocities were calculated from this model and used to estimate the time at which each measured stage at St. Joseph had passed well 12. Additionally, river level was adjusted to account for the slope of the river, 1.013 feet/mile, based on differences in gage elevations at Payne's Landing and St. Joseph.

A similar process was used to estimate river stage at river mile 188 for Overton North, using data collected simultaneously with the current study at NWIS gages at Booneville, Missouri (11 miles upstream of Overton) and Jefferson City, Missouri (44 miles downstream) (U.S. Geological Survey, 2014). Data yielded a model for travel time between Booneville and mile 188 based on the recorded stage at Booneville:

$$Travel \ Time \ (hr) = 25.237 * e^{-0.061 * stage \ ft}, R^2 = 0.59$$

As at Forest City, river level was adjusted to account for the slope of the river, 0.83 ft/mile, based on the difference in gage elevations at Booneville and Jefferson City. Using this method, the river stage of 19 feet

at Booneville that is associated with flow through the first constructed chute and flow across the floodplain from the second constructed chute and to the Diana Scour translates to a local river elevation of 175.4 m. River stage associated with flow through the breached and rebuilt levee (24 feet) corresponds to a local river elevation of approximately 176.9 m. It is acknowledged that local river stage is determined by channel morphology, such that the methods used here are unable to estimate stage in a manner sufficient to determine flood probability or for other purposes where more accurate estimates may be needed; however, they are sufficient for estimating the time of peak flow and assessing the relative response of groundwater level at each well.

Groundwater data analysis

Data were examined to identify discreet flow pulses that could inform analysis. The start of each flow pulse was identified as the lowest stable river stage just prior to flood pulse estimated using the stage-velocity relationships described above. The starting depth for each groundwater monitoring well was defined as the simultaneous water depth of each sensor. The end of a flow pulse was defined as the point at which river stage either dropped below the starting stage for that pulse or at the next local minimum, just before a new flow pulse was detected. The end of the groundwater response for each well was defined as either the point at which water depth dropped below the initial value following a discernable peak attributable to peak river stage, or when a response to a succeeding flow pulse was detected.

Changes in river stage and well water depths were calculated by subtracting the starting stage or depth from the stage or depth for each reading throughout the course of each flow pulse. From these calculations, the date, time and magnitude of the largest river stage change was extracted. The Groundwater Response Factor (GWRF) at each well was calculated by dividing each recorded change in water depth by the maximum change in stage for the river during that flow pulse. In instances for which well groundwater elevation was descending as the flow pulse initiated, negative GWRF values were recorded, often up to and including the maximum GWRF for that flow pulse (identified as the first peak GWRF following flow-pulse initiation).

From these above data, the following metrics were derived for each well: the date, time, and magnitude of the maximum GWRF, the duration of the groundwater response, and the number of days that

the GWRP exceeded 0.10, 0.25, and 0.50 (representing 10, 20, and 50 percent of the maximum river stage change). Additionally, the peak lag ratio—defined as the pulse start to peak time for each well divided by the pulse start to peak time for the river—and the ratios between the number of days during which the GWRP exceeded 0.10, 0.25, and 0.50 and the flood pulse duration were calculated (hereafter called the 0.10, 0.25, and 0.50 exceedance ratios, respectively). Along with the maximum GWRP value, these latter four metrics enabled between-well comparisons of groundwater response using data from floods of varying magnitude and duration.

Differences in mean values were tested for significance using Analysis of Variance with Bonferroni *post hoc* multiple-comparison tests. Additionally, for each site, a regression model relating each of the above metrics (maximum GWRP, lag ratio, and each exceedance ratio) to distance from the river was derived. Each site-specific model for maximum GWRP was examined for consistency with mean GWRP values derived from previous groundwater simulations for the Missouri River (Kelly, 2000). All models were used to assess deviations in groundwater response at individual wells from site-specific models based on soil drainage classification. (Throughout the results and discussion sections that follow, color coding for wells indicates SSURGO soil drainage classification, with a warm-to-cool color scheme corresponding to a gradient from excessively drained soils to very poorly drained soils.)

Relationships between LCPI and vegetation

Background

The theory supporting the development of the LCPI as a decision support tool for management of floodplain habitat was discussed in the literature review. In brief, elevation and soil drainage are critical factors related to the distribution of herbaceous and woody species and broad community types. Additionally, the underlying elements of the LCPI form the basis for classifying wetlands, for identifying suitable sites for habitat restoration and management, and for determining management actions at large and small scales. This portion of the thesis examines the underlying assumptions of the LCPI by quantifying the relationships between LCPI flow-return interval and soil drainage classes and the distribution of species and communities on the Missouri River floodplain.

Specific null hypotheses examined in this section include:

1. The likelihood of occurrence for species does not vary between LCPI flow-return intervals or soil drainage classes.
2. Mean percent foliar cover for species does not vary between LCPI flow-return intervals or soil drainage classes.
3. The likelihood of a species becoming abundant does not vary between LCPI flow-return intervals or soil drainage classes
4. The likelihood of occurrence for communities does not vary between LCPI flow-return intervals or soil drainage classes.
5. Mean area occupied by communities does not vary between LCPI flow-return intervals or soil drainage classes.

Though not designed to test the efficacy of management actions for particular species or communities, it is assumed that the analyses presented here can inform decision making to increase resource management efficiency in more intensively managed area.

Analyses here focus on vegetation that has established naturally following abandonment of agricultural practices. This abandonment was often a response to severe flooding that had significantly altered surface soils or local hydrology, or otherwise made continued management of the site for agricultural purposes untenable (for example, by washing out access roads). The major event that precipitated a reevaluation of floodplain management and the removal of many of the study sites from production was the great flood of 1993. Additional flooding in 1995 and 1997, as well as flooding within the last decade have driven acquisition of additional lands by state and federal agencies and made management of floodplain habitat a priority. Many of the study sites also include locations that have never been used for agricultural production. These include lands that have accreted following development of the levee and dike system designed to maintain a navigable stream, and lands that were left outside of protective levees during the development of that system. The analyses presented here do not distinguish among sites based on land-use history.

The research that follows explores where species and communities are likely to occur and to become abundant as a result of fluvial processes and soil conditions. Such information can be used to identify locations likely to support desired species and communities, and to identify locations susceptible to invasion by non-native, invasive species. At broad scales, the information can be used for acquisition planning to increase the likelihood that lands suitable for a broad spectrum of habitat types or for particular

target communities are represented in the conservation portfolio. At smaller scales, such as the sampling sites described below, the information can be used to develop focused early-detection/rapid response programs to limit the impact of non-native species and to identify where target species and communities are most likely to occur with minimal management effort. Such information is critical to effective allocation of limited management resources.

The results presented here do not address the likely success or failure of management efforts designed to limit exotic species expansion or to promote target species and communities. However, there is an underlying assumption that the distributions of species described here indicate the soil conditions and exposure to fluvial processes that are likely to either favor or hinder the long-term survival of species on a site. Research designed to assess the value of LCPI classes as a relevant parameter when considering specific management actions and the optimal allocation of resources would complement the research presented here.

Species and community data

Community occurrence and species cover data were compiled from various sources. A survey of bird habitat the Missouri River was conducted in three coarse habitat types between 2002 and 2004 (Bezzerides et al., 2003; Thogmartin et al., 2006). Plots were systematically established in wet prairies, early-successional forests, and mature forests, and species cover was estimated in 5 vegetative strata (emergent canopy, canopy, subcanopy, shrub, and groundflora). Data were collected on federal lands at Fort Leavenworth Military Reservation and 2 fish and wildlife refuges (Squaw Creek and Big Muddy), and at 2 Missouri state conservation areas (Eagle Bluffs and Howell Island) (Figure 9. Sites at which data used in this study were collected in relation to ecological provinces.). Data were collected on 4 units of Big Muddy: Lisbon Bottom, Jameson Island, Overton Bottoms, and St. Aubert Island. Data have previously been explored to model whether sites were likely to develop into either early-successional forests or wet prairie communities based upon soil drainage, flow frequency, elevation, and distance from the river (Thogmartin et al., 2009).

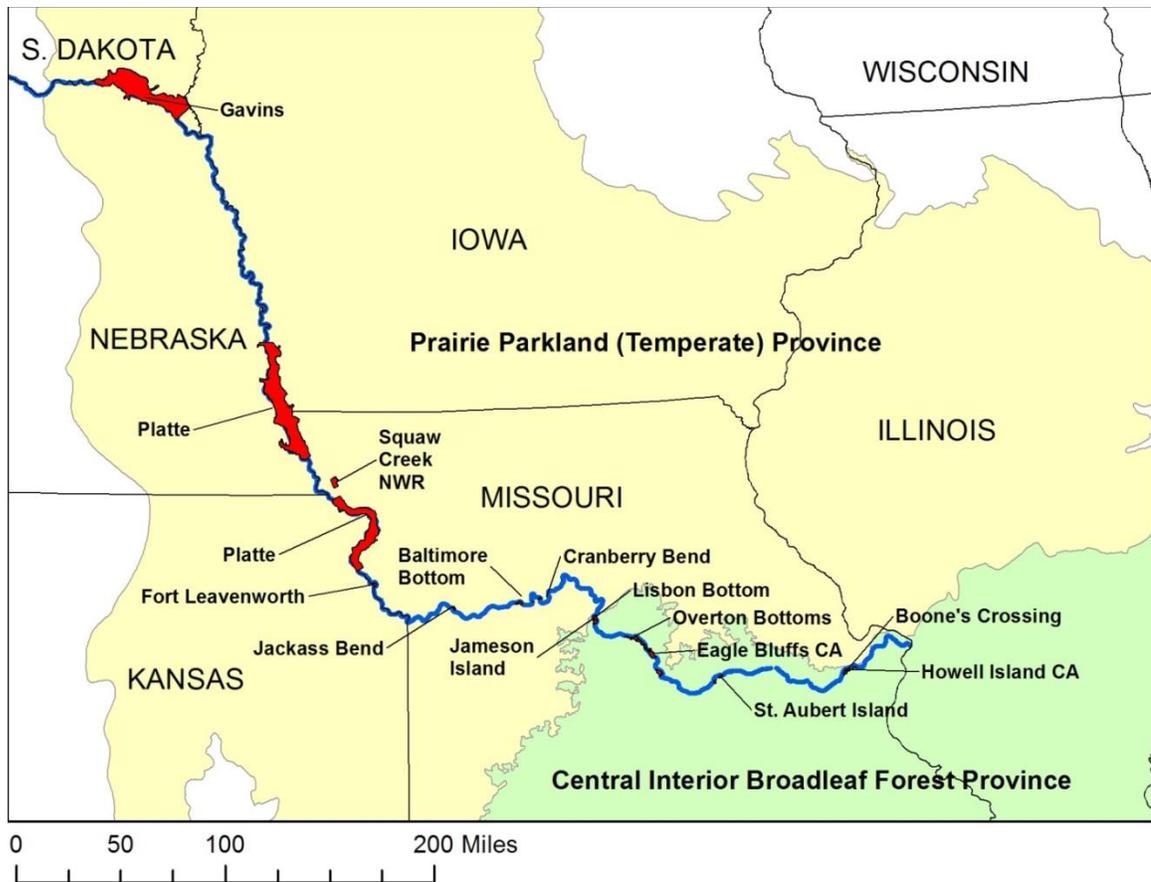


Figure 9. Sites at which data used in this study were collected in relation to ecological provinces.

From 2007 to 2009, data from these plots and newly established plots in herbaceous communities were used to classify and describe vegetation types and to map vegetation communities on the four sampled Big Muddy units, plus the then newly-acquired Boone's Crossing unit (Figure 9) (Struckhoff et al., 2011). New species-level data were collected at 48 of the plots sampled during the earlier study (Bezzerrides et al., 2003; Thogmartin et al., 2006) and at 19 new herbaceous plots, with species cover estimates in 3, 1 m² subplots and canopy species cover estimates for the entire 7.33 m radius plot. The analysis presented here uses the maximum cover value recorded for each species at each of the above plots during either of the two studies above. Additionally, during the latter study, stem counts and areal cover of exotic species were estimated as they were encountered when traversing between plots; the current study derives percent cover estimates for exotic species from data collected at these points.

Also between 2007 and 2009, plots were established and sampled across a forest age gradient in the upper reaches of the Lower Missouri River and above the Gavins Point Dam (Dixon et al., 2010).

Overstory composition and structure were sampled using a point-centered quarter method, fixed radius circular plots, and complete plot census methods. Shrub cover estimates were derived using belt transects and line-intercept sampling, and using 12 quadrats on 4 transects emanating from the plot center. Groundflora cover estimates were made from data collected at 24, 1 m² quadrats located on the same 4 transects. Data were collected at 59 plots in the Gavins section and 35 plots within Platte section of the area modeled by the LCPI, and were previously used to describe the status of and trends associated with one particular community type, cottonwood forests (Dixon et al., 2010). The analyses presented here use plot-level estimates of cover derived from these data.

The final data source was an expansion of the vegetation community map of Big Muddy National Fish and Wildlife Refuge to the previously unmapped areas of the refuge. These data were collected in 2012 as part of the current project in western units of the refuge (Jackass Bend, Baltimore Bottom, and Cranberry Bend) and at the north unit at Overton Bottoms (Struckhoff, 2013; Figure 9). Plot data were not collected, but cover of the 5 dominant species and 22 exotic species (Table 4) was estimated at 749 field sampling points used to classify map polygons derived from aerial photos. The 22 non-native species were selected because they are known noxious weeds (U.S. Department of Agriculture-Natural Resource Conservation Service, 2014) or were identified as species of concern by refuge biologists within the study area. Between sampling locations, cover of the same 22 exotic species was recorded between sampling locations along transects defined by LCPI polygon boundaries (i.e. while walking to the next sampling point, individual transects were recorded across each unique LCPI polygon encountered).

This thesis uses naming conventions for vegetation communities used in the two mapping efforts on Big Muddy National Fish and Wildlife Refuge (Struckhoff et al., 2011; Struckhoff, 2013). For natural and semi-natural communities, this follows the standards of the National Vegetation Classification System (NVCS) for mapping vegetation of federal lands (The Nature Conservancy and Environmental Systems Research Institute, 1994). Community concepts for the NVCS are curated by NatureServe (2014). Generally, the names of communities include one or two dominant or diagnostic species from the defining vegetative stratum (for example, the tree canopy for forests), as well as important species from other strata as needed to differentiate between similar community types. Cultural and other features associated with human activity are described in documents pertaining to the mapping efforts above (Struckhoff et al., 2011;

Struckhoff, 2013). Only 3 such communities (herbaceous old field, woody old fields, and Johnson grass communities) are included in analyses here. Plant nomenclature follows the Integrated Taxonomic Information System (2014).

Table 4. Alphabetical list of non-native species selected for detection during 2012 vegetation community mapping (Struckhoff, 2013)

Scientific name and author	Family	Common name
<i>Abutilon theophrasti</i> ¹ Medik.	Malvaceae	velvetleaf
<i>Alliaria petiolata</i> ¹ (Bieb.) Cavara & Grande	Brassicaceae	garlic mustard
<i>Cannabis sativa</i> L.	Cannabaceae	marijuana
<i>Carduus nutans</i> L.	Asteraceae	nodding plumeless thistle
<i>Celastrus orbiculatus</i> Thunb.	Celastraceae	oriental bittersweet
<i>Centaurea stoebe</i> L. ssp. <i>micranthos</i> (Gugler) Hayek	Asteraceae	spotted knapweed
<i>Cirsium arvense</i> (L.) Scop.	Asteraceae	Canada thistle
<i>Elaeagnus umbellata</i> ¹ Thunb.	Elaeagnaceae	autumn olive
<i>Euonymus fortunei</i> (Turcz.) Hand.-Maz.	Celastraceae	winter creeper
<i>Humulus japonicas</i> ¹ Sieb. & Zucc.	Cannabaceae	Japanese hop
<i>Lespedeza cuneata</i> ¹ (Dum.-Cours.) G. Don	Fabaceae	Chinese lespedeza
<i>Lonicera maackii</i> (Rupr.) Herder	Caprifoliaceae	Amur honeysuckle
<i>Lythrum salicaria</i> ² L.	Lythraceae	purple loosestrife
<i>Melilotus officinalis</i> ¹ (L.) Lam.	Fabaceae	sweetclover
<i>Microstegium vimineum</i> ² (Trin.) A. Camus	Poaceae	Nepalese browntop
<i>Phalaris arundinacea</i> ¹ L.	Poaceae	reed canarygrass
<i>Phragmites australis</i> ² (Cav.) Trin. ex Steud.	Poaceae	common reed
<i>Polygonum cuspidatum</i> Sieb. & Zucc.	Polygonaceae	Japanese knotweed
<i>Pueraria montana</i> (Lour.) Merr. var. <i>lobata</i> (Willd.) Maesen & S. Almeida	Fabaceae	kudzu
<i>Pyrus calleryana</i> Decne.	Rosaceae	Callery pear
<i>Ranunculus ficaria</i> L.	Ranunculaceae	fig buttercup
<i>Sorghum halepense</i> ¹ (L.) Pers.	Poaceae	Johnsongrass

¹ recorded at community classification point(s)

² otherwise detected during sampling

GIS-derived data variables

A geographic information system (GIS) was used to identify or derive independent variables to relate to species cover and community data. First, exotic species transect data from 2012 (Struckhoff, 2013) were converted to point data at the transect midpoint with percent cover estimates for each species. These points were then combined with point locations for plot data from the other studies (Bezzerrides et al., 2003; Thogmartin et al., 2006; Dixon et al., 2010; Struckhoff et al., 2011). Each point was then attributed with the flow-return interval, drainage class, and available water capacity (AWC) for the top 25, 50, 100, and 150

cm of soil by spatially joining the point data with the LCPI model. Additionally, the elevation of each point was determined from the gridded land-surface model used to develop the LCPI.

Next, GIS was used estimate to the nearest meter the distance from each point to roads, levees, the Missouri River, and other water features such as oxbows, scours, tributaries, and ponds. Distance to roads and levees was included because human-made features are often associated with exotic species (Heimann, 2001; Larson, 2002; Heimann and Mettler-Cherry, 2004). Additionally, these features affect local hydrology (as is evident from the earlier site descriptions in the section of this thesis addressing variation in groundwater processes associated with soil drainage classes). Distance from the river has been demonstrated to be an important determinant of species and community distribution on the Missouri River and in other fluvial systems (Vannote et al., 1980; Wharton et al., 1982; Malanson, 1993; Turner et al., 2004; Thogmartin et al., 2009). More generally, water bodies can be susceptible to invasion by exotic species (Henderson et al., 2006), increasing propagule pressure in their vicinity.

Vegetation community classifications were linked to LCPI classes using two methods for two distinct subsets of data. Within mapped areas of Big Muddy National Fish and Wildlife Refuge, the LCPI model was spatially joined with the vegetation map (Struckhoff et al., 2011; Struckhoff, 2013), and both the relative frequency and relative area of each community within each flow-return interval or drainage class was examined. Because greater than 95 percent of all mapped polygons were visited and field-classified during the map production, this provides a far more comprehensive picture of the distribution of communities within the mapped area than do sampling points. Vegetation polygons sharing the same classification within the same polygon from the original SSURGO data set (Soil Survey Staff, 2012) or the same flow-return interval (Chojnacki et al., 2012) were treated as a single unit in order to avoid double counting community occurrences for frequency and area estimates.

For sampling locations outside on the mapped area, plots were attributed with LCPI class attributes as described above and vegetation community classifications based upon classifications that had been made when the data were collected or upon interpretation of field data and notes indicating dominant species and structure. This latter set of data included all of the vegetation plots that are not on Big Muddy National Fish and Wildlife Refuge, including widely dispersed plots in the Gavins and Platte sections of the river (Dixon et al., 2010), and points sampled as part of the bird habitat study at Squaw Creek, Fort

Leavenworth, and the Eagle Bluffs and Howell Island Conservation Areas (Figure 9) (Bezzerrides et al., 2003; Thogmartin et al., 2006).

Analysis of vegetation data

Identification of dominant environmental variables using Non-metric

Multidimensional Scaling

Nonmetric multidimensional scaling (NMS) was used to identify those environmental variables with the highest correlation to the vegetation composition of plots. Analysis using NMS determines the best fit of data into a reduced number of dimensions (McCune et al., 2002). It is advantageous for ecological community data in that it avoids the assumption of linear relationships among variables, uses rank distances to linearize distances measured in species and environmental space, and allows the use of any distance measure or relativization (McCune et al., 2002). Outputs from NMS include a measure of final stress (lack of fit; scale of 1 to 100) and a graphical output of plots, species, or both according to their ordination scores.

Analyses using NMS that yield stress values less than 10 are unlikely to yield ambiguous or misleading results (McCune et al., 2002). Stress values above 10 indicate that results should be interpreted with more caution, but are fairly reliable until stress values approach 20 (McCune et al., 2002). The strength of the relationship between environmental variables and the ordination solution is indicated by the multiple r-square value (calculated as the square root of the sum of the r-square values for the variable and each axis). When considering the NMS graphical output, the proximity of sampling points to one another reflects their similarity in terms of species composition and abundance. Environmental variables can be displayed as vectors indicating direction of increase, with the length indicative of the multiple r-square value, or the overall correlation of that variable with the data structure.

Species occurring on less than 5 percent of the sample units were excluded from NMS analysis, because infrequently occurring species can exert exaggerated leverage on the results. Analyses were run using the “Medium” parameters of PC-Ord v. 6.07 (distance measure = Sorensen, maximum number of iterations = 250, runs with real data = 50; runs with randomized data = 50; maximum number of dimensions = 6, stability criterion for standard deviation over 15 iterations = 0.00001). In order to assess

relationships between community composition and elements of the LCPI model, plots were attributed with ordinal numbers representing increasing flow-return interval (1 to 9) and increasing drainage capacity (1 to 7), corresponding to decreasing wetness potential. Plots were also assigned ordinal numbers representing geomorphologic river segment (Jacobson et al., 2009), tributary-defined segments (Chojnacki et al., 2012), and sampling sites (Figure 9) in an upstream to downstream order.

Statistical tests of variation in species and community abundance between LCPI

classes

For each species or community, a percent similarity score was generated that compares the species or community distribution base on presence/absence data with that of the sampling distribution. Percent similarity is calculated by summing the shared percent of sampling locations and species (or community) occurrences in each flow or drainage class. A species or community has a score of 100 if its distribution amongst classes perfectly matches the distribution of sampling points. Species and communities distributions were assessed for differences between the expected distribution and actual distribution using Chi-square tests. To illustrate the relative susceptibility of flow and drainage classes to invasion by non-native species or occupancy by desired species or communities, the probability that each flow or drainage class would be occupied by a given species or community was calculated. For species for which Chi-squared analyses indicated significant deviation for expected distributions, differences between classes were assessed using a *post-hoc* Marascuilo (1966) procedure multiple comparison test.

Differences between classes in the distribution of cover values (for species) or relative area (for communities) were tested for statistical significance using Kruskal-Wallis one way analysis of variance on ranks for non-parametric data, with *post-hoc* Dunn's multiple comparison tests. In accordance with non-parametric data and Kruskal-Wallis analyses, comparisons of quantile distributions (rather than of means) are used to describe variation in the distribution of cover values between flow and drainage classes. Additionally, the distribution of locations where select exotic species and native species groups are abundant, defined here as having a collective cover value greater than 15 percent, were tested for differences from expected distribution using Chi-square tests in a manner similar to the presence/absence data above.

The primary data used for community-level analyses were those derived by intersecting the vegetation map for Big Muddy with the LCPI model; community classifications derived from plot data outside of the refuge were used only to determine if patterns detectable on the refuge were evident in other sections of the river. Only communities that appeared to be occurring as a combined result of fluvial processes and natural succession were examined; cultural features such as levees, plantations, roads, and communities that have been promoted through management activities were excluded from analysis.

In addition to the exotic species described above, subgroups of native species were selected for analysis based on their status as indicators for the community types within which they are found. Cottonwood (*Populus deltoides*) was treated individually because it is the target of the Missouri River Recovery Program Cottonwood Management Plan (U.S. Army Corps of Engineers, 2011). Additionally, the absence or presence of cottonwood frequently defines community types within the study area (Struckhoff et al., 2011). Willow species (primarily *Salix nigra* and *Salix interior*) were treated as a group because they are closely affiliated with cottonwood (Struckhoff et al., 2011). Smartweeds (*Polygonum* spp.) and sedges (*Carex* spp. and *Cyperus* spp.) were aggregated into two groups representing herbaceous wetland communities. Oaks (*Quercus* spp.), hickories (*Carya* spp.), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), and a few other species (Table 5) were aggregated into a class representing mid- and late-successional communities (Steyermark, 1963; Yatskievych, 1999; Nelson, 2005; Yatskievych, 2006, 2012).

Table 5. Species selected to represent late-successional communities

Scientific name and author	Common name
<i>Acer saccharum</i> Marsh.	Sugar maple
<i>Asimina triloba</i> (L.) Dunal	Paw paw
<i>Carya illinoensis</i> (Wangenh.) K. Koch	Pecan
<i>Carya</i> Nutt.	Hickory
<i>Cornus drummondii</i> C.A. Mey.	Roughleaf dogwood
<i>Fraxinus americana</i> L.	White ash
<i>Fraxinus pennsylvanica</i> Marsh.	Green ash
<i>Juglans nigra</i> L.	Black walnut
<i>Quercus macrocarpa</i> Michx.	Bur oak
<i>Ribes missouriense</i> Nutt.	Missouri gooseberry
<i>Robinia pseudoacacia</i> L.	Black locust
<i>Tilia americana</i> L.	American basswood
<i>Ulmus americana</i> L.	American elm
<i>Ulmus rubra</i> Muhl.	Slippery elm
<i>Zanthoxylum americanum</i> P. Mill.	Common prickly ash

Potential future LCPI class abundance

The dynamic context of floodplain systems means that current conditions may soon be transformed, altering the biotic and abiotic components of the system to which species respond. The most obvious examples of this are erosion and deposition of soils and vegetation associated with flood events. Less obvious, though no less profound examples would include alteration of the hydrologic regime, such that the conditions under which communities develop are no longer extant. Such changes have been identified along numerous rivers following dam construction (Vannote et al., 1980; Rood and Mahoney, 1990; Malanson, 1993; Auble et al., 1994; Hughes, 1997; Johnson, 1999; Nakamura and Shin, 2001; Nilsson and Svedmark, 2002; Hupp et al., 2010). Alteration of the Missouri River hydrologic regime (Johnson et al., 1982; Galat et al.; Jacobson et al., 2009) has been linked to declines in the abundance of cottonwood forests (Johnson et al., 1982; National Research Council, 2002; Dixon et al., 2010; Dixon et al., 2012a).

Climate change has the potential to induce changes in hydrology as well. Ensemble global circulation models obtainable from the Climate Wizard web tool maintained by The Nature Conservancy, estimate changes in precipitation across the Missouri River basin ranging from -2.5 percent to 19.6 percent, with a mean increase of 12.4 percent under the A1B emissions scenario (Girvetz et al., 2009). Additionally, changing temperature regimes can affect the timing of snow melt, vegetation growth, evaporative demand, and land use practices, thereby affecting both the quantity of water that enters fluvial systems and the timing of its delivery.

This section of the thesis quantifies the potential effects of climate change on the distribution of LCPI classes on the Lower Missouri River. A detailed exploration of the Soil-Plant-Atmospheric Continuum (Philip, 1966) is beyond the scope of this thesis, so no effort is made to quantify the relative contribution of rainfall, snowmelt, evaporative demand, or land use practices to the future potential discharge patterns of the Missouri River. Instead, this exploration relies on the results of a single study modelling the potential effects of climate change on many of these factors, and ultimately on the monthly discharge patterns of the Missouri River for the time period 2040 to 2069 (Gangopadhyay et al., 2012). The final section addresses the management implications, particularly for cottonwood forests.

Future changes in LCPI class abundance resulting from climate change were modeled by adjusting water surface elevations for each flow-return interval upward based on predicted changes in discharge from the Climate Change Analysis for the Missouri River Basin (Gangopadhyay et al., 2012). That study estimated future change in mean monthly discharge (years 2040-2069) compared to historical discharge (1950-1999) based on 112 simulations using three climate emissions scenarios and 16 climate models at 9 Missouri River stream gages within the study area (Table 6).

Table 6. Percent change in mean monthly discharge between the historic period (1950-1999) and future (2040-2069) conditions based on modeled effects of climate change for 9 gages within the area modeled by the LCPI (Table A.9 in Gangopadhyay et al., 2012)

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Sioux City, IA	13.1	17.8	23.8	28.6	30.0	15.2	-5.3	-3.0	-0.1	1.7	4.3	6.5
Omaha, NE Nebraska City, NE	13.5	19.2	26.0	26.7	29.3	16.0	-3.7	-2.4	1.9	1.4	6.6	8.2
Rulo, NE St. Joseph, MO	14.0	18.8	23.7	22.4	25.0	14.5	-4.3	-1.5	1.2	0.8	5.6	9.6
Kansas City, MO	13.8	18.9	21.8	20.7	24.5	14.8	-3.2	-1.3	1.8	0.4	5.5	11.0
Waverly, MO	11.6	15.8	19.1	16.3	22.9	15.2	-0.3	1.3	2.3	0.0	5.3	10.5
Boonville, MO	11.4	15.6	17.9	16.3	22.5	15.6	-0.1	1.2	2.7	-0.5	5.4	10.5
Hermann, MO	10.6	14.3	13.2	15.7	22.5	16.5	-0.3	1.3	3.1	1.5	4.7	11.4
	11.4	11.6	10.9	14.7	20.6	16.3	0.1	2.4	3.6	0.7	4.9	11.3

Modeled changes in monthly discharge were applied to historical monthly discharge values for each station. Historical monthly discharge values were limited to the period of dam operation (1967 to 2012) and were obtained from National Water Information System (NWIS) river gage data for each station used in the climate change analysis (U.S. Geological Survey, 2014). Application of the monthly change predictions from the Climate Change Analysis for the Missouri River Basin (Gangopadhyay et al., 2012) to historic discharge values indicated that the for all gages in the LCPI-modeled area, either May or June will yield the highest monthly discharge. Therefore, analyses of changes in stage associated with LCPI flow-return intervals are limited to those two months under the assumption that they are most likely to determine

future flow return interval. Whichever month (May or June) yielded the higher future discharge was then used to calculate the percent change in maximum monthly discharge compared to historical values. Values ranged from 14 percent to 19.14 percent, with the largest values evident at the farthest upstream and farthest downstream stations (Table 7). For each river mile (U.S. Army Corps of Engineers, 1995a, b), the percent change in discharge was interpolated from the change data for each station, and was applied equally to the discharge values associated with each flow-return interval, based on data from the Upper Mississippi River System Flow Frequency Study (U.S. Army Corps of Engineers, 2004).

It is recognized that an increase in mean discharge does not necessarily account for the variability that may surround maximum flow values, such that the values applied here maybe a poor indicator of the likelihood of flow during any given year. Nor does this method account for greater variation or increased likelihood of extreme events that could increase the probability of large-discharge events without affecting mean and median values. However, the naïve approach used here was necessary because the historic flow data for the Missouri River are insufficient to allow calculations of exceedance probabilities for every point on the floodplain; the same is true for future modeled discharge. Modeled future relationships also assume no shifts in reservoir management that would alter the frequency of the given discharges.

Following methods used in the original LCPI development (Chojnacki et al., 2012), adjusted discharge values were applied to stage-discharge relationships for each river mile to identify the water elevation associated with each flow-return interval. (An example for Boonville, Missouri at mile 192 is shown in Figure 10.) Points representing each river mile (U.S. Army Corps of Engineers, 1995a, b) and corresponding points delineating the left and right valley walls (based on their proximity as nearest neighbors to the river-mile points) were attributed with the water-surface elevations corresponding to flow-recurrence intervals to create water-surface elevations that slope with the river valley (Jacobson et al., 2007). Relevant water-surface elevations were used as the height source to convert the points to triangulated irregular networks, which were then converted to grids with 5-m cells representing water surface elevation associated with each flow-recurrence interval for the entire LCPI-modeled area.

The area inundated during flows representing each recurrence interval was identified by subtracting the land surface elevation grid used in the original LCPI development (Chojnacki et al., 2012) from the water surface elevation grids based on modeled future discharges (positive values for any given

flow-recurrence indicate inundated areas); a conditional function in ArcGIS was used to reclassify cells into the appropriate flow-recurrence interval. From this grid, the area in each modeled future flow-return interval was calculated and compared to historical area at the scale of geomorphologic sections (Jacobson et al., 2009) and tributary-defined segments (Chojnacki et al., 2012) used to analyze the current distribution of LCPI classes (see earlier section).

Table 7. Change in mean monthly discharge and maximum monthly discharge between historic period and as modeled under climate change (Gangopadhyay et al., 2012)

Shaded cells indicate months with maximum discharge during each period; the change in these values was used to calculate change in maximum monthly discharge.

Location (river mile)	Historic (1967-2012) discharge (cfs)		Predicted change (2040-2069) (Gangopadhyay et al., 2012)		Future (2040-2069) discharge (cfs)		Change in maximum monthly discharge
	May	June	May	June	May	June	
	Sioux City (732)	35,100	38,300	30%	15%	45,630	
Omaha (662)	40,800	45,200	29%	16%	52,632	52,432	16.4%
Nebraska City (557)	50,200	56,600	26%	14%	63,252	64,524	14.0%
Rulo (493)	55,200	62,100	25%	14%	69,000	70,794	14.0%
St. Joseph (448)	60,400	66,900	24%	15%	74,896	76,935	15.0%
Kansas City (361)	74,500	83,500	23%	15%	91,635	96,025	15.0%
Waverly (293)	78,500	87,300	22%	16%	95,770	101,268	16.0%
Boonville (192)	97,800	103,000	22%	16%	119,316	19,480	16.0%
Hermann (93)	127,000	130,000	21%	16%	153,670	150,800	18.2%

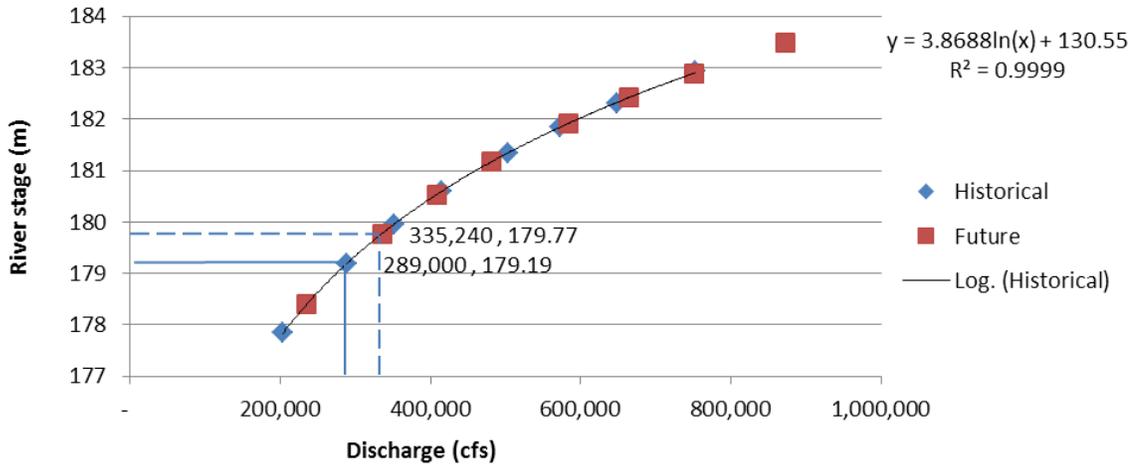


Figure 10. Change in river stage associated with the 5 year flow-return interval from historic (1967-2006; solid lines) to modeled future conditions (2040-2069; dashed lines) assuming a 16 percent increase in discharge at Boonville, Missouri (Gangopadhyay et al., 2012).

Chapter III:

Results

Current distribution of LCPI Classes

Maps depicting the distribution of LCPI soil drainage and flow-return intervals reveal a few obvious trends. Regarding soil drainage, the Big Sioux River, the Little Sioux River, the Grand River and the Chariton River are associated with a greater abundance of soils with lower drainage capacity (Figure 11). Better drained soils increase in abundance below the Kansas River, and downstream of the Chariton River in the area of transition from the Prairie Parkland Province to the Central Interior Broadleaf Forest Province (Figure 11). Below the Gavins Point Dam and extending for hundreds of miles downstream, lands with longer flow-return intervals dominate (Figure 12). These decrease in abundance downstream, with noticeable reductions associated with the inflow of the Floyd River, Little Sioux River and the Platte River (Figure 12). A similar trend is evident from the Kansas River to approximately 100 miles downstream, where longer flow-return intervals are more common (Figure 12).

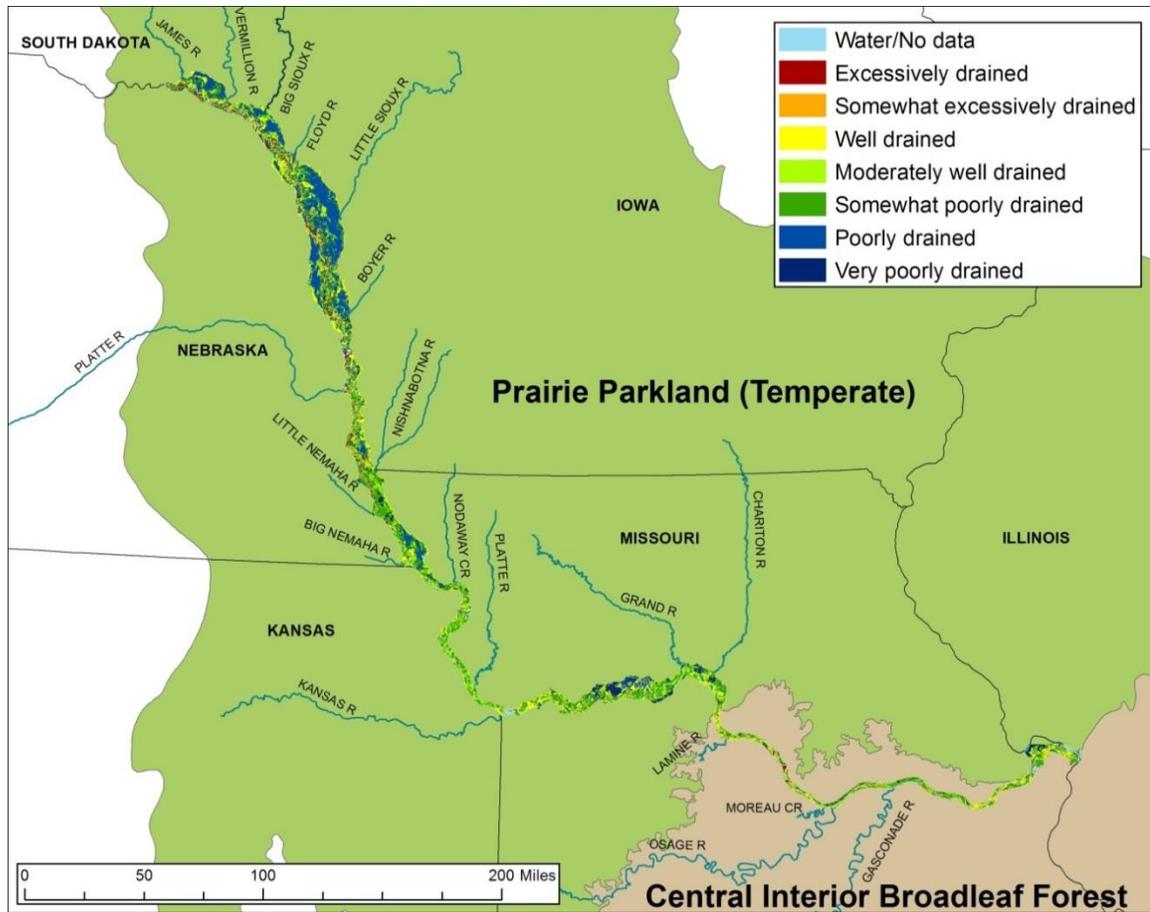


Figure 11. Map of LCPI soil drainage classes for the entire Lower Missouri River.

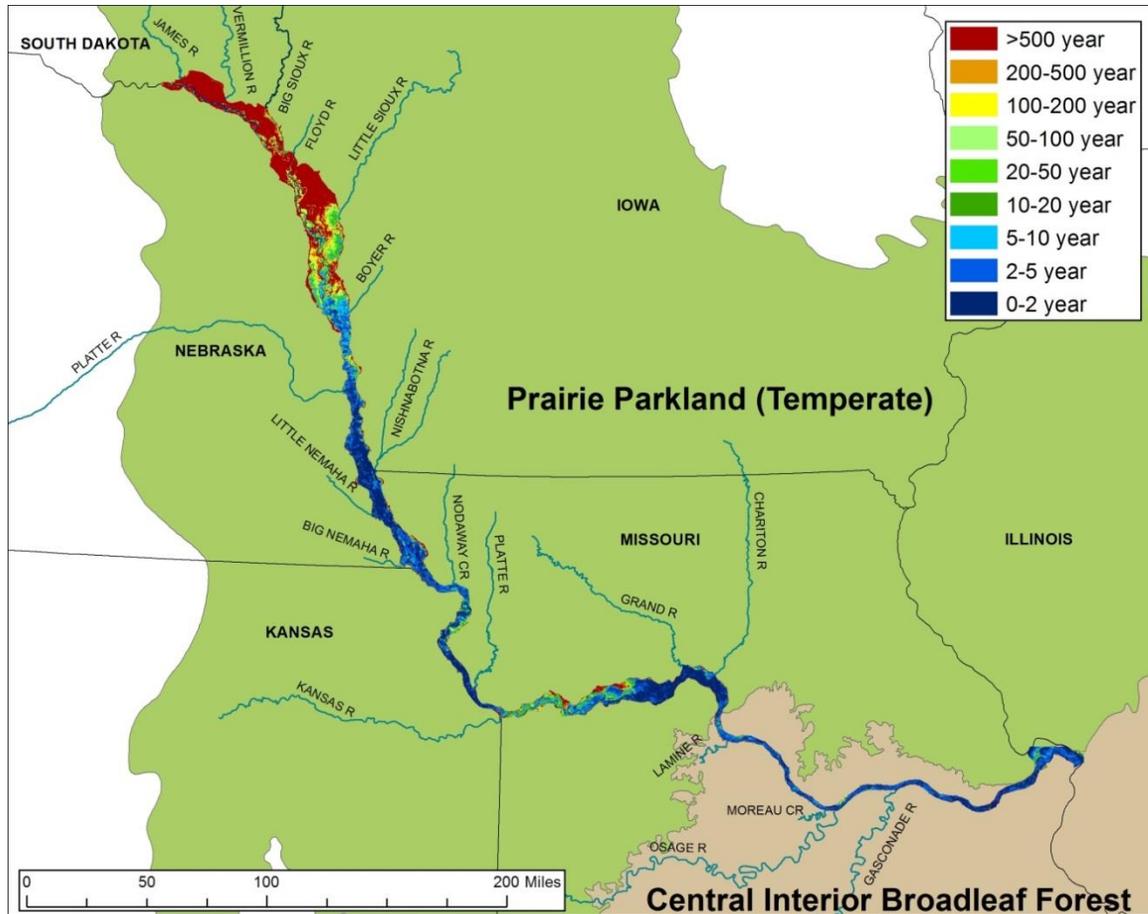


Figure 12. Map of LCPI flow-return intervals for the entire Lower Missouri River.

A perhaps more informative way of viewing the data is by relative abundance of LCPI classes. For flow-return interval, the most obvious trend is one of decreasing relative area of longer flow-return interval downstream from the Gavins Point dam (mile 811) (Figure 13). Omaha, Nebraska (mile 646) is associated with a spike in relative area occupied by lands with longer flow-return intervals (Figure 13). The Platte River (mile 595) is associated with an increase in relative area with flow-return intervals less than 5 years (Figure 13). A similar increase in relative land area with shorter flow-return intervals is seen in the stable/aggrading section approximately from mile 290 to mile 220 (Figure 13). The downstream terminus of that section exhibits effects of the transition from the prairie province to the forest province, where there is a small increase relative in area for lands with flow-return intervals greater than 500 years (Figure 13).

As distance from the Gavins Point Dam increases, the most poorly drained soil types occupy a smaller percentage of the valley and a larger percentage of the floodplain is modeled as water (Figure 14).

The Missouri cities of St. Joseph (mile 454-444), Kansas City (mile 369-356), Jefferson City (mile 150-135), and the St. Louis metropolitan area (beginning at mile 50) are associated with increases in the relative area of urban areas (Figure 14). In many urban areas, better drained soils occupy more relative area. The approach to Omaha, Nebraska (beginning at mile 646) is associated with an increase in areas with better drained soils that persists for nearly 100 miles (Figure 14). The Kansas River (mile 368) and the transition between ecological provinces (mile 220) are associated with large and persistent increases in better drained (Figure 14) soils.

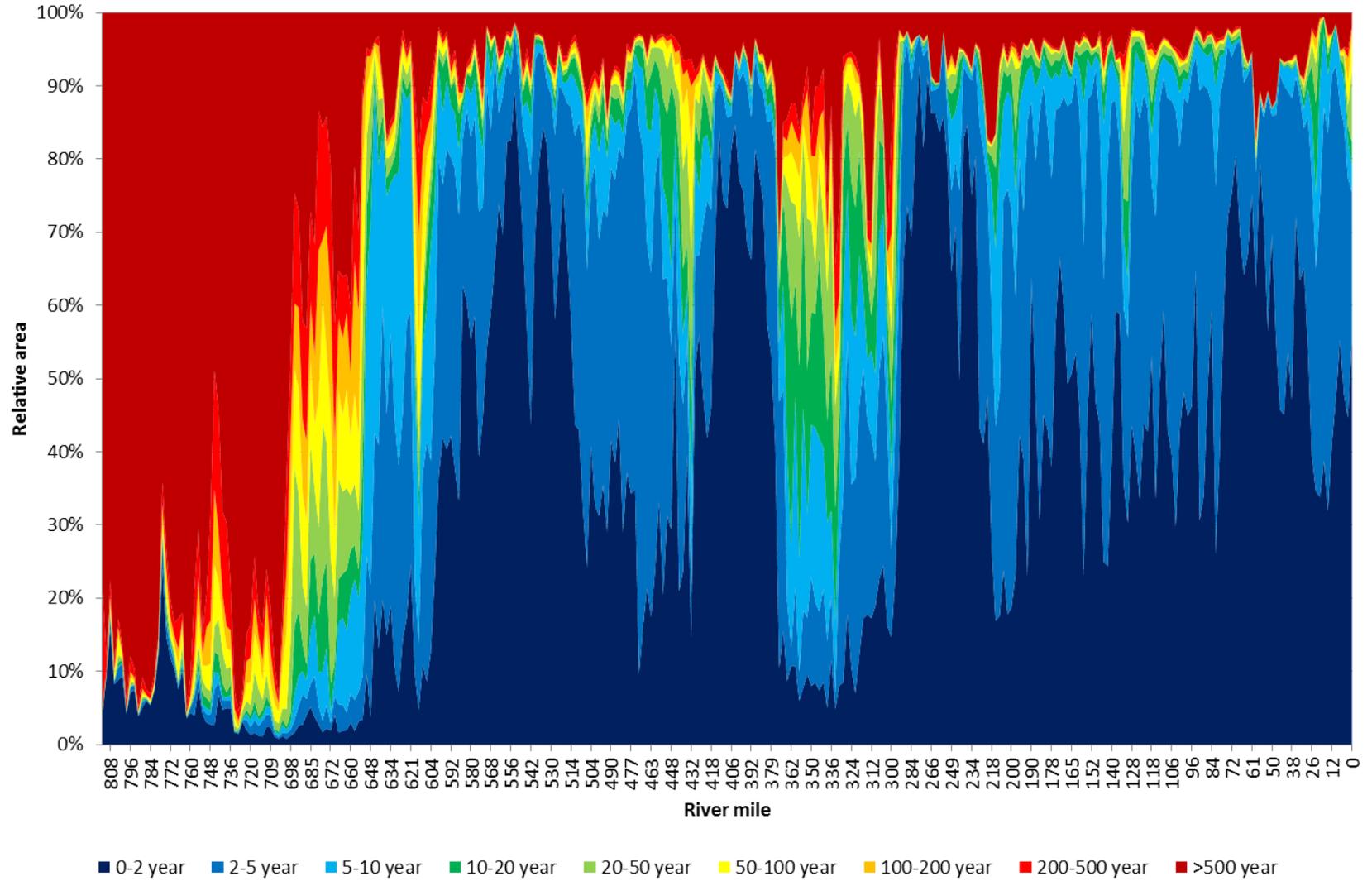


Figure 13. Relative area of LCPI flow-return intervals by valley cross-section for the Lower Missouri River.

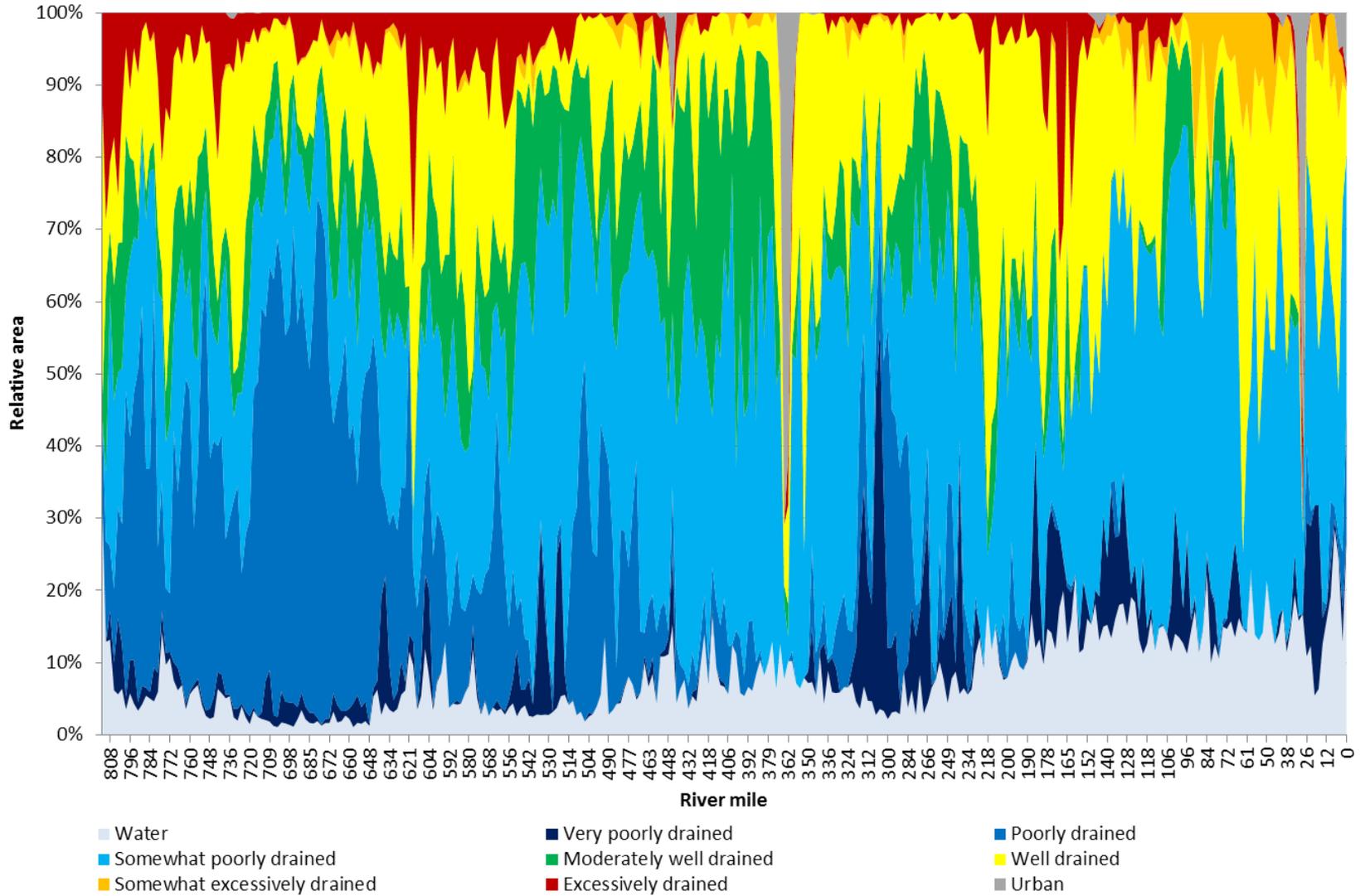


Figure 14. Relative area of LCPI soil drainage classes by valley cross-section for the Lower Missouri River.

Differences between ecological provinces

Between Ecological Provinces, there are large differences in the relative area occupied by LCPI flow-return intervals. The Prairie Parkland Province is dominated by infrequently flooded lands (Figure 15). Thirty-two percent of the floodplain is characterized by flow-return interval greater than 500 years; the area with flow-return intervals less than 5 years is less than 40 percent. By contrast, in the Central Interior Broadleaf Forest Province, lands with flow-return intervals less than 5 years comprise 83 percent of the floodplain; lands with flow-return intervals in excess of 500 years comprise just 5 percent of the floodplain. These differences in flow-return interval class abundance are evident in the map illustrating that dominance by infrequently-flooded classes decreases as distance downstream from the Gavins Point Dam increases (Figure 12). This trend continues approximately until the mouth of the Platte River (Nebraska) at mile 594. When analyzed using cross sections of the river over this span, linear regression confirms a strong negative relationship between the relative abundance of the greater than 500 year flow-return interval and distance downstream from the dam (Figure 16). Complementing the decrease in infrequently flooded lands, shorter flow-return intervals increase in relative abundance over this same stretch of river (data not shown).

The differences between provinces in the relative area occupied by soil drainage classes are less pronounced than those for flow-return intervals (Figure 17). Together, poorly and very poorly drained soils represent 34 percent of the Prairie Parkland Province valley floor, but only 9 percent of the Central Interior Broadleaf Forest Province valley floor (although very poorly drained soils occupy slightly more relative area in the latter). Complementing this decrease in poorly drained soil types in the forest province is an increase in better drained soil types compared to the prairie province. Somewhat excessively drained soils, which are barely present in the prairie province, represent 5 percent of the forest province; well drained soils increase from 18 to 31 percent. Patterns relating to distance from the Gavins Point Dam are not evident for drainage classes as they are for flow-return interval.

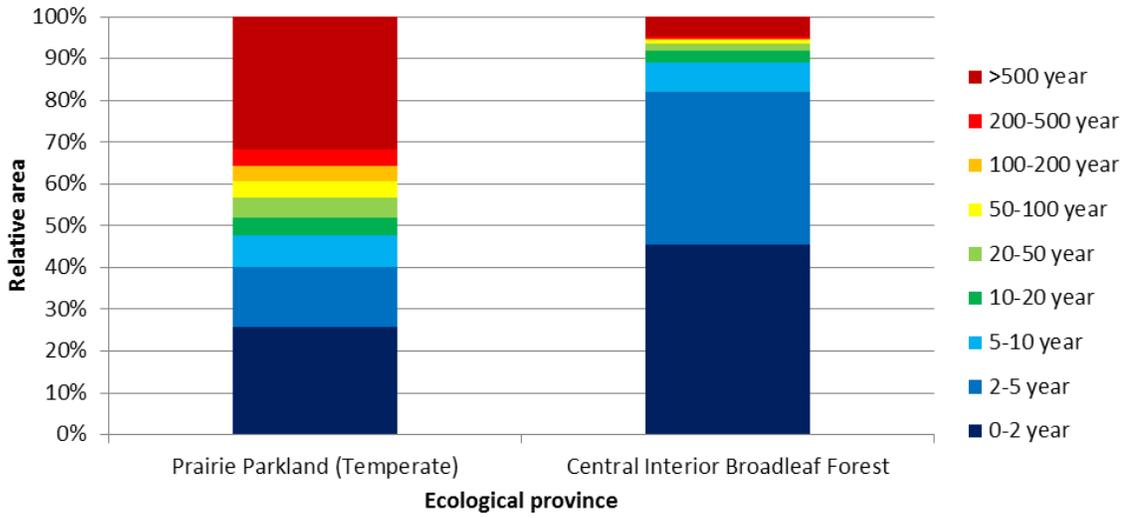


Figure 15. Relative area of Land Capability Potential Index flow-return intervals by ecological province (Cleland et al., 2007).

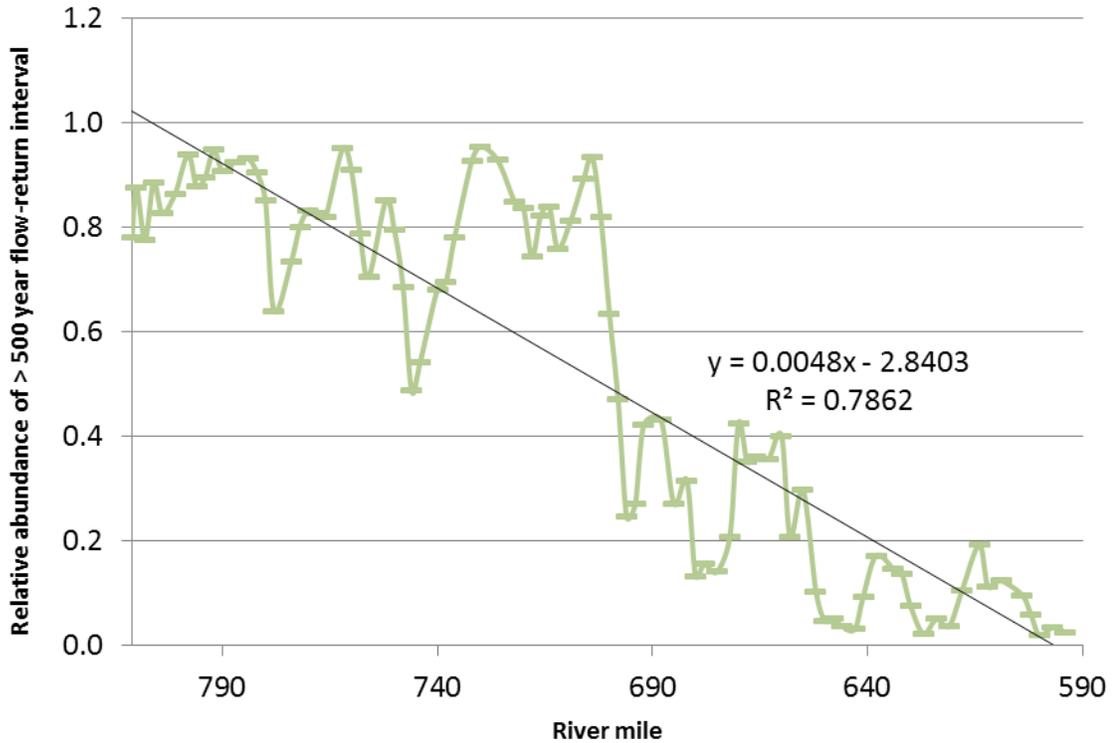


Figure 16. Graph showing decreasing relative area of the greater than 500 year flow-return interval as distance from the Gavins Point Dam (mile 811) increases.

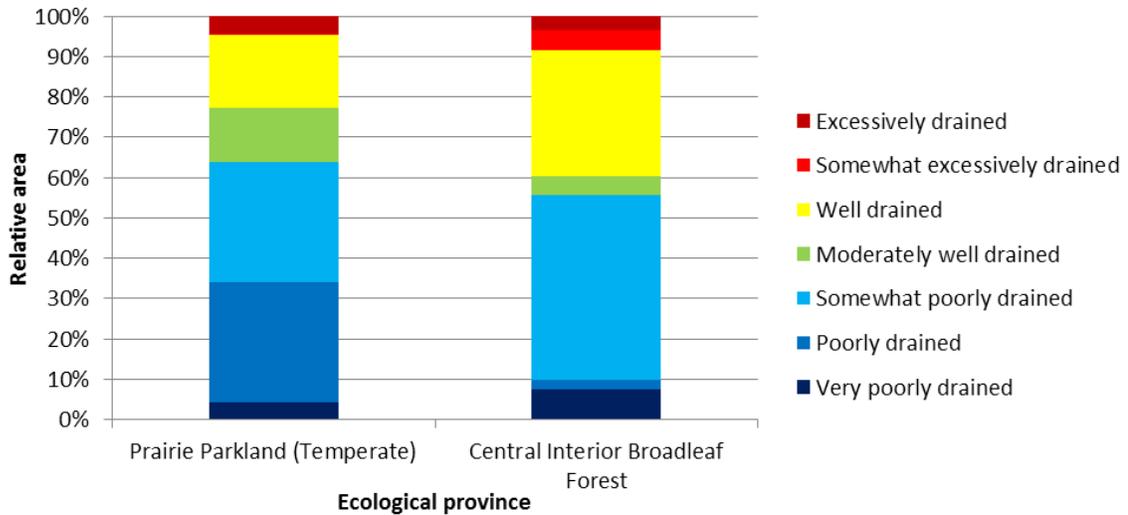


Figure 17. Relative area of Land Capability Potential Index soil drainage classes by Ecological Province (Cleland et al., 2007).

At the transition between the prairie and forest regions there is a shift toward less frequently flooded lands with better drained soils (Figure 18, Figure 19). Within the cross-section including the transition point and adjacent cross-sections, the relative area of both well drained soils and lands with longer flow-return intervals increases in association with the constriction of the river valley. Additionally, although the area in these classes drops somewhat in farther downstream polygons, they continue to represent a greater proportion of the floodplain than they do upstream of the transition zone. The combined area of lands with a flow-return interval of less than 5 years shows a weak increasing trend downstream from the transition point; other flow-return intervals trend downward in relative area. Comparing the mean area within each class from 40 miles upstream of the transition to 40 miles below the transition, a large decrease in relative area in the less than 2 year flow-return interval is associated with an increase in all other classes, with the largest increases in the 2 to 5 and 5 to 10 year classes (Table 8). Regarding soil drainage classes, the relative areas of the moderately well and all poorly drained soil classes are lower downstream of the transition point than upstream, while those of well and excessively drained soils are greater (Table 9).

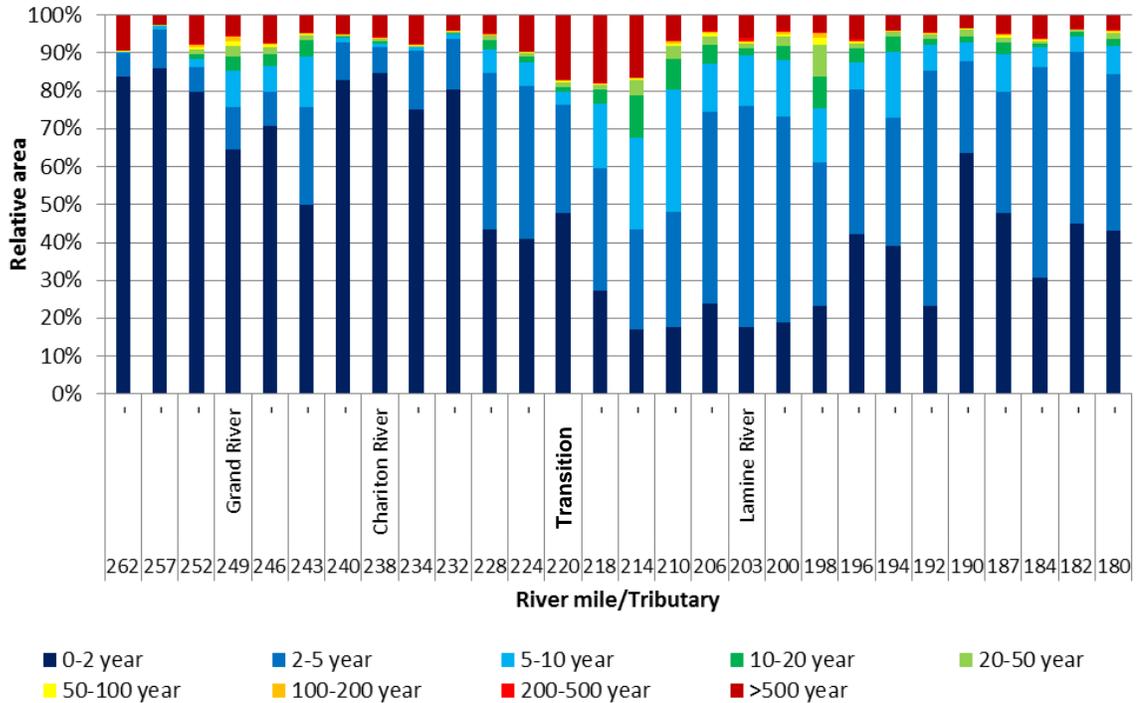


Figure 18. Relative area of flow-return intervals within 40 miles of the transition between the Prairie Parkland (Temperate) and Central Interior Broadleaf Forest Provinces showing a shift to less frequently flooded lands.

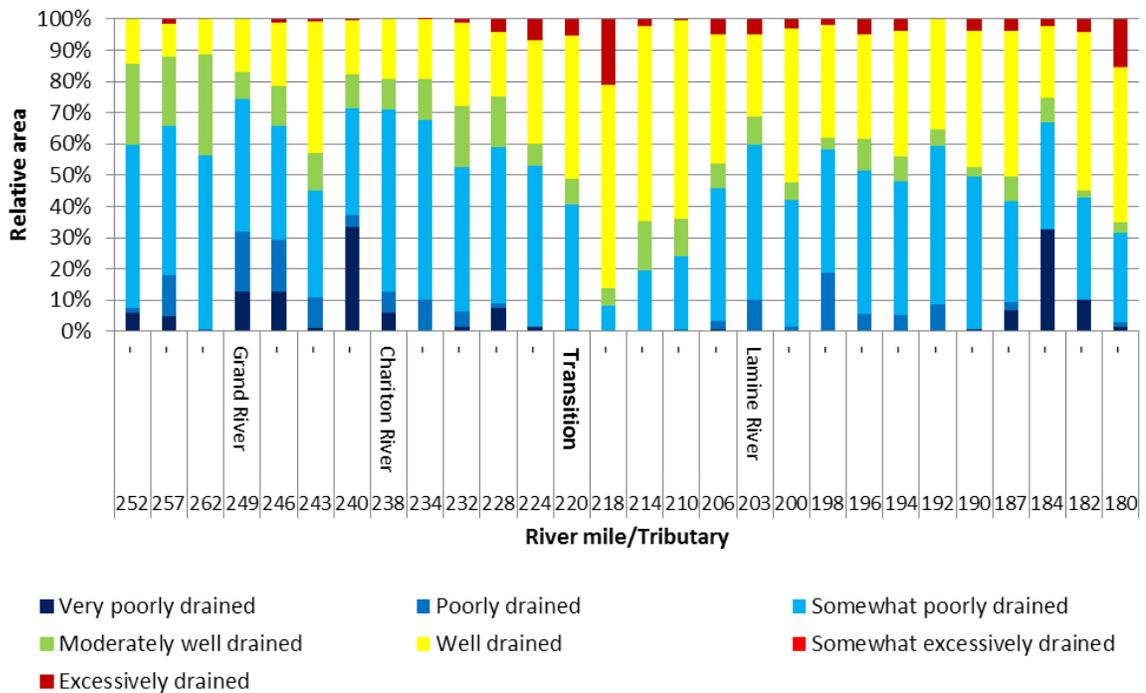


Figure 19. Relative area of soil drainage classes within 40 miles of the transition between the Prairie Parkland (Temperate) and Central Interior Broadleaf Forest Provinces showing a shift to better drained soils.

River names indicate cross section at mouth of the indicated stream.

Table 8. Comparison of mean relative area for flow-return interval classes within 40 miles of the transition between ecological provinces.

Flow-return Interval	Ecological province mean relative area	
	Prairie Parkland (Temperate)	Central Interior Broadleaf Forest
>500 year	5.9%	7.2%
200-500 year	0.2%	0.3%
100-200 year	0.2%	0.3%
50-100 year	0.4%	0.5%
20-50 year	1.0%	2.1%
10-20 year	1.6%	3.9%
5-10 year	4.5%	12.5%
2-5 year	17.3%	40.5%
0-2 year	68.9%	32.2%

Table 9. Comparison of mean relative area for soil drainage classes within 40 miles of the transition between ecological provinces.

Drainage Class	Ecological Province Mean Relative Area	
	Prairie Parkland (Temperate)	Central Interior Broadleaf Forest
Excessively drained	1.3%	3.8%
Somewhat excessively drained	0.0%	0.0%
Well drained	20.1%	38.8%
Moderately well drained	13.2%	6.6%
Somewhat poorly drained	42.8%	32.6%
Poorly drained	7.4%	3.3%
Very poorly drained	7.4%	2.9%

Differences between geomorphological segments and tributary-defined sections

There are clear differences in the relative area occupies by LCPI flow-return intervals between hydrogeomorphic segments (Figure 20). Incising sections include more land with longer flow-return intervals compared to stable and aggrading sections immediately upstream from them; conversely, stable and aggrading sections have more lands with short flow-return intervals than incising segments immediately upstream from them. These effects tend to increase or remain stable farther downstream within sections (for example, lands with flow-return intervals less than 5 years are more abundant in the downstream portion of Stable-aggrading zone 1). Shorter flow-return intervals occupy more relative area toward the downstream portion of incising zones 1a and 1b. Overall, the trend is toward a greater

abundance of lands with shorter flow-return intervals from upstream to downstream. An exception to this trend can be seen in the upstream, incising half of the Kansas section, where there is an increase in less frequently flooded lands at the Kansas River and extending for about 100 miles downstream.

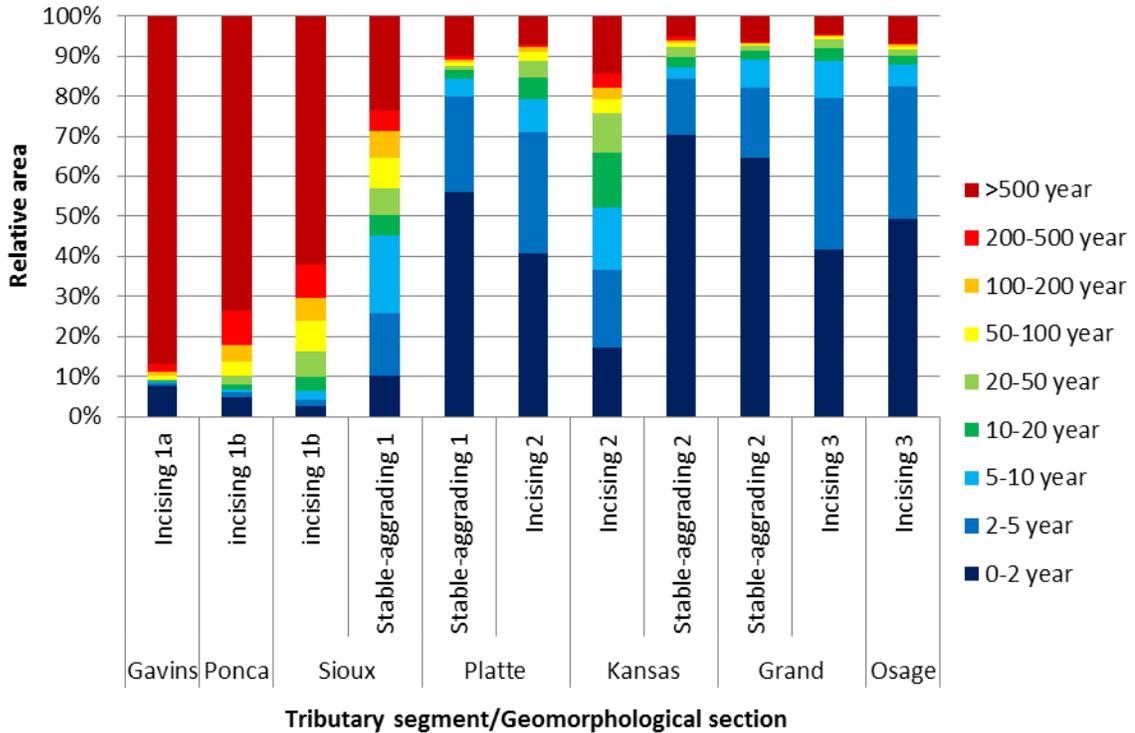


Figure 20. Relative area of Land Capability Potential Index flow-return intervals for segments of the Lower Missouri River defined by tributaries (Chojnacki et al., 2012) and by geomorphological criteria (Jacobson et al., 2009) (flow is from left to right).

As was the case for ecological Provinces, differences between sections in the abundance of soil drainage classes are less pronounced than for flow-return intervals (Figure 21). The relative area occupied by soils with poorer drainage increases through incising sections and decreases through stable or aggrading sections. Overall, lands with poor soil drainage diminish in abundance downstream, dropping from about 37 percent in the Gavins section to about 12 percent in the Osage section. The most poorly drained soil classes decrease in relative abundance as the river flows through stable and aggrading sections and increase through incising sections.

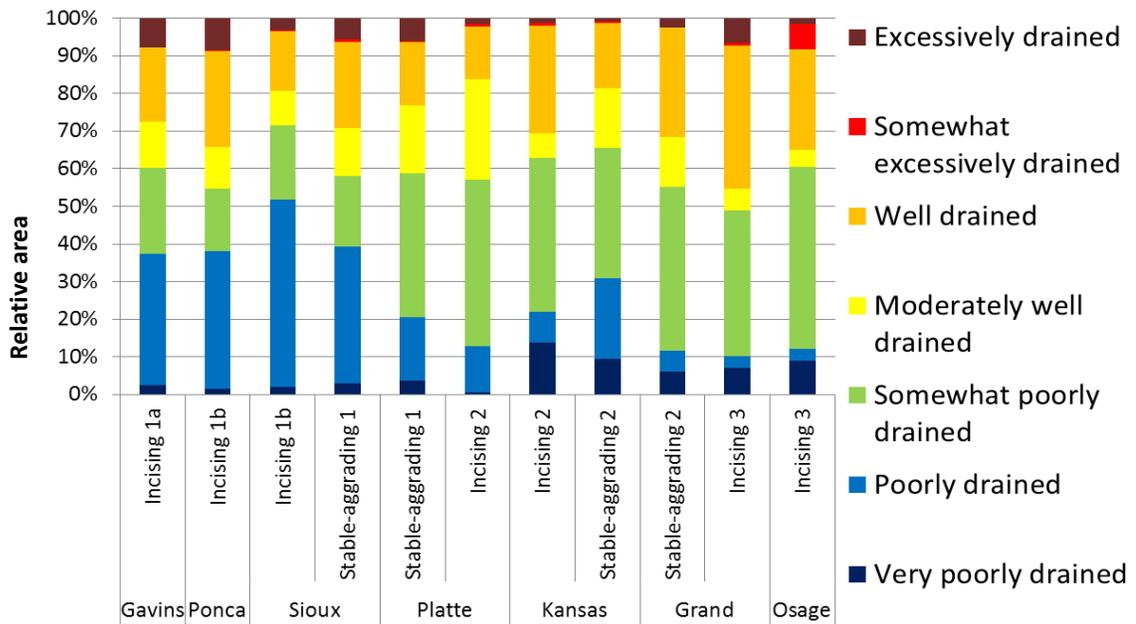


Figure 21. Relative area of Land Capability Potential Index soil drainage classes for of the Lower Missouri River defined by tributaries (Chojnacki et al., 2012) and by geomorphological criteria (Jacobson et al., 2009) (flow is from left to right).

Changes associated with tributary mouths

The mouths of tributaries are associated with varying shifts in the relative area occupied by LCPI classes. For the Big Sioux River, well-drained soils generally increase in abundance from where the Big Sioux enters the valley to the confluence with the Missouri, downstream of which better drained soils maintain an elevated abundance (Figure 22, Figure 23). Additionally, the Big Sioux River is associated with an increase in frequently flooded lands where it enters the valley until the mouth of the river, below which lands with longer flow-return intervals return to their previous abundances.(Figure 24).

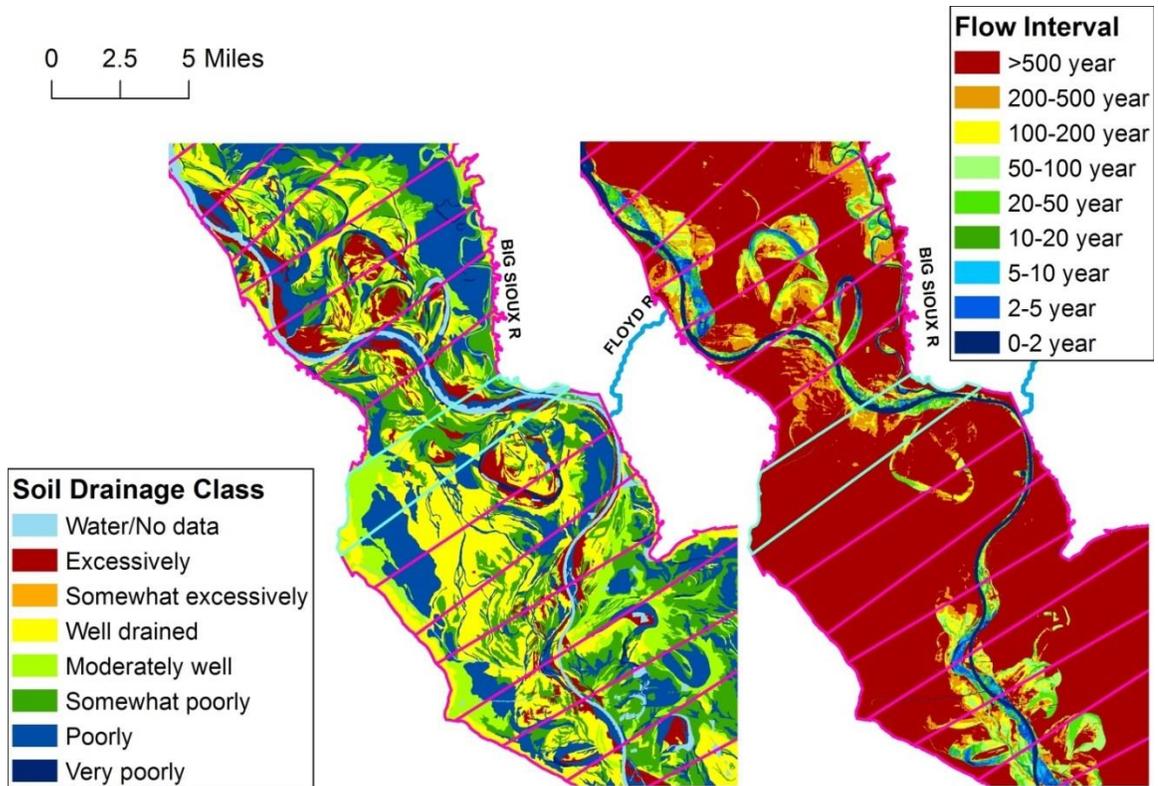


Figure 22. Soil drainage classes (left) and flow-return intervals (right) at the mouth of the Big Sioux River (within the blue-highlighted valley cross-section).

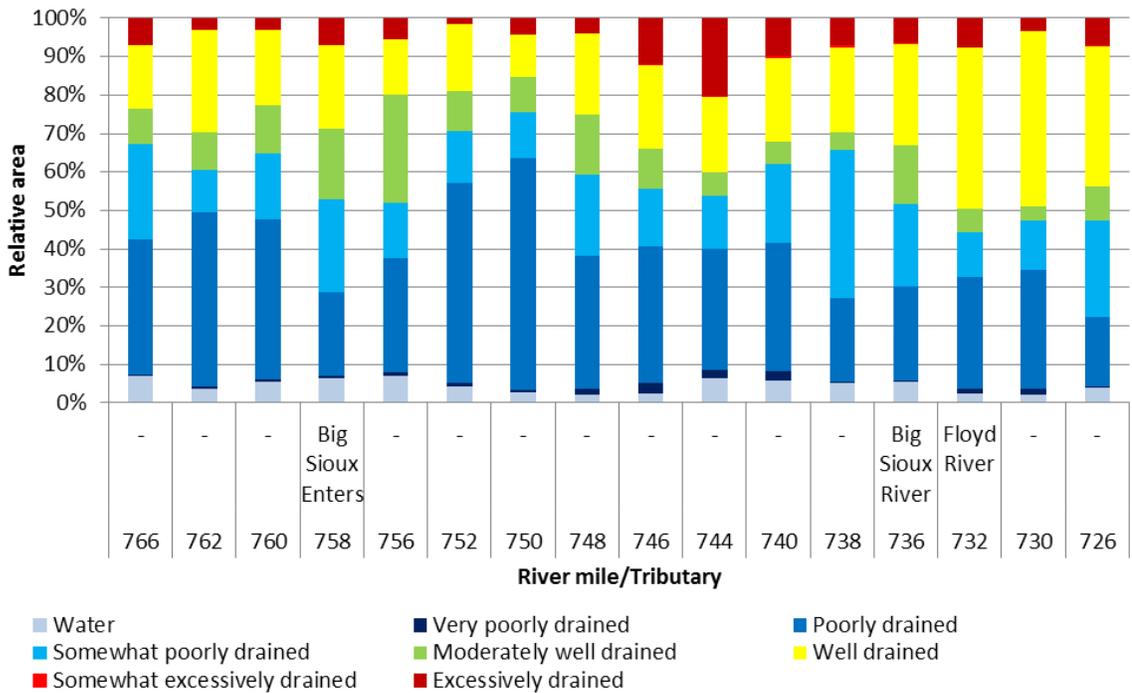


Figure 23. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Big Sioux River.

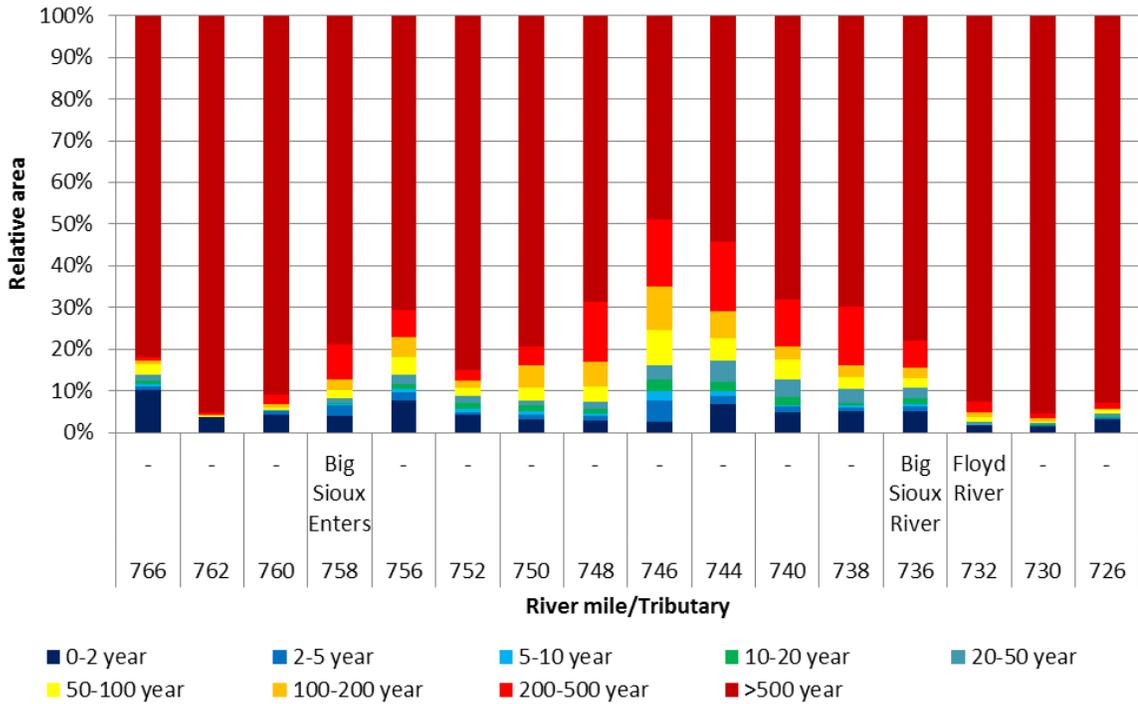


Figure 24. Relative area represented by flow-return intervals within valley cross-sections in proximity to the mouth of the Big Sioux River.

Shifts in LCPI class abundances are less pronounced near the Platte River [Nebraska] than at the Big Sioux River. The map of LCPI classes at the mouth of the Platte shows increased abundance of excessively drained soils west of the river, and a slight increase in moderately well-drained and somewhat poorly drained soils (Figure 25). There is a slight decrease in the most poorly drained soil classes that extends downstream from the mouth (Figure 26). Additionally, the flow-return intervals below 5 years increase in relative area from 55 percent to approximately 80 percent approximately 6 miles upstream of the mouth and remain elevated for many miles downstream (Figure 27).

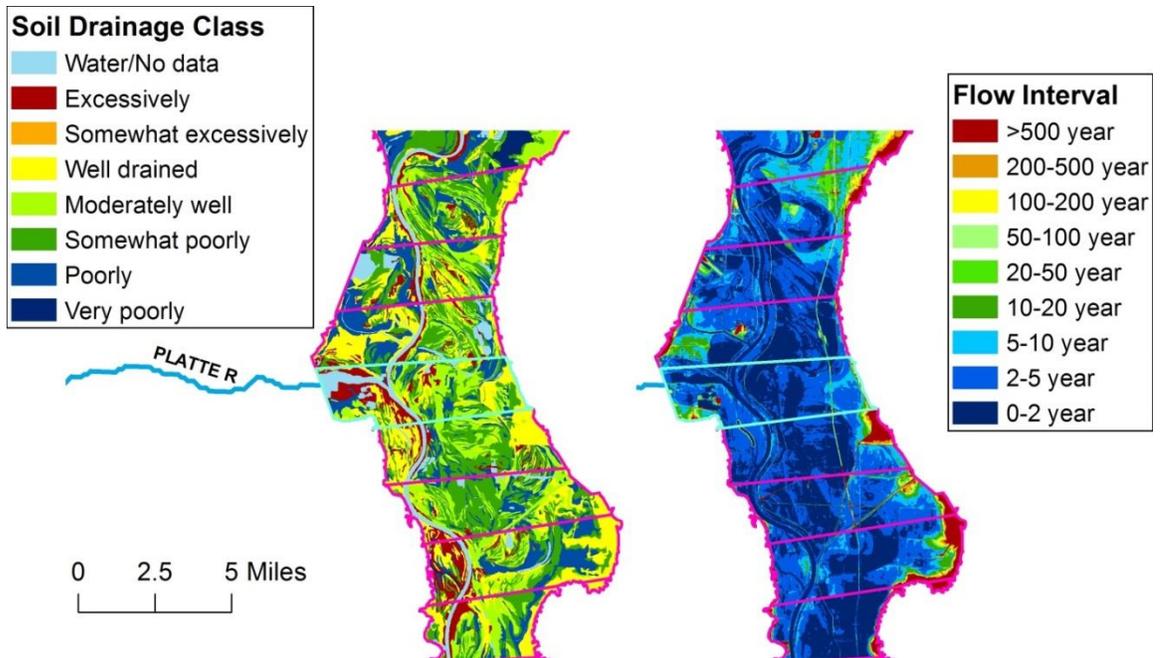


Figure 25. Soil drainage classes (left) and flow-return intervals (right) at the mouth of the Platte River (within the blue-highlighted valley cross-section).

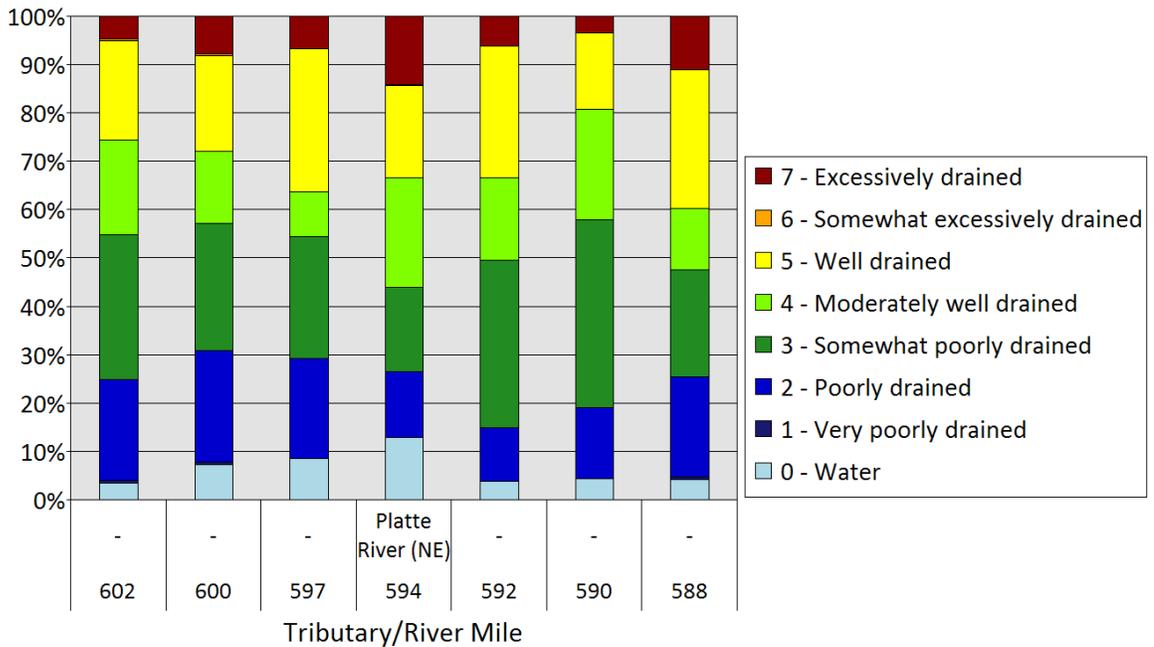


Figure 26. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Platte River.

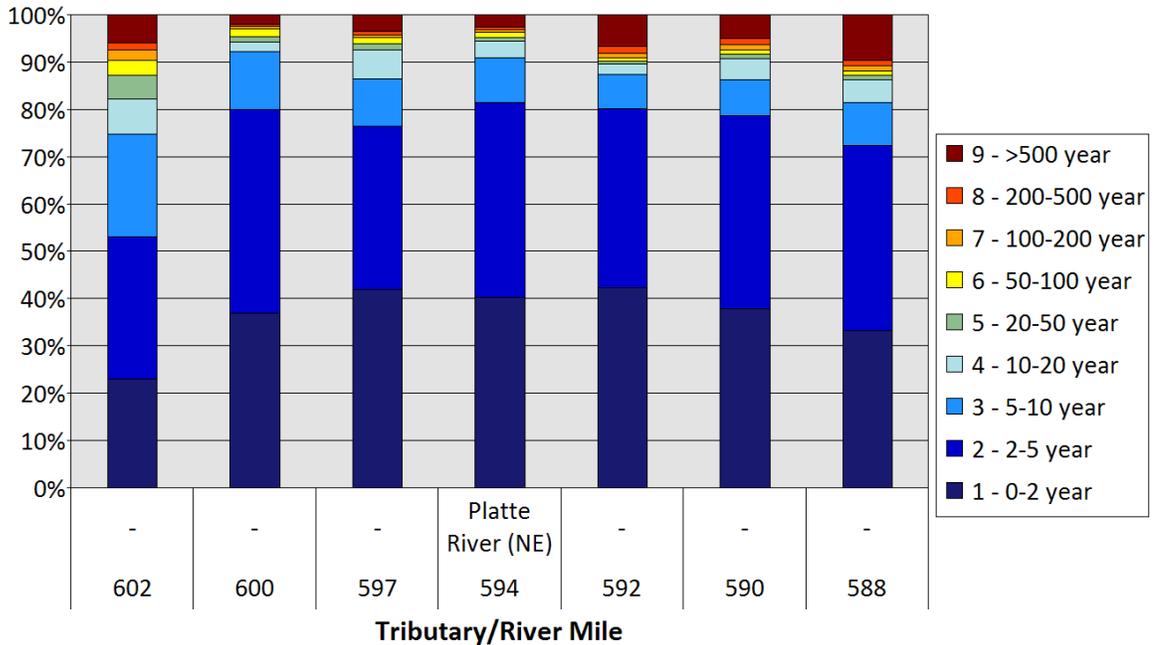


Figure 27. Relative area represented by flow-return intervals within valley cross-sections in proximity to the mouth of the Platte River.

The mouth of the Kansas River is somewhat anomalous among the streams examined here in that it occurs in close proximity to a transition from agriculture to urban lands at Kansas City, Missouri. A map of the mouth shows that the area of land represented by water or no data increases dramatically just below the mouth (Figure 28). By far, most of this increase includes urban lands and other human-modified soil types that have no functional drainage class (Figure 29). When these areas are excluded from analysis, soils with better drainage increase in relative area starting just upstream of the mouth and maintain elevated abundance below the mouth (Figure 30). There is an unequivocal reduction in dominance by lands with shorter flow-return intervals beginning with a large terrace on the south floodplain just upstream of the mouth of the Kansas and continuing downstream as a more diffuse increase in lands with longer flow-return intervals (Figure 28). The relative area of lands with flow-return intervals below 10 years decreases from almost 90 percent to less than 50 percent. The abundance of lands with longer flow-return intervals remains elevated for approximately 100 miles downstream.

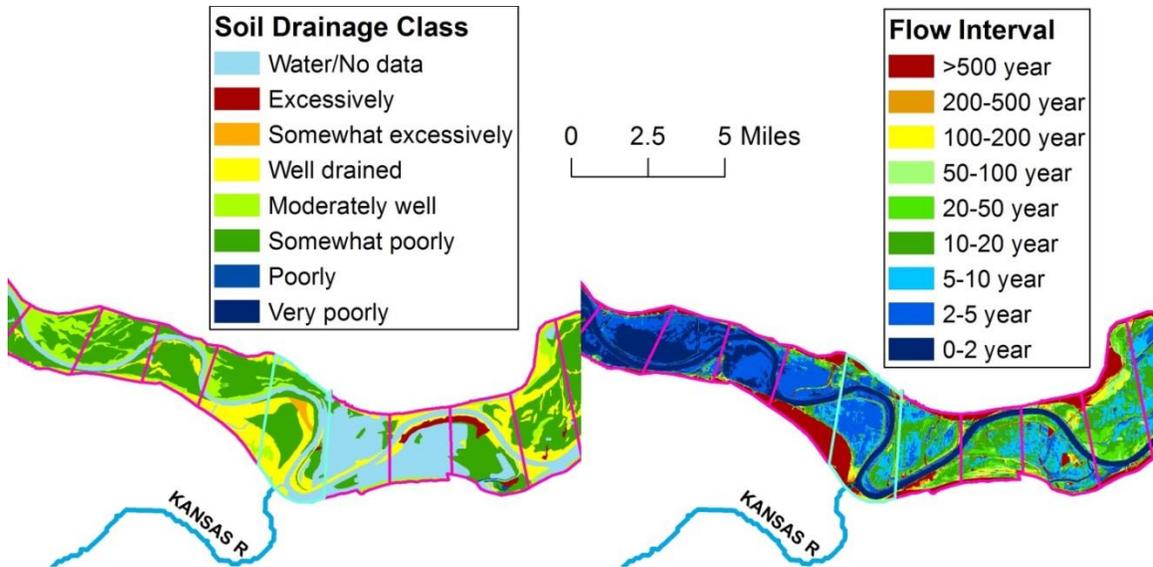


Figure 28. Soil drainage classes (left) and flow-return intervals (right) at the mouth of the Kansas River (within the blue-highlighted valley cross-section).

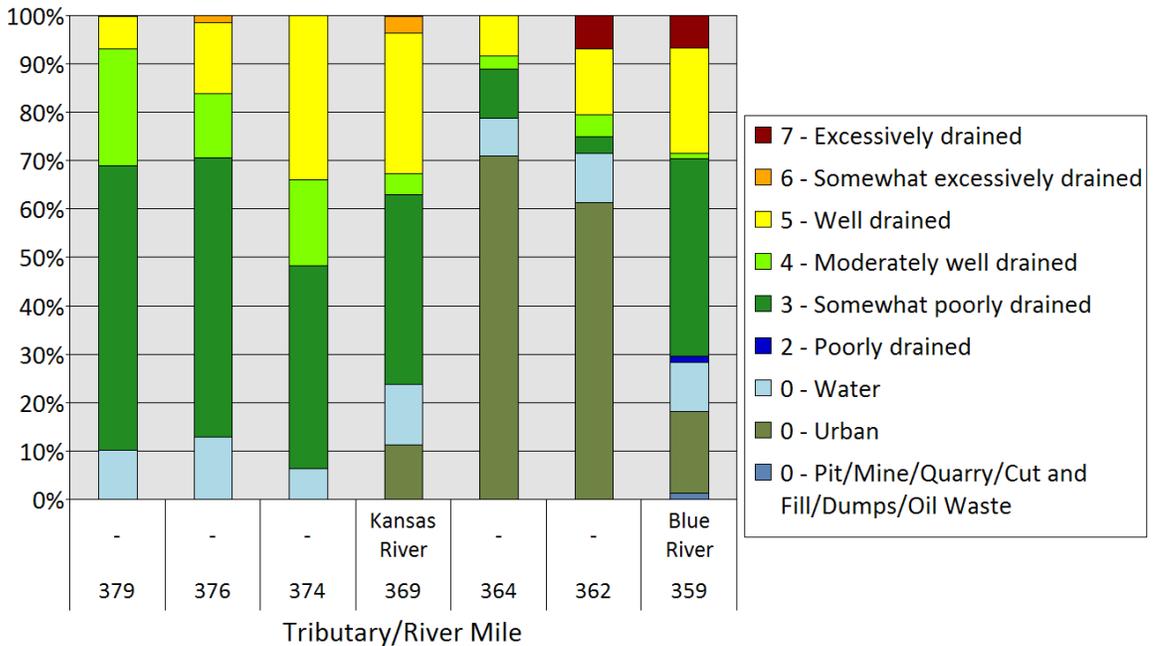


Figure 29. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Kansas River.

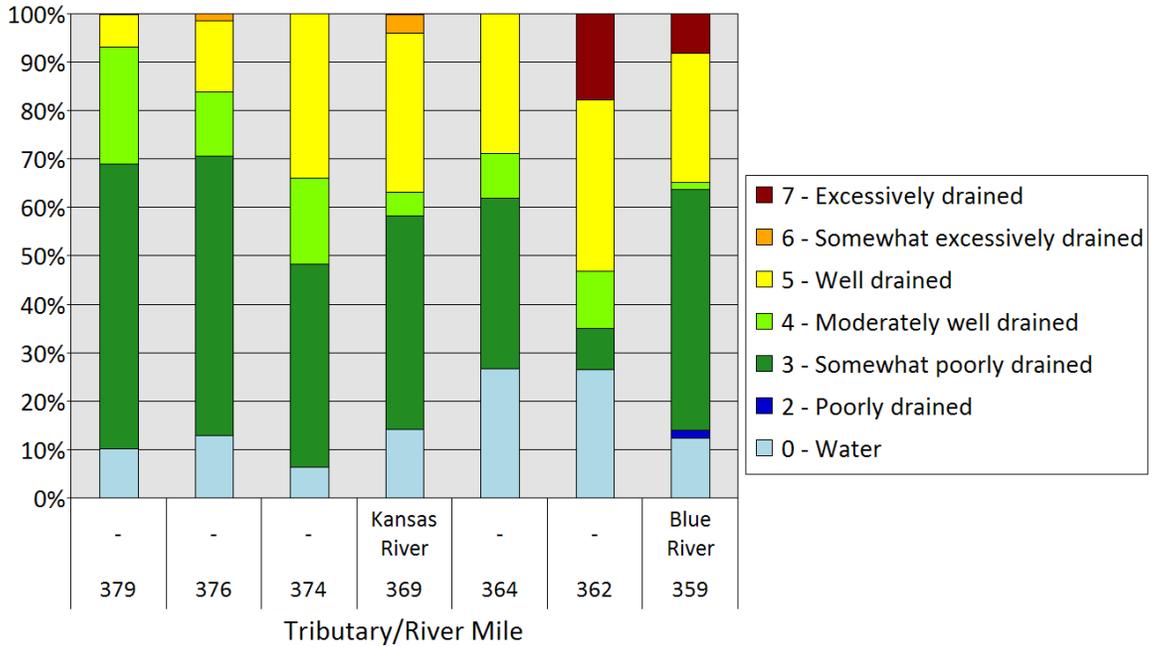


Figure 30. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Kansas River, excluding urban and other human-modified soil types.

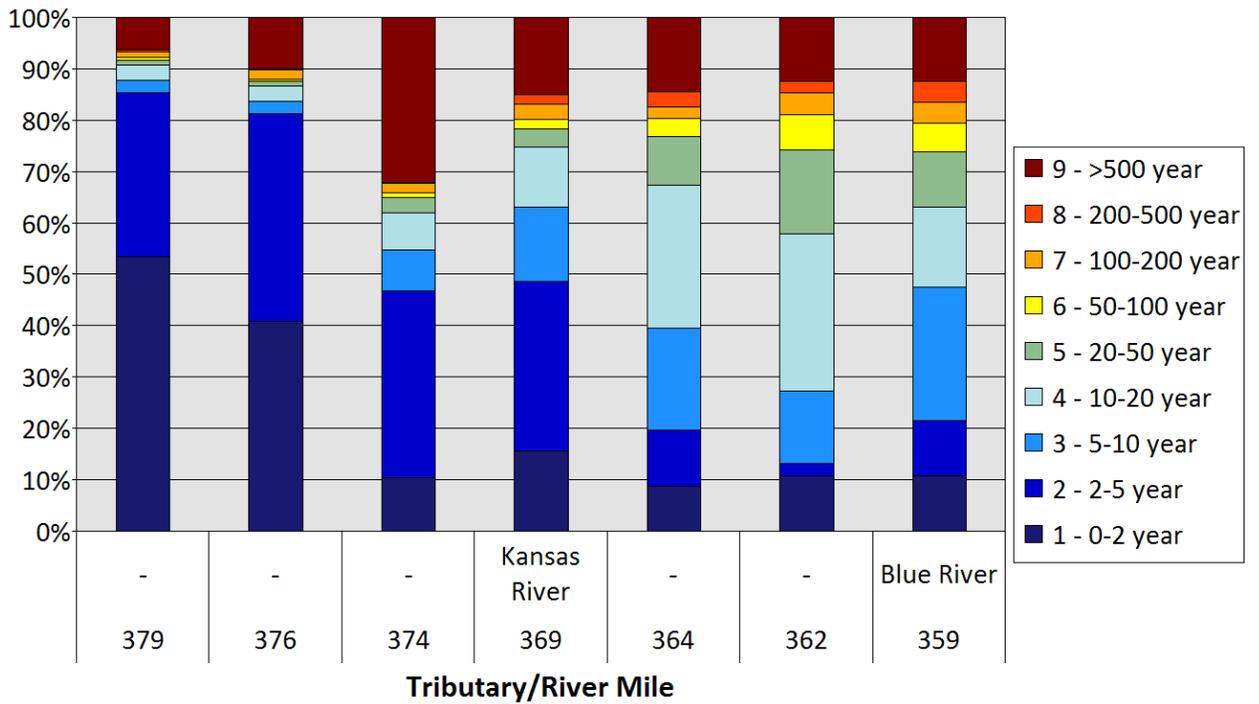


Figure 31. Relative area represented by flow-return intervals within valley cross-sections in proximity to the mouth of the Kansas River.

The Grand River is associated with a spatially limited increase in poorly and very poorly drained soils at the mouth, and an increase in well drained soils below it (Figure 32, Figure 33). The relative area with longer flow-return intervals also increases for a short distance downstream of the mouth (Figure 32, Figure 34). The soil drainage map (Figure 24, left) also captures the effects of the Chariton River entering the valley. Like the Grand River, this is associated with an increase in area represented by poorly drained soils types.

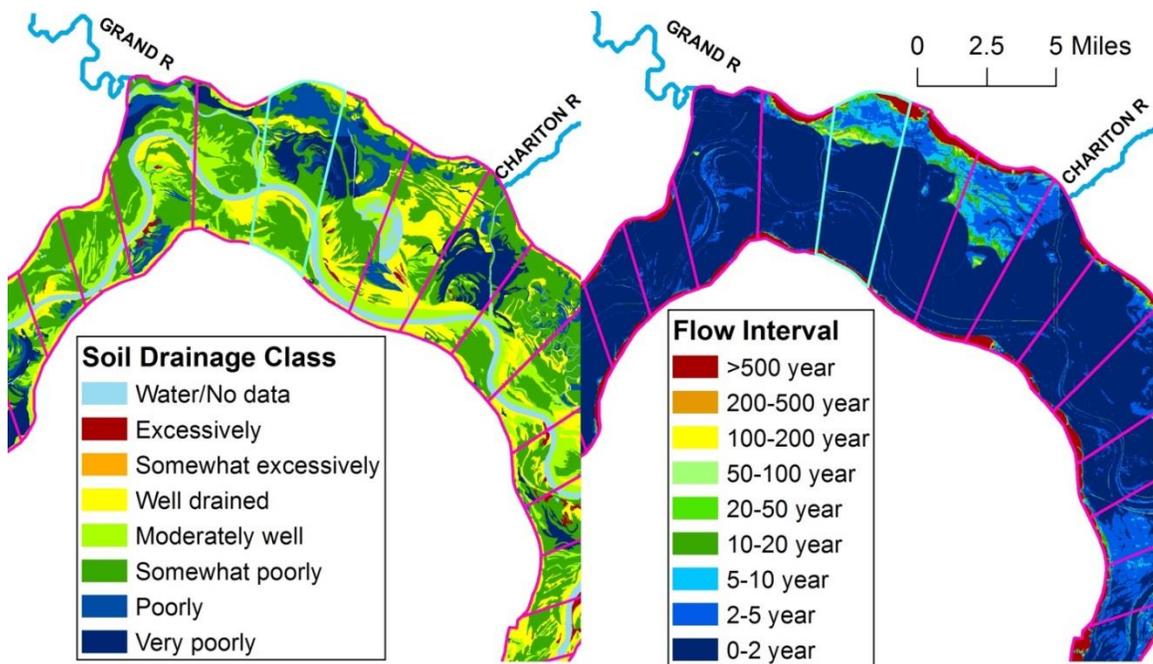


Figure 32. Soil drainage classes (left) and flow-return intervals (right) at the mouth of the Grand River (within the blue-highlighted valley cross-section).

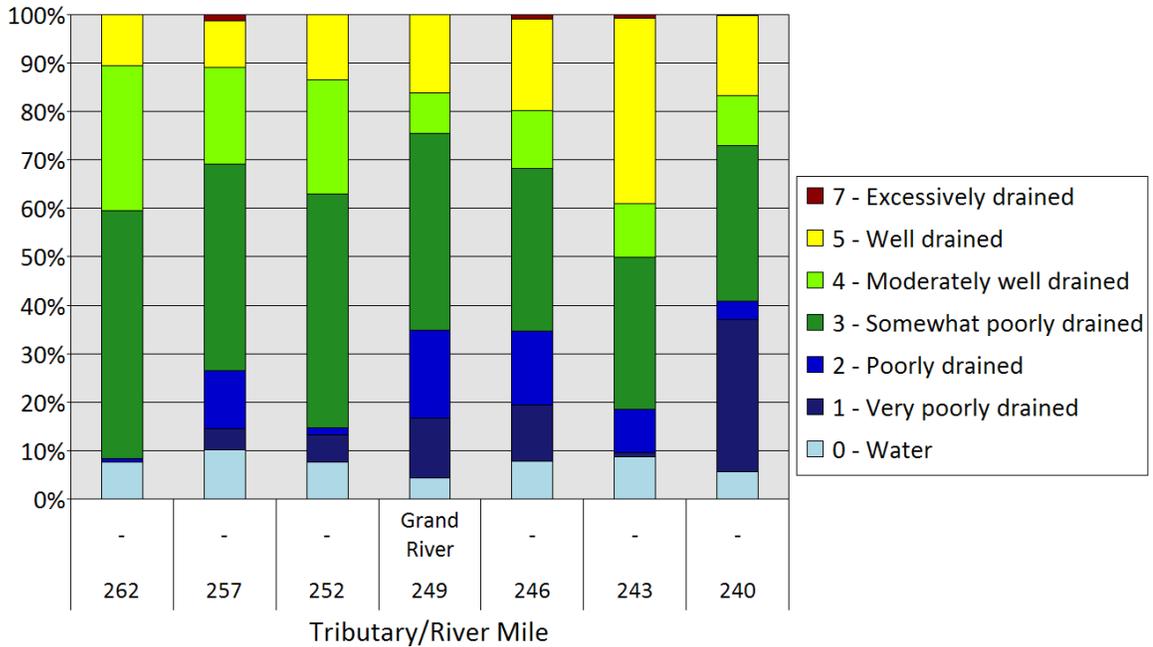


Figure 33. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Grand River.

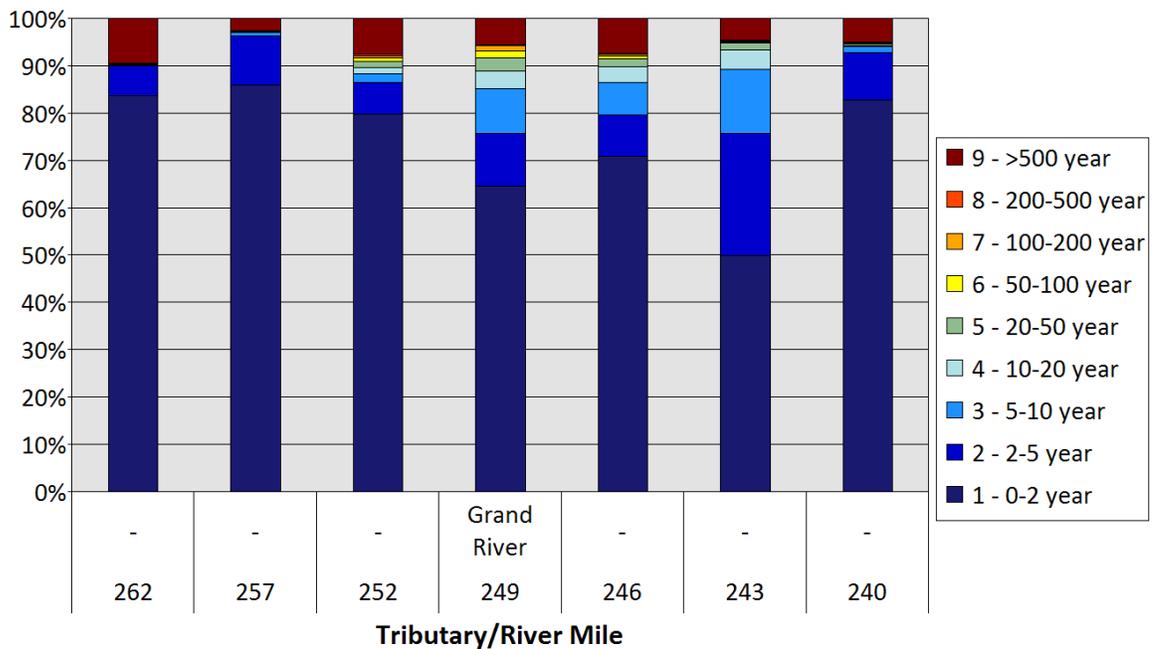


Figure 34. Relative area represented by flow-return intervals within valley cross-sections in proximity to the mouth of the Grand River.

The mouth of the Osage is associated with a shift toward drier conditions, with better drained soils and a reduction in dominance by the lands with short flow-return intervals (Figure 35). There is a slight but persistent increase in the relative abundance of soils that are well drained or better, offset by a decrease in the most poorly drained soil classes (Figure 36). There is a large drop in relative area with flow-return intervals less than 10 years, from above 90 percent to about 63 percent (Figure 37). Collectively, these higher lands return to their previous dominance within a few miles downstream of the mouth, although the area with flow-return intervals below 2 years remains depressed for a greater distance downstream (Figure 37).

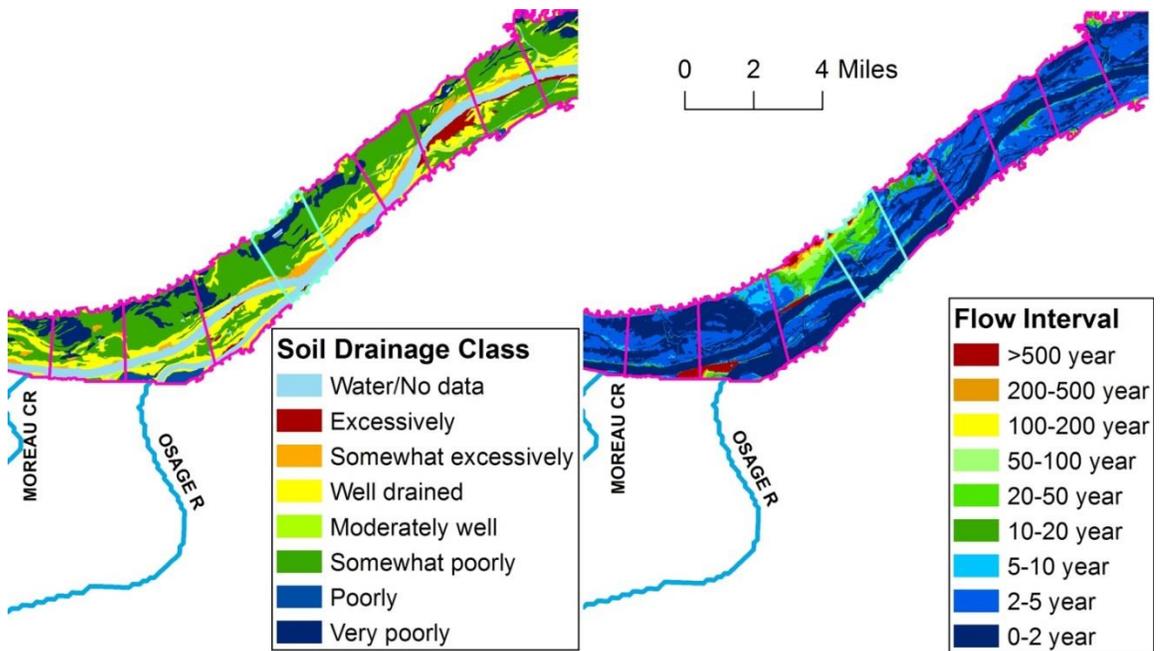


Figure 35. Soil drainage classes (left) and flow-return intervals (right) at the mouth of the Osage River (within the blue-highlighted valley cross-section).

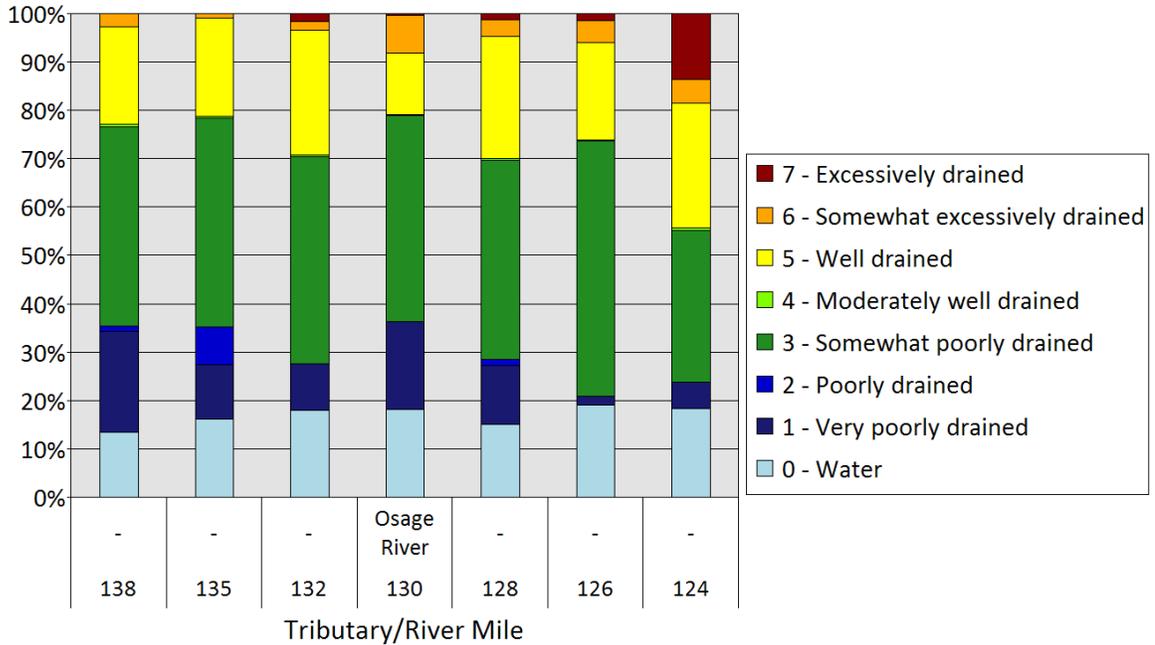


Figure 36. Relative area represented by soil drainage classes within valley cross-sections in proximity to the mouth of the Osage River.

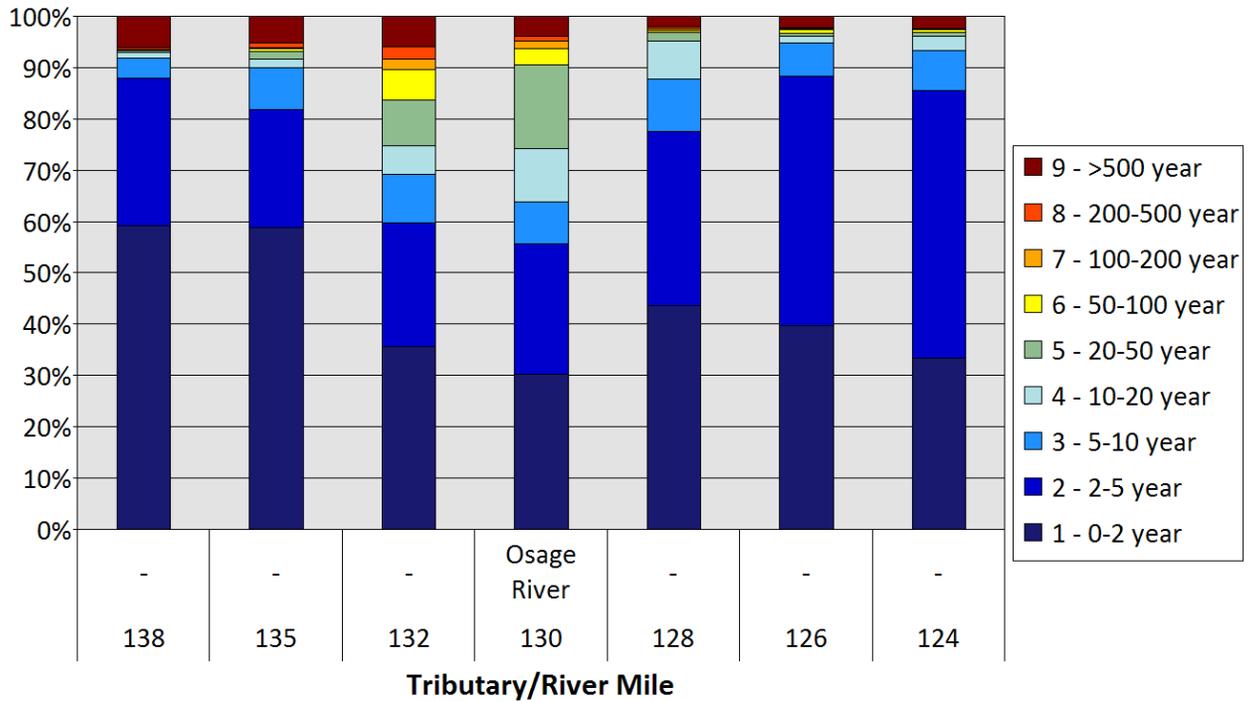


Figure 37. Relative area represented by flow-return intervals within valley cross-sections in proximity to the mouth of the Osage River.

The area-weighted wetness indices allow assessments of the relationships between LCPI class abundance and tributaries regardless of variation in the dominant conditions upstream of each. Of the five tributaries examined above, all of them except the Platte River are associated with an increase in area with longer flow-return intervals (Figure 38). The magnitude of change is greatest for the Kansas River, for which the Flow-return Interval Index more than doubles from 2.1 to approximately 4.5, indicating a shift in area weighted mean flow-return interval from approximately 5 years to 20 years. Flow-return interval index increases from 7.4 to 9.8 (indicating a shift in area-weighted mean flow return intervals from approximately 150 years to longer than 300 years) near the Big Sioux and from 2 to 3 (from 5 years to 10 years) at the Osage River. The elevated Flow-return Interval Index values persist well below the Kansas River and the Big Sioux River, but do not extend far downstream from the Osage River. The Flow-return Interval Index decreases from 3.7 to 2 in association with the mouth of the Platte, corresponding to a decrease in area-weighted mean flow-return interval from about 20 years to about 5 years; the Flow-Return Interval Index recovers somewhat at the downstream end of the analyzed area.

For all five major tributaries except the Grand River, soil drainage capacity increases from above the mouth to below (Figure 39). The largest magnitude increases corresponding to an improvement in soil drainage by one class (for example from poorly drained soils to somewhat poorly drained soil) are associated with the Kansas River and Osage River; increases at both tributaries persist downstream. Although there is a large increase two cross-sections below the mouth of the Grand River, soil drainage capacity shows a clear downward trend from approximately 3.5 upstream of the mouth to approximate 2.5 downstream (a shift of one soil drainage class). In general, Soil Drainage Index values around the mouths of tributaries are more erratic than are Flow-return Interval Index values.

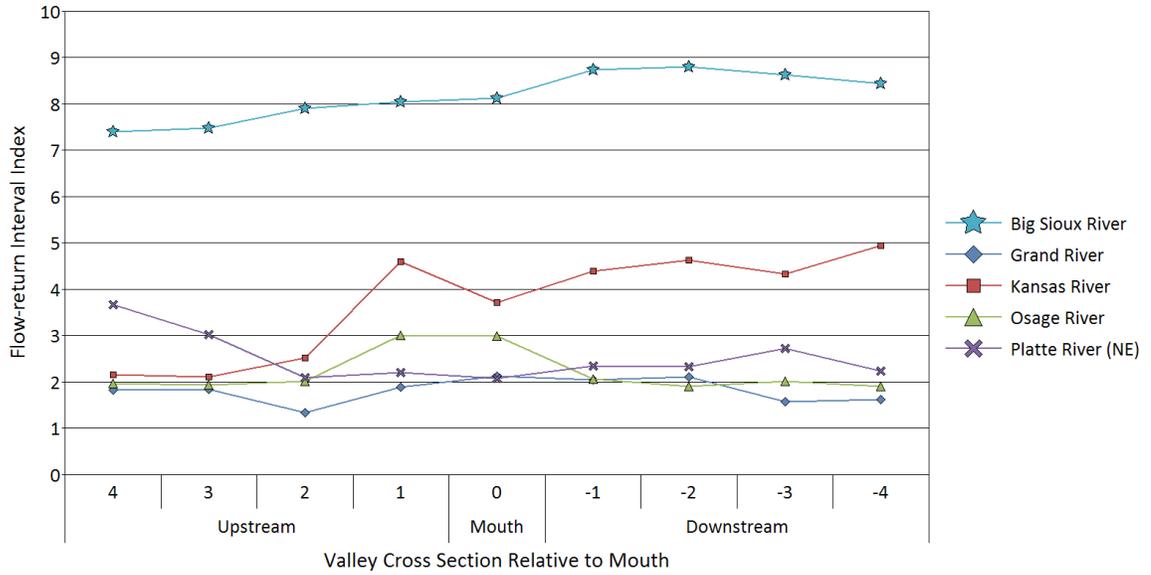


Figure 38. Comparison of changes in Flow-return Interval Index associated with the mouths of 5 major tributaries of the Missouri River.

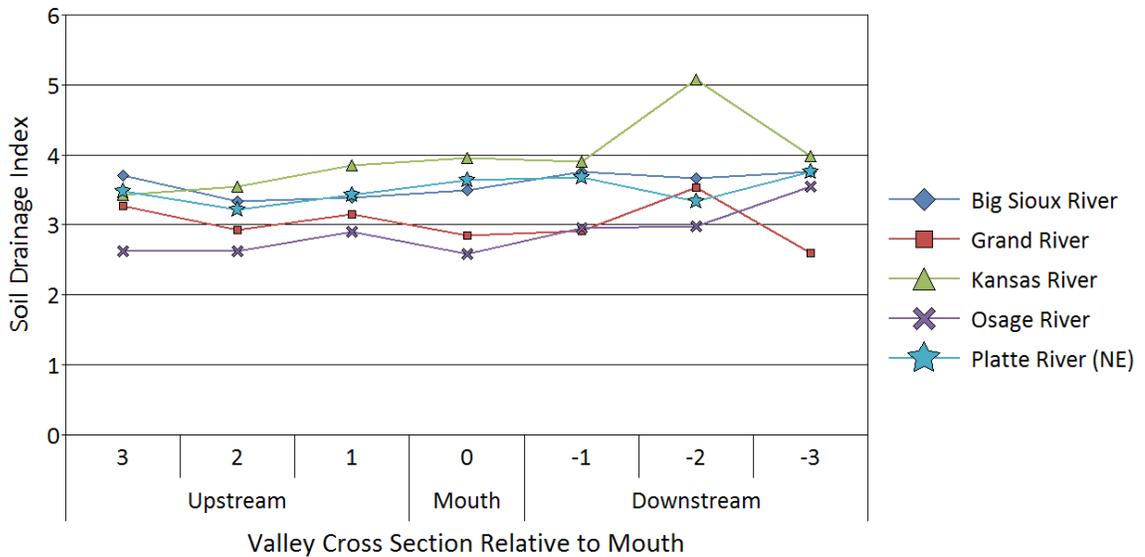


Figure 39. Comparison of changes in Soil Drainage Index associated with the mouths of 5 major tributaries of the Missouri River.

Examination of the effect of tributaries on soil drainage and flow-return interval indicates minor differences depending on the area drained by tributaries. Tributaries from the Northern Plains, Central

Plains, and Ozark Highlands are associated with local increases in areas with infrequent flows, with effects in the Northern plains being somewhat more persistent downstream; a similar trend is not evident for tributaries draining the Western Prairies (Figure 40). The mouths of tributaries draining the Northern Plains and Western Prairies are associated with local increases in soil drainage capacity; tributaries from the Ozark Highlands are associated with diminished local soil drainage capacity (Figure 40). When examined at the Ecological Province, streams draining the Central Interior Broadleaf Forest Province (incorporating Ozark Highland streams) are associated with a large magnitude local reduction in soil drainage capacity (Figure 41); tributaries from the Prairie Parkland Province (incorporating all other tributaries) are associated with a slight increase in drainage capacity. Tributaries from both ecological provinces are associated with large local increases in flow-return intervals, but values return to levels comparable to those upstream within a short distance of the mouth (Figure 41).

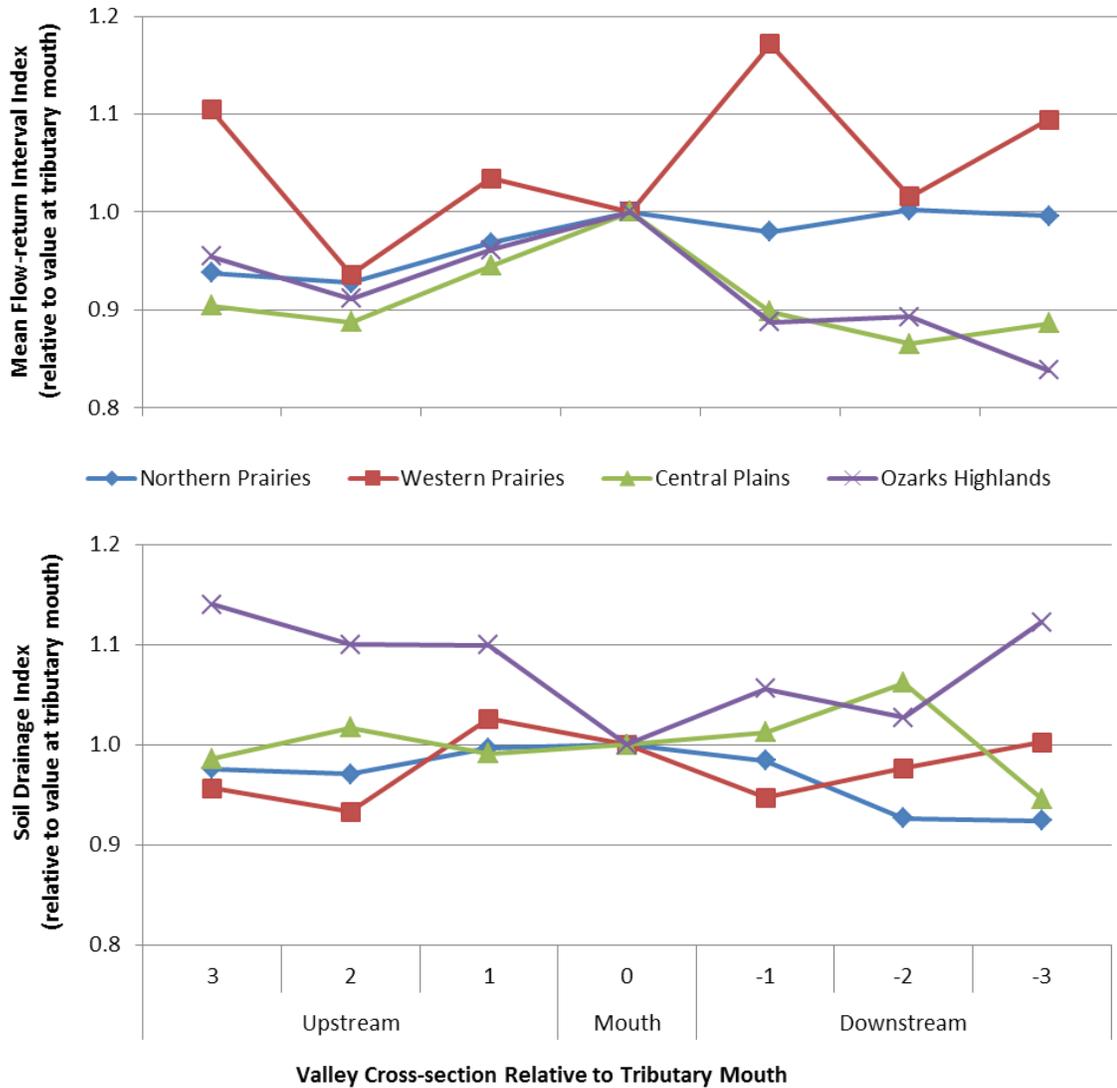


Figure 40. Mean Flow-return Interval Index and mean Soil Drainage Index for tributaries (bottom) draining four ecological regions.

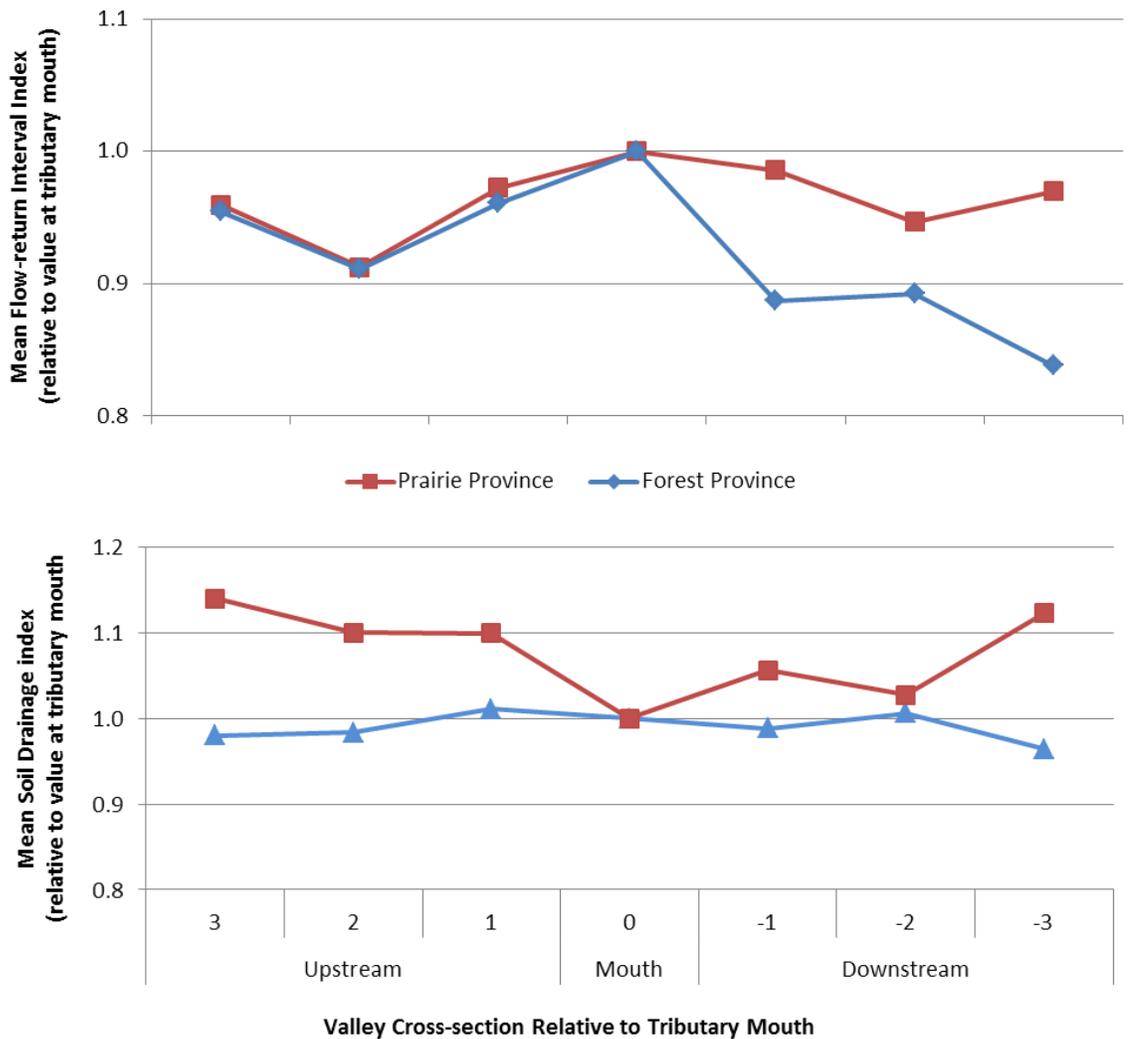


Figure 41. Mean Flow-return Interval Index and mean Soil Drainage Index for tributaries (bottom) draining four ecological regions.

Potential future LCPI class abundance

All sections of the river show a shift toward increased likelihood of overland flow during any particular year, a pattern consistent with higher water surface elevations for each flow-return interval class resulting from projected increases in discharge (Table 10, Figure 42). The largest increases in relative area tend to occur in the 0 to 2 year class, reflecting the fact that this class can only expand in area as water elevations associated with each return interval rise (Table 10). For the same reason, the area represented by the greater than 500 year flow class decreases in all segments; however, the reduction is not uniform

through the study area. For example, the Ponca, Sioux, and Kansas sections exhibit an expansion of area in the frequently flooded classes primarily at the expense the greater than 500 year class; in other sections of the river, the expansion of area with shorter return intervals is accompanied by a reduction in area for middle classes and a more limited reduction in area for the longest flow interval class.

The effects of climat change induced alteration of flow regime on LCPI class abundance are examined in closer detail for three sections of the river. In the Gavins section, the land area with flow return intervals greater than 500 years is expected to decrease by nearly 3,000 hectares; all other flow-return intervals (except the 5 to 10 year interval) are expected to increase in area (Table 10). Most of this change is limited to the active channel (Osterkamp and Hupp, 1984) immediately adjacent to the Missouri River flowing along the south edge of the valley and Clay Creek flowing along the north edge (Figure 43). Within the Grand Stable-aggrading segment of the river, only the 0 to 2 year flow-return interval is expected to increase in area; most of that increase is offset by reductions in area for other flow-return intervals lass than 20 years (Table 10). By contrast, in the Sioux Stable aggrading section,increased area for flow returns less than 2 years is offset by reductions across a broader range of flow-return intervals.

Table 10. Area (ha) of land represented by each LCPI flow-return interval class in tributary-defined sections (Chojnacki et al., 2012) and geomorphological zones (Jacobson et al., 2009) during the period of reservoir management (1967-2012) and as modeled based on anticipated future discharge patterns under climate change (2040-2069; Gangopadhyay et al., 2012), and the percent change between periods.

Values are not cumulative and exclude land area that would be inundated at river stages associated with shorter flow return intervals.

Tributary section	Geomorphological zone	Area (ha)														
		0-2 year			2-5 year			5-10 year			10-20 year			20-50 year		
		1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change
Gavins	Incising 1a	6,618	7,068	6.79	780	938	20.31	159	120	-24.49	289	319	10.53	449	778	73.25
Ponca	Incising 1b	1,339	1,585	18.32	576	1,369	137.94	324	237	-26.65	557	538	-3.39	909	1,381	51.90
Sioux	Incising 1b	3,522	4,782	35.80	2,932	4,107	40.10	4,233	7,759	83.30	6,198	9,663	55.90	11,899	13,361	12.29
Sioux	Stable-aggrading 1	12,918	22,968	77.80	21,944	23,019	4.90	28,042	27,653	-1.39	7,632	7,378	-3.33	10,655	9,961	-6.51
Platte	Stable-aggrading 1	70,241	88,767	26.38	29,994	14,990	-50.02	5,554	4,172	-24.88	2,757	2,281	-17.28	1,122	949	-15.41
Platte	Incising 2	40,648	58,509	43.94	30,525	18,240	-40.25	7,740	5,947	-23.16	4,647	3,398	-26.88	3,231	2,660	-17.67
Kansas	Incising 2	10,036	15,486	54.31	15,405	19,165	24.41	12,406	13,027	5.01	10,996	7,534	-31.49	7,711	4,698	-39.07
Kansas	Stable-aggrading 2	40,799	46,209	13.26	8,366	4,967	-40.62	1,831	1,821	-0.55	1,515	1,172	-22.63	1,494	997	-33.26
Grand	Stable-aggrading 2	21,577	24,485	13.48	6,588	5,295	-19.62	2,509	1,626	-35.21	900	501	-44.39	437	300	-31.31
Grand	Incising 3	15,763	23,494	49.05	16,032	11,579	-27.78	3,795	1,748	-53.93	1,270	810	-36.17	865	519	-39.95
Osage	Incising 3	49,744	69,542	39.80	33,870	18,608	-45.06	5,495	3,032	-44.81	2,590	1,890	-27.02	1,531	1,340	-12.50

Tributary section	Geomorphological zone	Area (ha)											
		50-100 year			100-200 year			200-500 year			>500 year		
		1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change	1967-2012	2040-2069	% Change
Gavins	Incising 1a	886	999	12.74	944	1,270	34.49	1,991	3,156	58.53	79,057	76,003	-3.86
Ponca	Incising 1b	1,383	1,938	40.10	1,699	2,726	60.44	3,544	4,163	17.48	24,848	21,243	-14.51
Sioux	Incising 1b	13,899	15,074	8.45	11,093	12,726	14.72	14,757	12,944	-12.28	113,682	101,798	-10.45
Sioux	Stable-aggrading 1	11,396	11,913	4.54	10,428	8,180	-21.56	7,783	7,263	-6.68	33,657	26,122	-22.39
Platte	Stable-aggrading 1	1,195	946	-20.86	932	815	-12.56	1,049	911	-13.17	11,442	7,809	-31.75
Platte	Incising 2	1,766	1,175	-33.44	1,062	696	-34.51	828	656	-20.80	6,836	6,012	-12.06
Kansas	Incising 2	3,032	2,372	-21.79	2,290	2,119	-7.47	2,699	2,421	-10.30	11,494	9,249	-19.54
Kansas	Stable-aggrading 2	696	448	-35.62	541	261	-51.76	438	138	-68.41	2,437	2,104	-13.66
Grand	Stable-aggrading 2	172	118	-31.22	119	78	-34.43	95	72	-23.72	2,499	2,420	-3.16
Grand	Incising 3	367	223	-39.21%	220	177	-19.19%	248	174	-30.05%	1,874	1,713	-8.58%
Osage	Incising 3	780	509	-34.75%	556	315	-43.26%	373	308	-17.47%	6,941	6,343	-8.61%

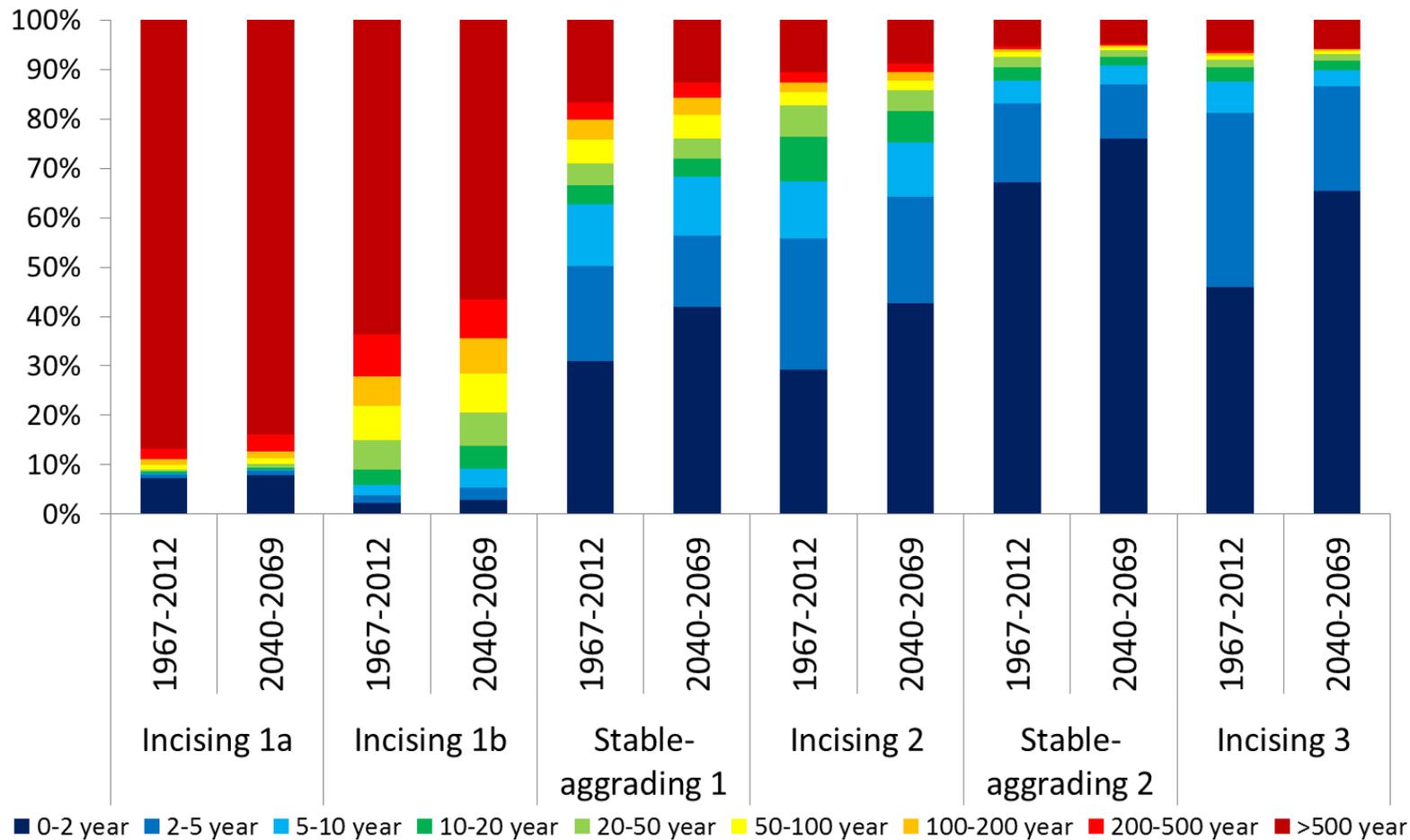


Figure 42. Bar graph of the relative abundance of LCPI flow-return intervals illustrating a shift toward more frequent flooding between the flow regime under dam management (1967-2006) and the flow regime based on modeled future changes in discharge resulting from climate change (2040-2069) (Gangopadhyay et al., 2012).

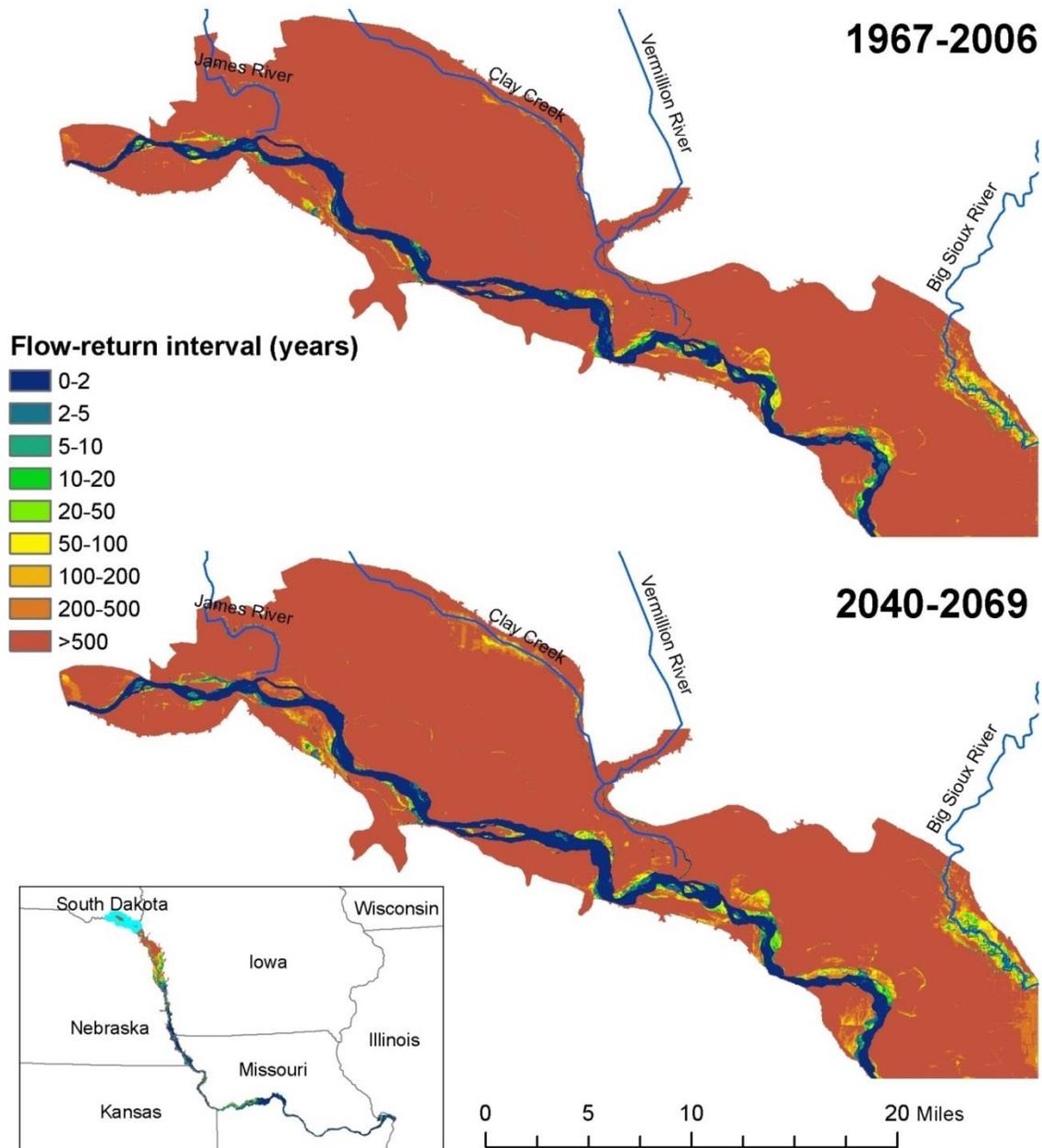


Figure 43. Comparison of LCPI flow-return interval class distribution between the period of reservoir management (1967-2006) and as modeled based on anticipated future discharge patterns under climate change (2040-2069; Gangopadhyay et al., 2012) for the Gavins, Incising 1a section of the Missouri River (highlighted in inset).

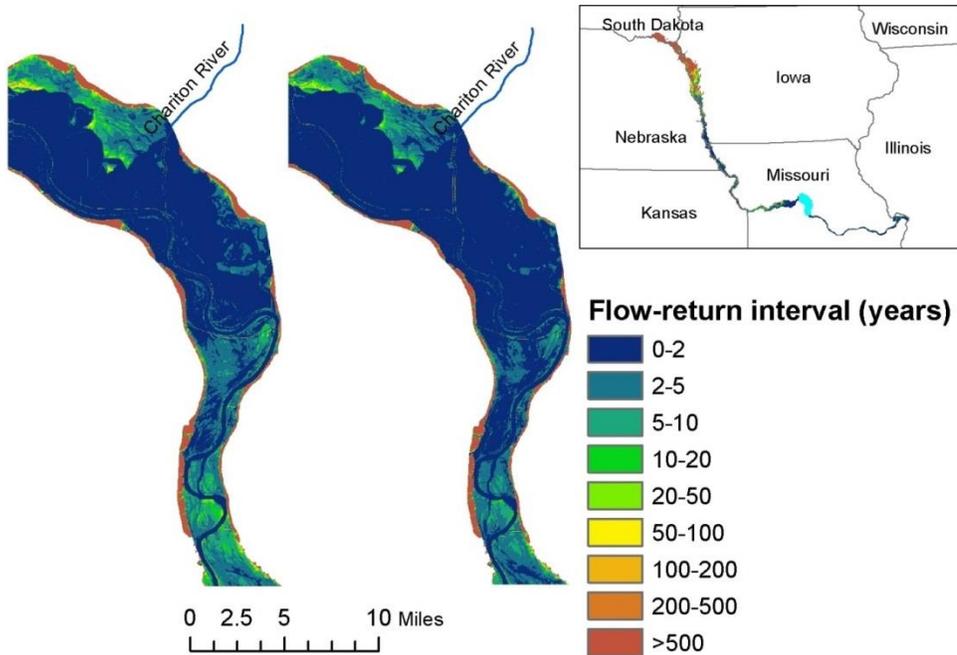


Figure 44. Comparison of LCPI flow-return interval class distribution between the period of reservoir management (1967-2006; left) and as modeled based on anticipated future discharge patterns under climate change (2040-2069; right; Gangopadhyay et al., 2012) for the Grand, Stable-aggrading 2 section of the Missouri River (highlighted in inset).

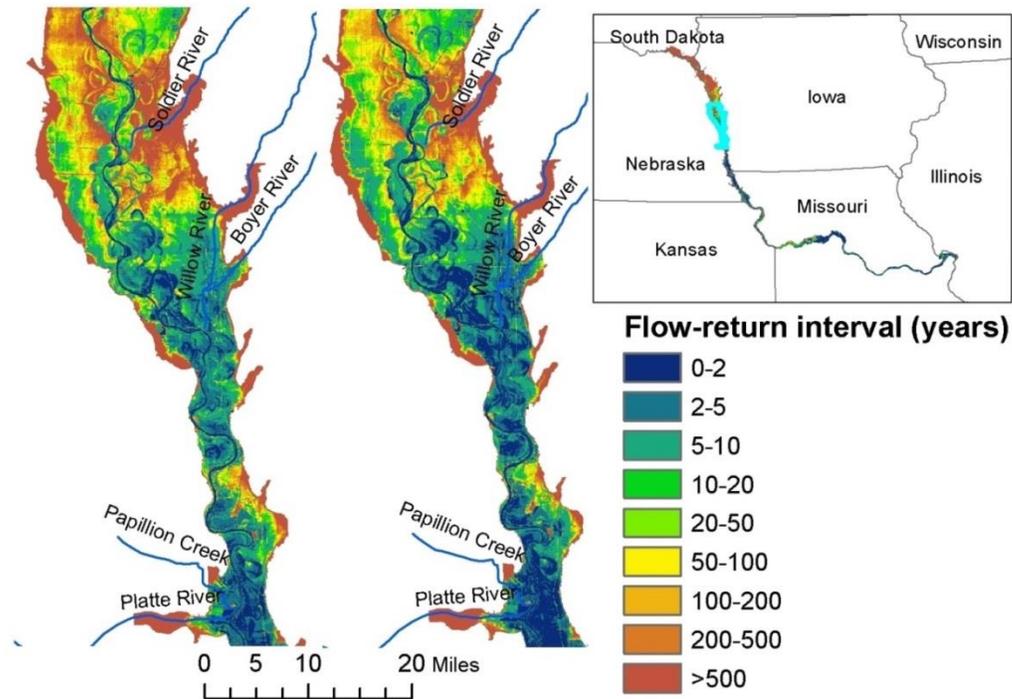


Figure 45. Comparison of LCPI flow-return interval class distribution between the period of reservoir management (1967-2006; left) and as modeled based on anticipated future discharge patterns under climate change (2040-2069; right; Gangopadhyay et al., 2012) for the Sioux, Stable-aggrading 1 section of the Missouri River (highlighted in inset).

Variation in groundwater processes by soil drainage classes

Forest City summary

At Forest City, data were collected from February 7, 2012 to October 25, 2013 (Figure 46). No shallow wells recorded any fluctuations attributable to flow events; all of the Forest City results that follow pertain to deep wells only. The sensor used to measure barometric pressure demonstrated fluctuations that were not attributable to changes in atmospheric pressure throughout the study period, suggesting a malfunction of unknown type. Therefore, data from shallow well FC11 were used to adjust data from other wells for barometric pressure (this sensor showed no variation in readings that could be attributed to inundation and showed fluctuations consistent with barometric readings obtainable from a nearby weather station in St. Joseph (University of Missouri Agricultural Extension, 2014). The sensor in well FC10 reached capacity on March 29, 2013 and those in wells FC11 and FC12 reached capacity on July 21, 2013; these sensors recorded no data until they were reset on August 5. There is a data gap for the sensor in well FC9 from June 26 to August 22, 2012 and periods of erratic readings from May 26 to June 26, 2012 and from June 3 to September 11, 2013; these time periods are excluded from analyses for that sensor.

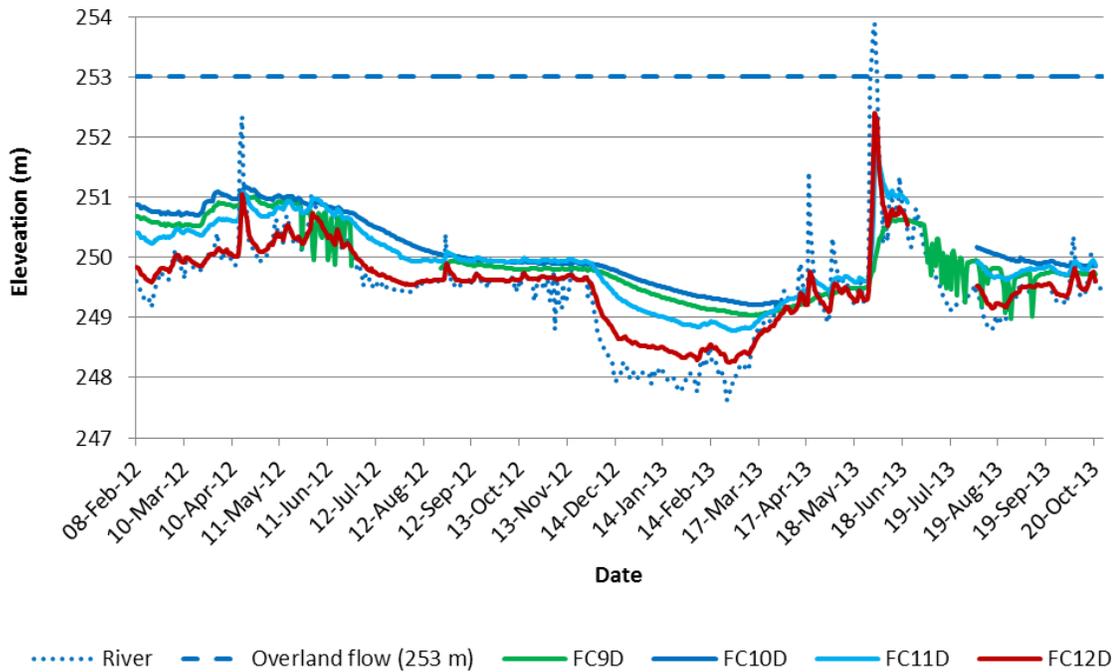


Figure 46. Average daily estimated river and groundwater elevation (m) for deep wells at the Forest City site relative to water surface elevation (253 m) at which overland flow cuts off wells FC11 and FC12 from the rest of the floodplain.

Thirteen discrete flow events were identified for analysis from the available data at Forest City (Table 11). Of these, maximum stage change exceeded 1 meter for 6 pulses and 2 meters for 2 pulses. The largest flow pulse approached 5 meters (May 25 to June 5, 2013), exceeding the estimated threshold at which overland flow cuts off wells FC11 and FC12 from the rest of the floodplain. Mean flow pulse magnitude was 1.41 m and mean pulse duration was 8.2 days.

Table 11. Summary groundwater data for 13 flow events selected for analyses at the Forest City, Missouri.

Pulse start date and time	Days from start to peak	Pulse duration (days)	Initial river elevation (m)	Peak river elevation (m)	Pulse magnitude (m)
4/14/12 22:00	1.04	9.583	250.067	252.874	2.806
5/5/12 21:00	2.88	3.333	250.184	250.652	0.468
5/13/12 12:00	1.67	7.917	250.173	250.739	0.565
5/25/12 03:00	6.42	17.125	250.107	251.129	1.022
8/23/12 17:00	2.88	7.833	249.577	250.529	0.952
10/13/12 05:00	2.25	7.375	249.584	249.852	0.267
2/5/13 12:00	2.88	4.792	247.732	248.309	0.578
4/9/13 00:00	4.04	8.167	249.158	250.029	0.870
4/17/13 04:00	1.21	6.250	249.163	251.622	2.459
5/1/13 21:00	1.75	7.500	248.892	250.439	1.547
5/25/13 19:00	5.25	10.833	249.257	254.129	4.871
10/2/13 14:00	3.92	8.875	249.211	250.416	1.205
10/14/13 12:00	4.13	7.458	249.411	250.075	0.664
Mean	3.10	8.23			1.41

A typical flood pulse at Forest City yielded the largest and most rapid GWRF response for FC12, a smaller and slightly slower maximum GWRF for FC11, and a muted and much delayed maximum GWRF for wells FC9 and FC10 (Figure 47). Comparison of mean maximum GWRF, mean lag ratio, and the mean exceedance ratios all show significant differences between wells (Table 12). Well FC12 had a significantly higher GWRF than all other wells, followed by wells FC11, FC9, and FC10; the latter two wells were not significantly different from each other. Also as predicted by previous GWRF simulations (Kelly, 2000), the ratio of well lag time to river lag time generally increased as a function of distance from the river; wells further from the river had a longer relative lag time than did wells closer to the river. One exception was well FC9, which had a slightly greater mean lag ratio than did well FC10, which was farther from the river; however, these differences were not significant.

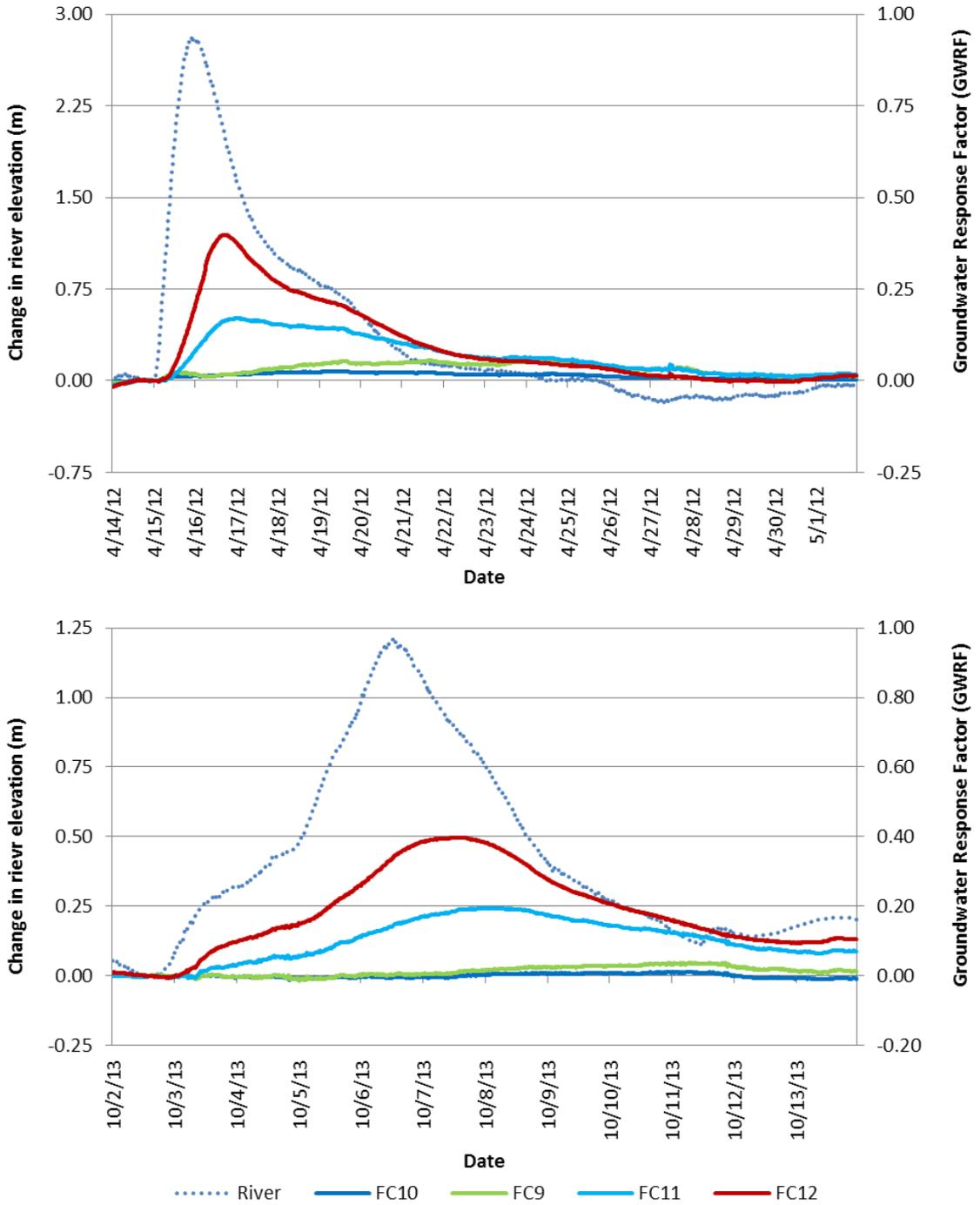


Figure 47. A large flow pulse from April, 2012 and a moderate flow pulse from October, 2013, with the typical pattern of GWRF for wells at Forest City, Missouri.

Table 12. Mean maximum groundwater response factor, lag ratio, and exceedance ratios for wells at Forest City, Missouri.

Values in the same column with different letters are significantly different (Analysis of Variance with *post hoc* Bonferroni multiple comparison test; $\alpha = 0.05$). No tests for differences were performed on 0.5 exceedance values.

Well	n	Mean Maximum Groundwater Response Factor (GWRF)	Mean Lag Ratio (Well start to peak time/ River start to peak time)	Mean 0.5 exceedance ratio (Days GWRF > 0.5/ pulse duration)	Mean 0.25 exceedance ratio (Days GWRF > 0.25/ pulse duration)	Mean 0.10 exceedance ratio (Days GWRF > 0.1/ pulse duration)
FC09	11	0.06 ^a	3.65 ^a	0.00	0.00 ^a	0.10 ^a
FC10	9	0.04 ^a	2.09 ^{ab}	0.00	0.00 ^a	0.09 ^a
FC11	13	0.21 ^b	1.67 ^b	0.00	0.11 ^a	0.61 ^b
FC12	13	0.41 ^c	1.41 ^b	0.02	0.47 ^b	0.83 ^b

Exceedance ratios decreased with distance from the river. Only one flood event elicited a maximum GWRF greater than 0.5, and this only in well FC12; accordingly, no test of differences between wells was performed for the 0.50 exceedance ratio. The mean 0.25 exceedance ratio for Well FC12 was significantly greater than for all other wells ($\alpha = 0.05$). The 0.25 exceedance threshold was surpassed following 12 flow pulses for well FC12, 3 pulses for well FC11, and no pulses for wells FC9 and FC10.

Mean 0.10 exceedance ratio also decreased with distance from the river, and wells FC12 and FC11 had significantly greater values than did wells FC9 and FC10 ($\alpha = 0.05$). For wells FC11 and FC12, this exceedance threshold was surpassed during all flow pulses except during the April 17, 2013 pulse for well FC11. The only flow pulse for which the 0.10 exceedance threshold was surpassed in wells FC9 and FC10 occurred on May 5, 2012. That event is unique in that it was associated with relatively extended durations above the 0.10 threshold for all wells, perhaps due to high antecedent soil moisture conditions resulting from an earlier flood pulse of more than 0.5 meters and a rain event exceeding one inch on May 3, according to precipitation data from a nearby weather station in St. Joseph (University of Missouri Agricultural Extension, 2014).

Overton summary

At Overton North, data were collected from February 8, 2012 to October 24, 2013. Of the unvented sensors used at wells OV1 and OV3 during the first few months of the study, only that from deep well OV1 recorded any change in water depth prior to their replacement on June 23, 2012 (the sensor in deep well 3 malfunctioned and those in the shallow wells were not deep enough to reach the groundwater).

On March 26, 2013, sensors at deep wells OV2, OV6, OV7, and OVTC reached capacity and failed to collect additional data until they were reset on August 6. This data gap spans the time period during which the highest river stages were recorded during this study. The shallow sensor at well OVTC has a similar gap between June 16 and August 6, 2013.

During the sampling period, 17 discrete flow pulses were identified for analyses from the available data (Figure 48, Table 13). Twelve pulses exceeding 1 meter were estimated based on stage at Booneville, Missouri. Of these, 7 pulses exceeded 2 meters and 1 exceeded 4 meters. Mean flow pulse was 1.7 m. Only two pulses exceeded the approximate threshold (175.4 m) at which flow is expected in the first constructed chute, across the floodplain to the Cottonwood Scour, or from the second constructed chute. The first, beginning April 17, 2013, induced groundwater elevation changes in both wells at OV1, the deep well at OV3, and the shallow well at OVTC. The second, on May 26, 2013, yielded obvious inflection points in the rate of water elevation change during both the rising and descending limbs of the flood pulse, as well as peak water elevations that were nearly simultaneous with that of the flow peak, suggesting that all wells were inundated. Therefore, because measured water depths in wells do not represent a groundwater response to flow pulse, this flow event is excluded from analyses comparing deep wells. Of the sensors placed in shallow wells, only those at wells OV1, OV3, and OVTC detected any rise that could be attributed to changes in river stage.

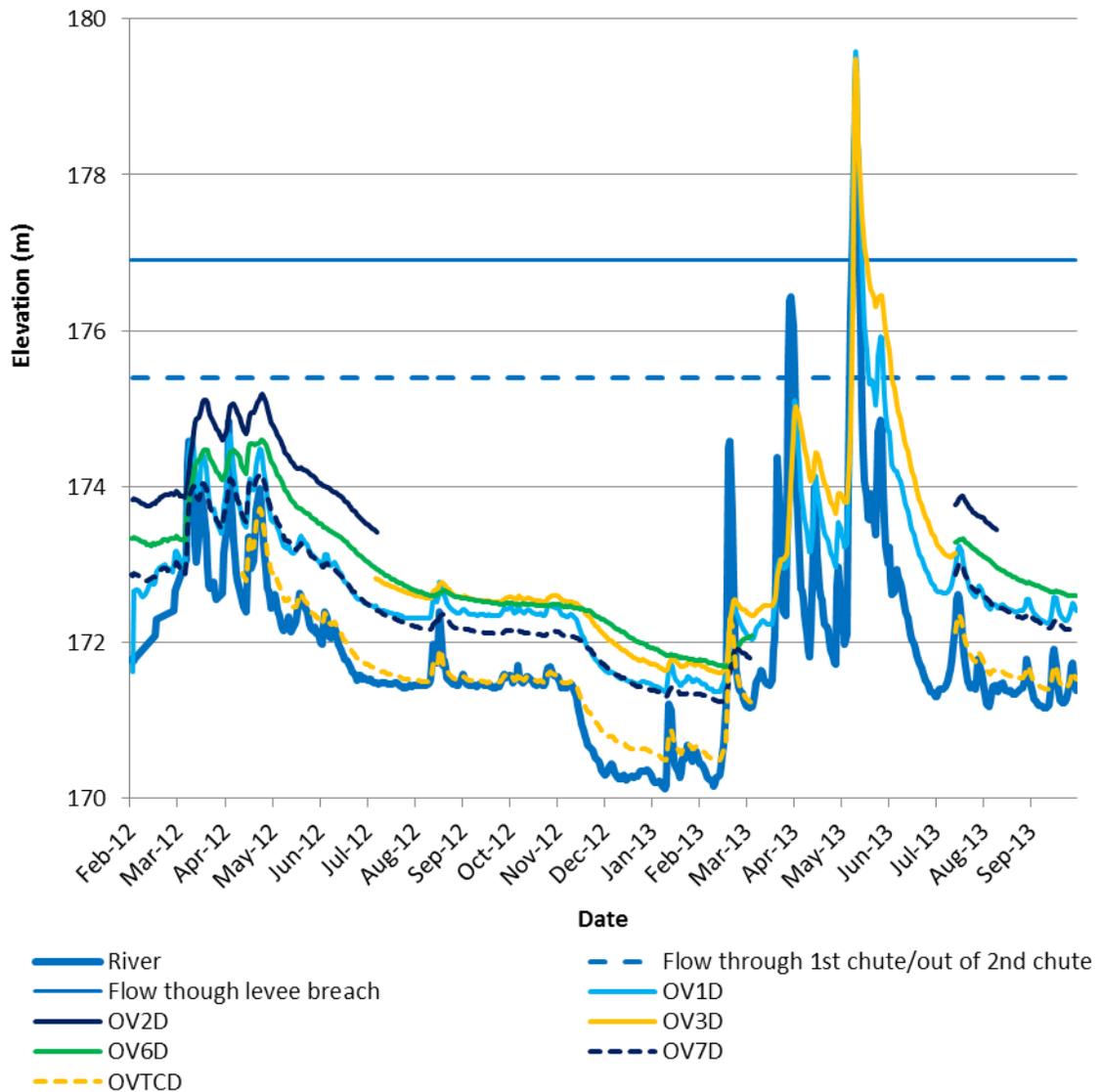


Figure 48. Average daily estimated river and groundwater elevation (m) for deep wells on the Big Muddy National Fish and Wildlife Refuge Overton North management unit, Missouri relative to water elevations at which overland flow occurs at chutes and the levee breach.
 Periods during which sensors were above groundwater elevation have been removed.

Table 13. Summary of groundwater data for 17 discreet flow events at Overton, Missouri.

Pulse start date and time	Days from start to peak	Pulse Duration (days)	Initial river elevation (m)	Peak river elevation (m)	Pulse magnitude (m)
3/19/12 12:00	3.50	8.50	172.023	174.633	2.610
4/13/12 12:00	4.50	15.50	172.369	174.909	2.540
4/29/12 2:30	2.93	4.54	172.380	173.447	1.067
5/3/12 15:30	4.90	9.02	172.840	174.023	1.183
8/28/12 6:00	2.02	3.41	171.505	172.033	0.527
9/1/12 2:30	2.32	4.48	171.676	172.463	0.786
11/10/12 17:30	3.35	11.41	171.445	171.694	0.250
1/29/13 8:30	2.31	9.67	170.113	171.304	1.192
3/8/13 13:45	3.28	18.42	170.686	174.849	4.164
4/17/13 22:00	2.84	12.61	172.283	176.559	4.276
5/3/13 14:00	3.08	14.23	171.795	174.066	2.271
5/26/13 21:15*	6.74	15.39	171.780	178.702	6.922
6/15/13 20:30	3.18	6.36	173.331	174.938	1.606
6/23/13 18:00	0.58	1.43	172.925	173.333	0.408
9/18/13 4:00	4.29	7.78	171.390	171.832	0.442
10/6/13 8:15	3.82	8.43	171.182	171.957	0.774
10/18/13 0:00	4.00	6.60	171.258	171.760	0.502
Mean	3.39	9.28			1.854

* excluded from analysis because all wells were inundated/

A typical flood pulse at Overton yielded the largest and most rapid GWRF response for OV1 and OVTC, smaller and slower responses from OV2, OV3 and OV7, and a muted and much delayed maximum GWRF for OV6 (Figure 49). Maximum GWRF decreased with distance from the river, and wells OV1D and OVTC had significantly greater maximum GWRF than all other wells ($\alpha = 0.05$). Lag ratios also increased with distance from the river, and wells OV1D and OVTC had significantly smaller lag ratios than well 6D ($\alpha = 0.05$). Exceedance ratios decreased with distance from the river (Table 14). The two wells closest to the river, OV1D and OVTC, were the only wells to experience periods during which GWRF exceeded 0.5. At well OV1D, mean 0.5 exceedance ratio was significantly greater than ratios at wells OV6D and OV7D ($\alpha = 0.05$). Wells OV1D and OVTC also had the greatest 0.25 and 0.10 exceedance ratios, with significantly larger values than well OV6D ($\alpha = 0.05$).

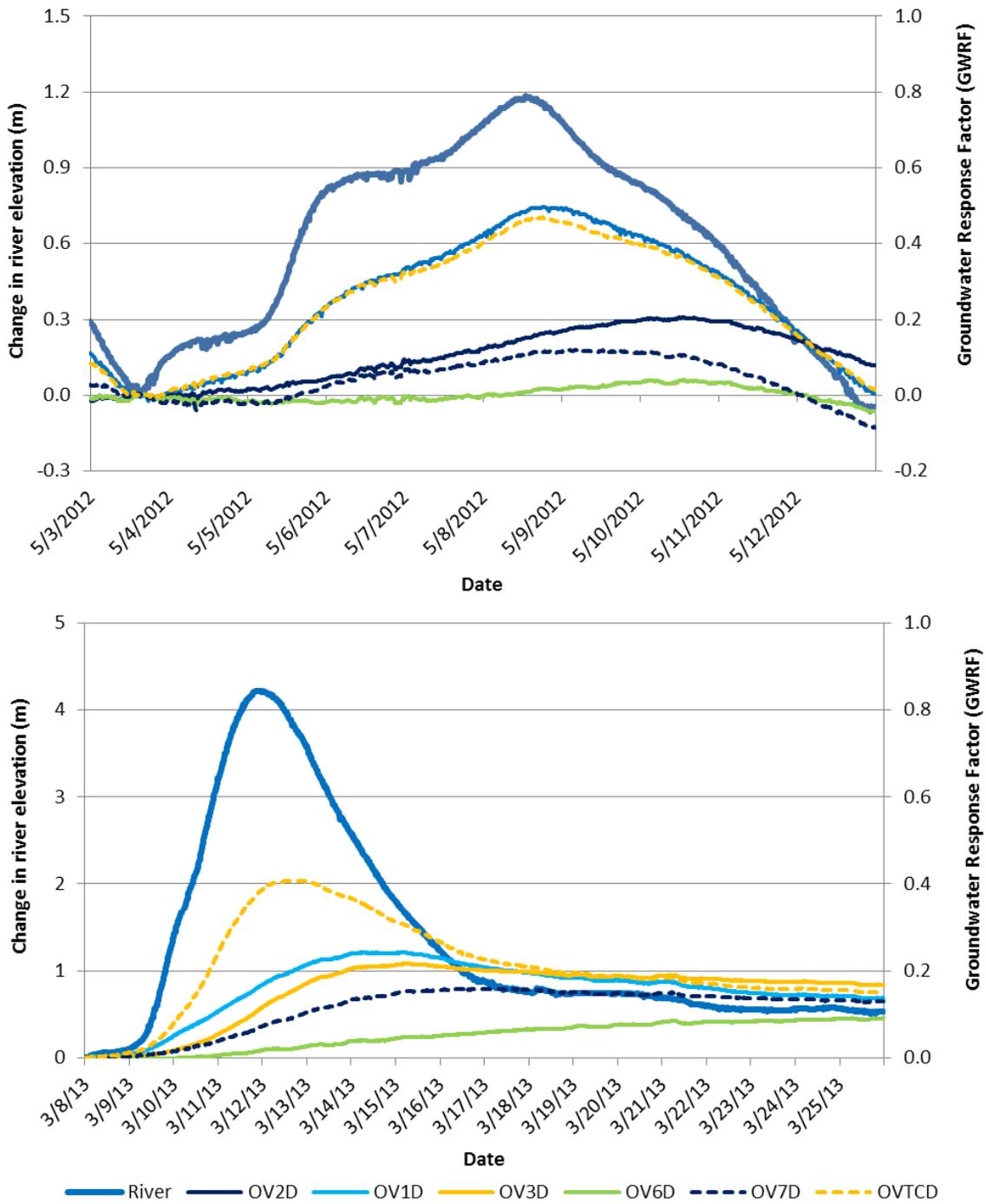


Figure 49. A moderate flow pulse from May, 2012 and a large flow pulse from March, 2013, with the typical pattern of GWR for deep wells at Overton, Missouri.

Table 14. Mean maximum groundwater response factor, lag ratio, and exceedance ratios for deep wells at Overton North, Missouri

Well	n	Mean Maximum Groundwater Response Factor (GWRF)	Mean Lag Ratio (Well start to peak time/ River start to peak time)	Mean 0.5 exceedance ratio (Days GWRF > 0.5/ pulse duration)	Mean 0.25 exceedance ratio (Days GWRF > 0.25/ pulse duration)	Mean 0.10 exceedance ratio (Days GWRF > 0.1/ pulse duration)
OV1D	16	0.47a	1.28a	0.10a	0.49a	0.88a
OV2D	5	0.20b	1.68ab	0.00ab	0.11ab	0.51ab
OV3D	9	0.20b	1.63ab	0.00ab	0.16ab	0.56ab
OV6D	12	0.10b	2.23b	0.00b	0.05b	0.22b
OV7D	12	0.22b	1.60ab	0.00b	0.16ab	0.51ab
OVTCD	9	0.44a	1.14a	0.02ab	0.50a	0.78a

Maximum GWRF

The site-specific relationships between mean observed maximum GWRF and distance from the river are described for each site by the following equations:

$$\text{Forest City: GWRF} = 0.4011 * e^{-0.002 \times \text{distance (m)}} \quad (R^2 = 0.67)$$

$$\text{Overton: GWRF} = 0.0004 * \text{distance (m)} + 0.5282 \quad (R^2 = 0.59)$$

At both Forest City and Overton, mean maximum GWRF had a significant negative relationship with distance from the river (Figure 50), consistent with simulated results for the Missouri River floodplain near Kansas City, Missouri (Kelly, 2000). At Forest City, mean pulse duration was 8.23 days, but the site model relating maximum GWRF to distance from the river tracks approximately midway between those of models based on simulated 1-day and 8-day flow pulses; at Overton, the site model based on a mean flow pulse duration of 9.26 days yields higher maximum GWRF values than the model based on data from 8-day flow pulse simulations (Figure 50) (Kelly, 2000).

At Forest City, the mean observed maximum GWRF for the excessively drained well FC12 is higher than the site-specific model for maximum GWRF based on distance from the river, and most responses to flood pulses were larger than what the site-specific model predicts (Figure 50). By contrast, the mean maximum GWRF and most individual responses to flood pulses at somewhat poorly drained FC11 were at or below modeled GWRF at their distances from the river. The mean maximum GWRF at FC9 was approximately equal to the value predicted by the site model. Although maximum GWRF values

were even distributed above and below the expected value for the the poorly drained FC10 1,235 m from the river, mean maximum GWRF was above model predictions. At Overton, mean maximum GWRF and the majority of groundwater responses to flood pulses at somewhat poorly drained well OV1 and the very poorly drained OV2 and OV7 are below what the site-specific model predicts. By contrast, mean maximum GWRF and the majority of groundwater responses at wells OV3 and OVTC exceed the model predictions (Figure 50). Mean maximum GWRF at moderately well drained OV6 is slightly below the site model, with the majority of responses below the site model as well.

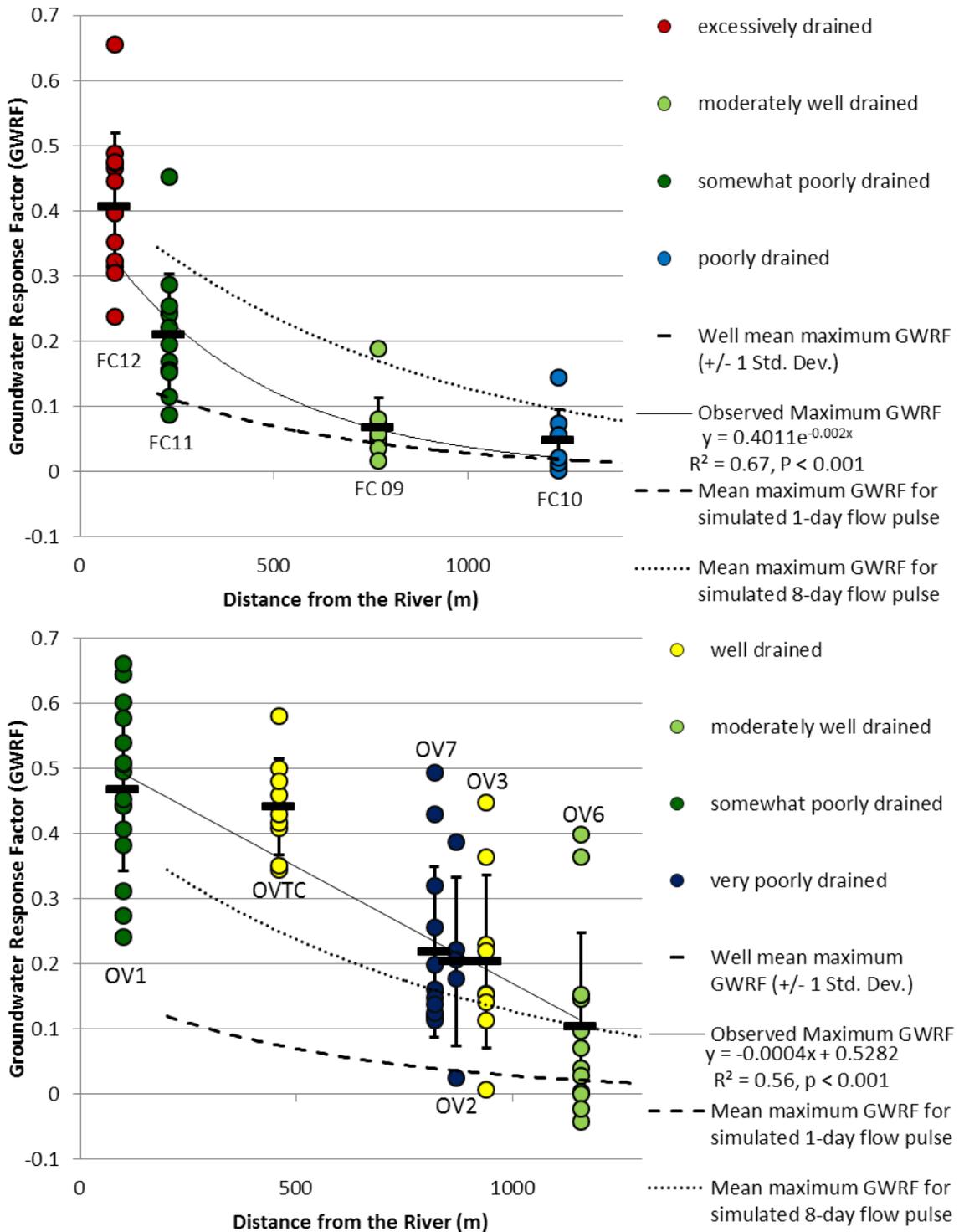


Figure 50. Maximum Groundwater Response Factor (GWRF) as a function of distance from the river at Forest City (top) and Overton (bottom) in relation to modeled maximum GWRF based on simulations for the Missouri River near Kansas City, Missouri (Kelly, 2000)
 Error bars indicate 1 standard deviation about the mean for each indicated well.

Lag ratio

Lag ratio is positively related to distance from the river, and there is some evidence that SSURGO soil drainage classification is related to lag values within a given site (Figure 51). Both sites have significant positive linear relationships between lag ratio and distance from the river ($p < 0.001$); however, these relationships are weak ($r^2 < 0.2$) and provide little predictive value. At both sites, the only wells with lag ratios smaller than what the site model predicts are those located on the better drained soil classes (FC12, OV3, and OVTC). At these wells, groundwater elevation reaches peak value faster than would be predicted on a model based on distance from the river alone. At Overton mean lag ratio for wells on soils with low drainage capacity tended to be greater than the site-specific model predictions. Two exceptions to the above trends include FC10 and OV7, wells on poorly drained soils at which the lag time was less than the site model predicts. These are the same wells for which mean maximum GWR values exceeded predictions for the site model.

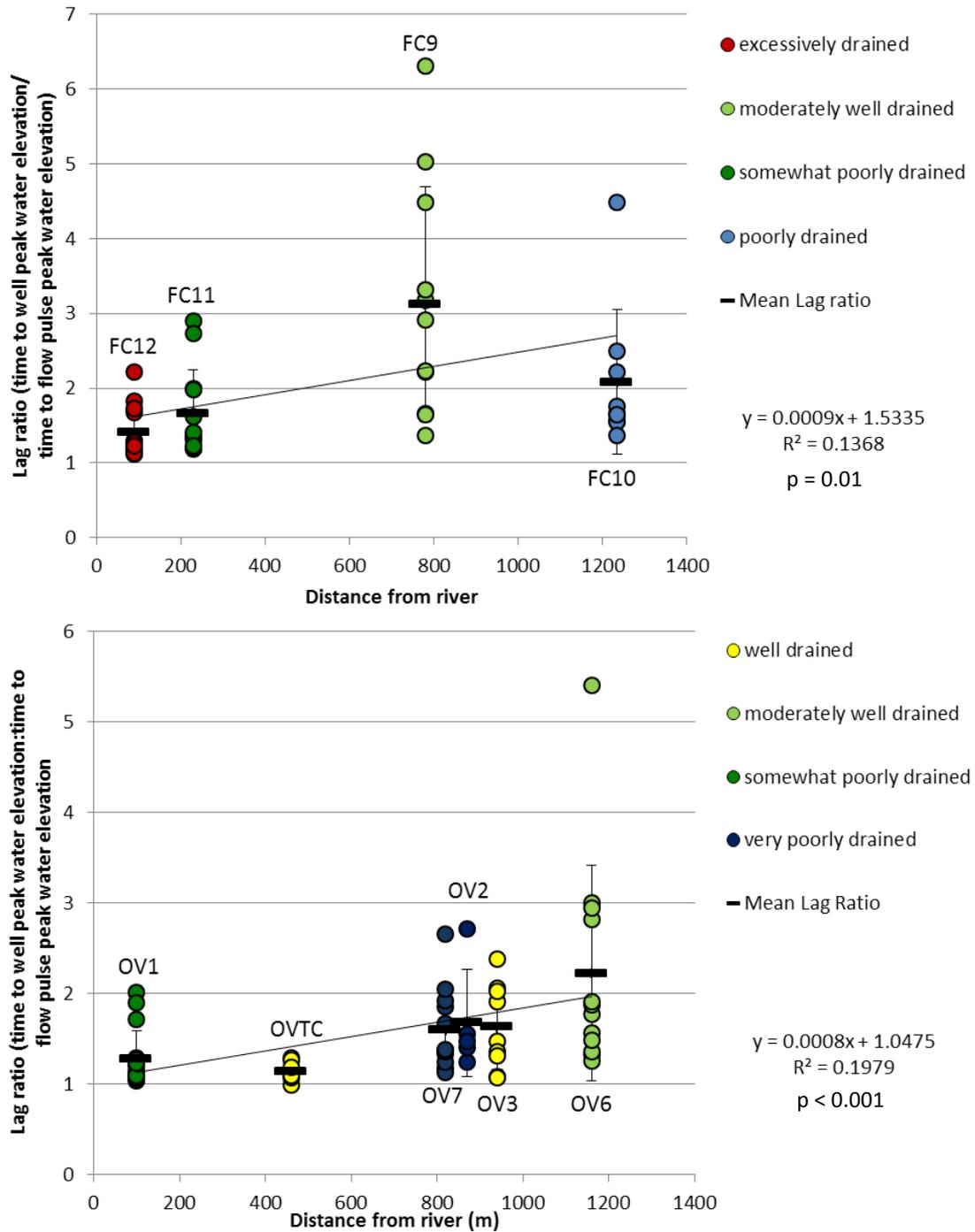


Figure 51. Positive linear relationship between lag ratio and distance from the river for wells at Forest City (top) and Overton (bottom).

Error bars indicate 1 standard deviation about the mean for each indicated well.

Exceedance ratios

At Overton, all exceedance ratios have significant negative linear relationships with distance from the river; at Forest City, the 0.1 and 0.25 exceedance ratios have significant negative logarithmic relationships with distance from the river ($p < 0.001$; Figure 52 and Figure 53). (The 0.5 exceedance ratio at Forest City was not significantly related to distance from the river). These relationships become stronger as the value of the exceedance threshold decreases, but are generally weak and provide little predictive value (the maximum r^2 value was less than 0.6). Mean exceedance values and the majority of observations for wells on better drained soils (FC11, FC12, OV2, OV3, and OVTC) tended to be equal to or higher than the site model predictions. By contrast, wells on soils with poorer drainage tended to have mean exceedance values below what the site model predicts. For example, 0.1 exceedance ratios for all but one flow pulse (May, 5, 2012) at wells FC9 and FC10 were below values suggested by the site model (that the mean value for well FC10 exceeds model predictions reflects the effect of a single outlier). Similarly, the majority of observations at wells on more poorly drained soil classes at Overton were below site model predictions.

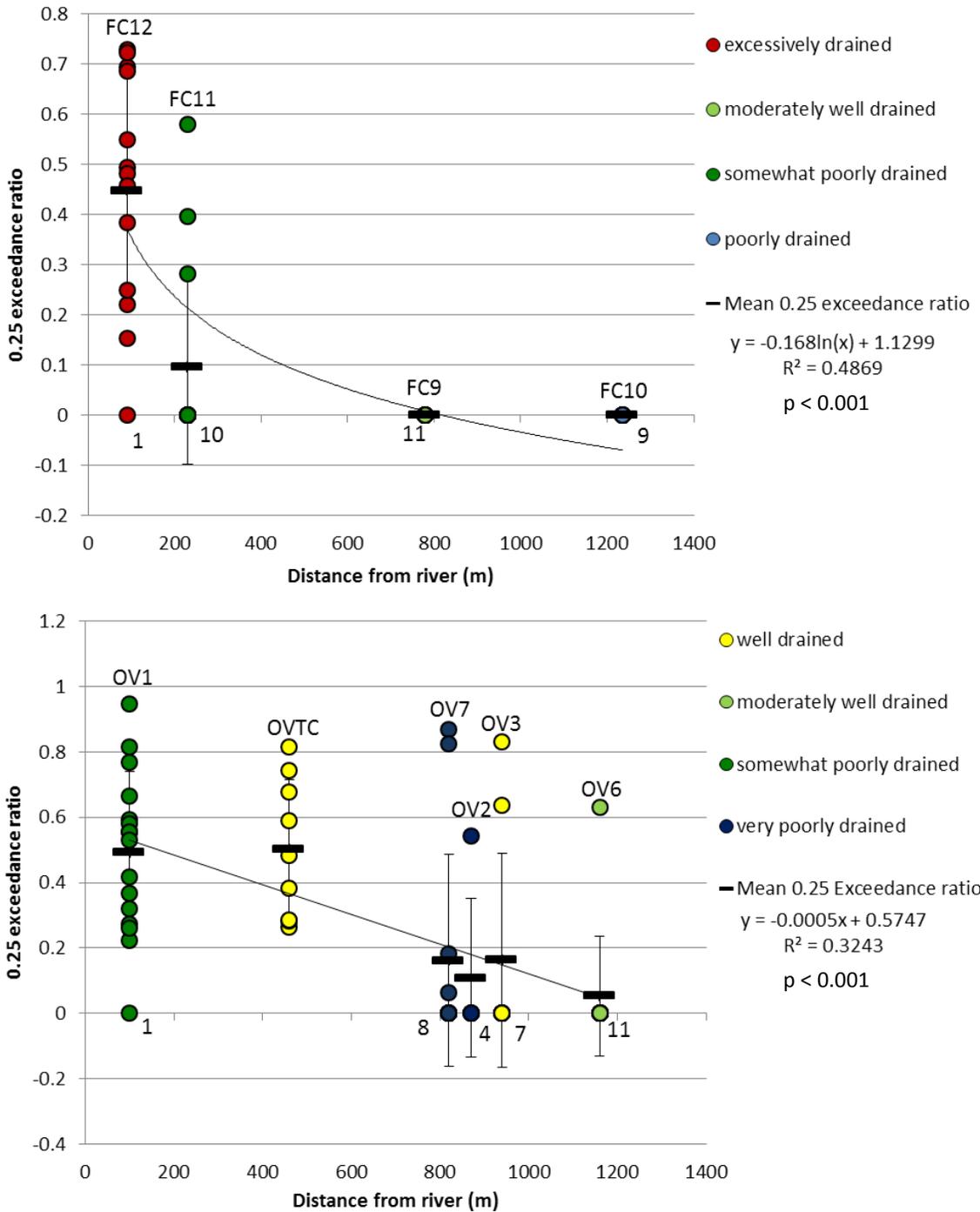


Figure 52. Negative relationship between the 0.25 exceedance ratio and distance from the river at Forest City (top) and Overton (bottom). Numbers next to 0 values indicate the number of flow pulses during which GWRP failed to exceed 0.25, and error bars indicate 1 standard deviation about the mean for each indicated well.

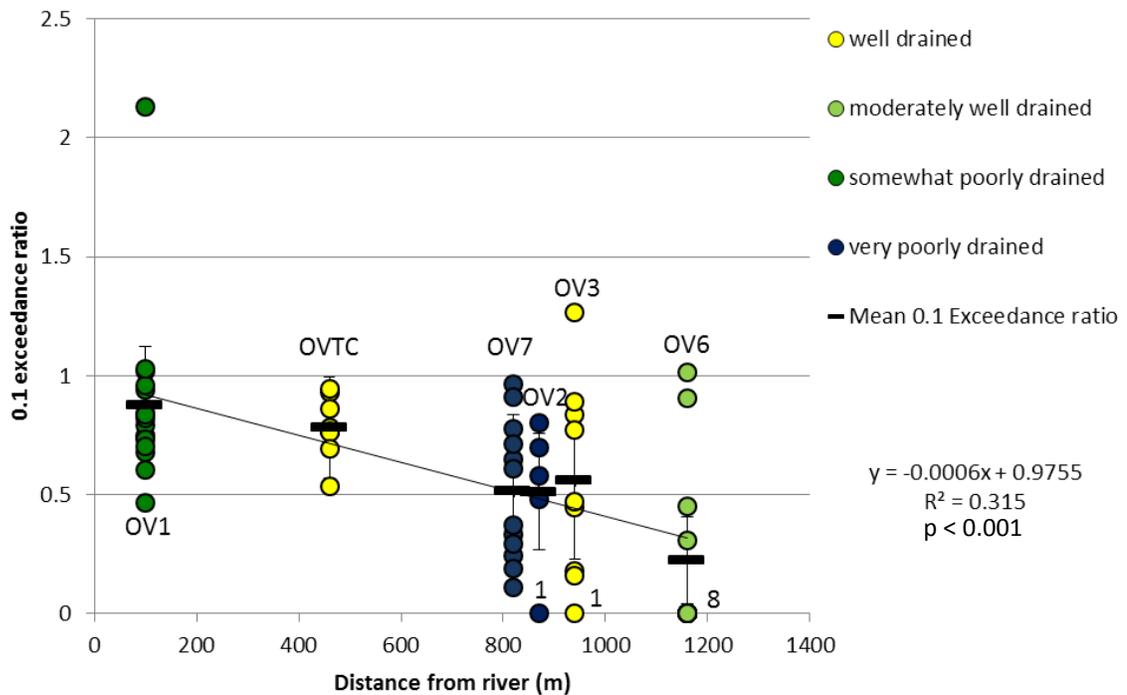
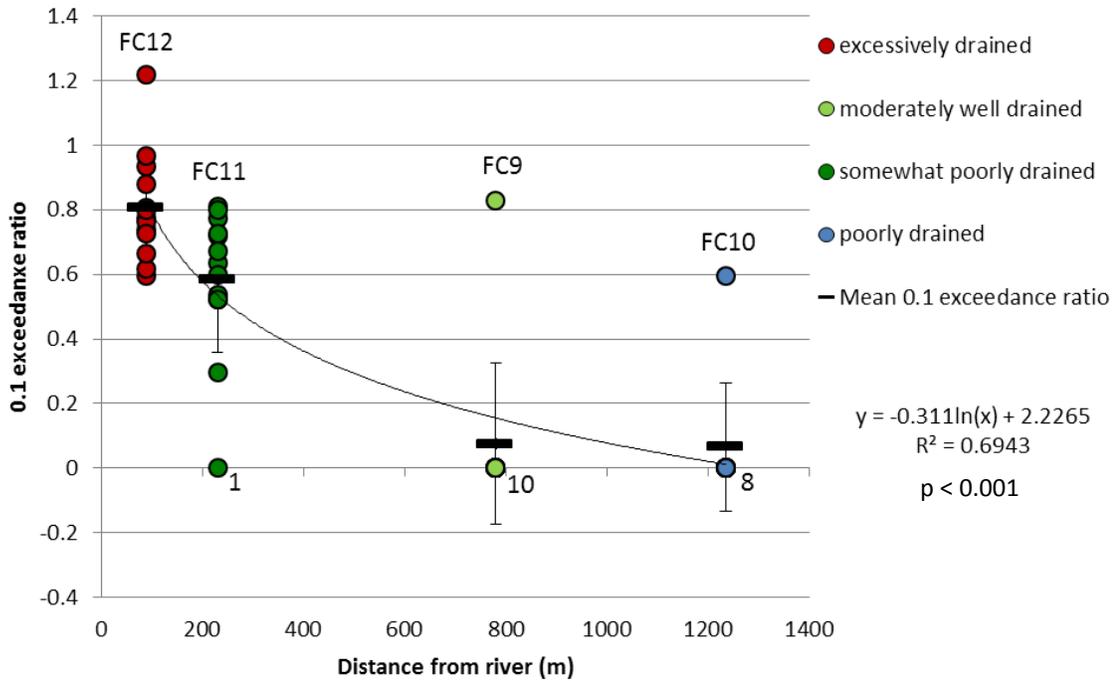


Figure 53. Negative relationship between the 0.1 exceedance ratio and distance from the river at Forest City (top) and Overton (bottom).

Numbers next to 0 values indicate the number of flow pulses during which GWRP failed to exceed 0.1, and error bars indicate 1 standard deviation about the mean for each indicated well.

Comparison of shallow and deep well groundwater response to flow pulses

Four flow pulses at Overton North were detected simultaneously by pairs of deep and shallow wells (Figure 54). The first and largest such pulse began May 27, 2013 and induced overland flow that appears to have inundated all wells; well inundation began shortly after estimated river elevation reached the approximate stage at which flow through the 1993 breach is expected (176.9 m at 11:00 pm, May 30). Wells were inundated in order of increasing distance from the river; this order was reversed as wells were exposed during the descending limb of the flow pulse. After wells were exposed, water elevation dropped fastest in the wells at OV1, and slowest in well TCS. During this time, GWRP tracks nearly perfectly between paired short and deep wells (linear regression yields r^2 values greater than 0.995; $p < 0.001$). Additionally, the maximum range of difference between deep and shallow wells, regardless of soil drainage class, is only 8 cm. During the three subsequent flow pulses that were detected by paired deep and shallow wells on June 11, 15 and 23, the fluctuations in groundwater elevation continue tracks closely between paired shallow and deep wells. Additionally, there is virtually no difference in lag time between shallow and deep wells. Groundwater dropped somewhat farther in well drained OV3 (1.69 m) relative to somewhat poorly drained OV1 (1.47 m).



Figure 54 Graph of average hourly river and well water elevation for 4 flood pulses detected by paired shallow and deep wells at Overton North

Also shown are river elevations at which flow is expected through the first constructed chute, from the second constructed chute, and through a breach in the levee. The starting dates of the pulses are May 26, June 11, June 15, and June 23, 2013. “D” = deep well, “S” = shallow well.

Relationships between LCPI and vegetation

The combined data sets included 410 plots at which cover data on individual species were collected between 2002 and 2012. Data from these plots form the basis for NMS analyses and for analyses of native species group distributions. An additional 94 plots included exotic species data as part of field notes or environmental description data. The remaining data points were from production of the vegetation map at Big Muddy National Fish and Wildlife Refuge, which yielded 435 community classification points during 2009 sampling (Struckhoff et al., 2011) and 749 points in 2012 (Struckhoff, 2013). These mapping efforts also yielded 2,394 exotic species mapping points with estimates of cover for the species of interest. Only 6 of the 22 exotic species of interest were encountered in sufficient quantity to allow analysis of their

abundance in relation to LCPI classes and other variables (Table 16, Table 18). Together, these data sets yielded 4,082 data points that were used to assess the distribution of exotic species.

Intersection of the vegetation map with the LCPI model yielded 6,445 unique flow-return interval/vegetation community polygons and 6,286 unique soil drainage/vegetation community polygons. These data were used to assess the relative frequency, relative area, and probability of occurrence for vegetation communities within the mapped area of the refuge.

To overcome analytical difficulties associated with small sample sizes in some LCPI classes and to facilitate interpretation of results, drainage classes and flow-return intervals were combined prior to analysis. For all species, soils with poorer drainage (very poorly, poorly, and somewhat poorly drained) were combined into a “Poorly drained” group. Similarly, excessively drained and somewhat excessively drained soils were aggregated in to an “Excessively drained” group, and well and moderately well drained soils were aggregated into a “Well drained” group.

Flow-return intervals were aggregated based upon the available data. Exotic species data used plot data and data from the community classification points and exotic species sampling locations. For garlic mustard, hops, reed canary grass, sweet clover, and Johnson grass, flow-return intervals greater than 50 years were combined into a single class. For sweet clover, the 10 to 20 and 20 to 50 year classes were also combined into a single class. All intervals greater than 5 years were aggregated into a single class for velvetleaf. Analysis of native species groups used only plot data for statistical analyses. This required aggregating the 20 to 50 year and 50 to 100 year flow classes into one class, and all intervals greater than 100 years into another.

Non-metric multi-dimensional scaling

In the sections that follow, results of NMS analysis are explored for relationships between environmental variables, species, and communities using graphical outputs of NMS results. Graphs include plots (and occasionally species) and vectors indicating direction of increase and strength of the relationship (indicated by length) for those variables with the strongest relationship to species’ distributions at each site. Results of these NMS analyses are summarized in Table 15 at the end of the section.

All plots

Ordination analysis using data from all of the plots yielded a 3-dimensional solution with a final stress of 16.5. Results indicate that the variables most correlated with differentiation among communities are tributary-defined and geomorphologic river segments, sampling sites, and elevation ($r^2 > 0.30$). All of these variables represent a longitudinal gradient from upstream to downstream. Among the remaining variables those with the strongest relationships to community composition were distance to the nearest levee ($r^2 = 0.18$) and flow-return interval ($r^2 > 0.13$). The graph of final community distribution (Figure 55) shows strong separation of communities based on tributary segment, with upstream plots located on the right of the graph; similar separation of plots are evident when grouped by geomorphologic section or sampling site (not shown). Flow-return interval also tends to increase toward the right of the graph, with nearly all of the plots on land with greater than 500 year flow-return intervals associated with the Gavins section (Figure 55, maroon points in upper right of bottom graph).

Given the longitudinal gradient affecting species distributions, data were further analyzed using ordination at intermediate scales of ecological province and river segments, as well as at the smallest scale of individual sites. The longitudinal gradient and differences between sites continued to exert significant influence on ordination results at intermediate scales, masking the local variables most closely related to ordination results (data not shown). Therefore, the results that follow explore those variables most correlated with ordination results on a site by site basis (there was insufficient data for analysis of plots from Boone's Crossing).

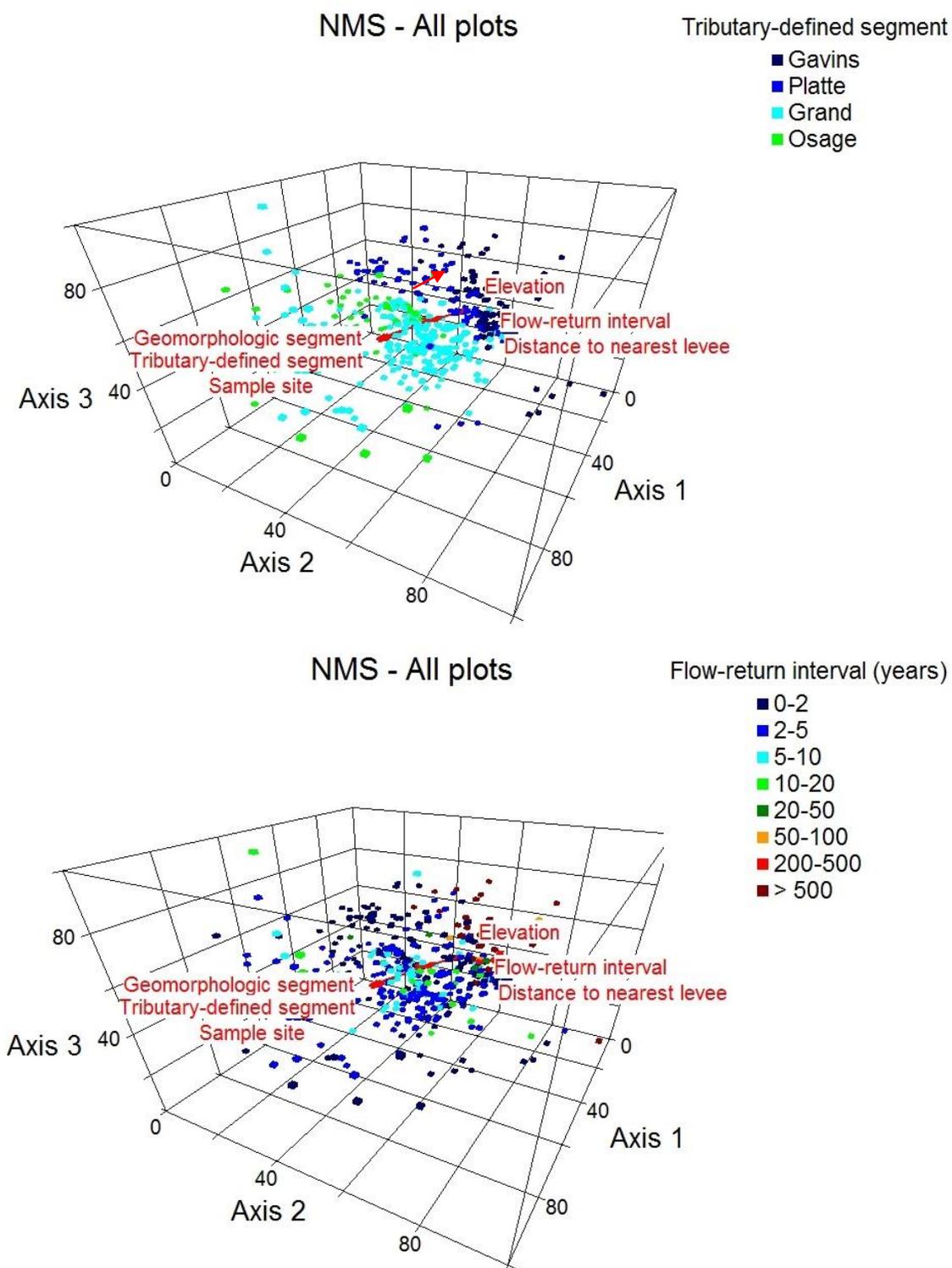


Figure 55. Non-metric Multidimensional Scaling results for all plots coded by tributary-defined river segments (top) (Chojnacki et al., 2012) and flow-return interval (bottom) showing aggregation of plots with long flow-return intervals in the Gavins section.

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Gavins

Data from the Gavins section yielded a 3 dimensional solution with a final stress of 11.7. Axis 1 explained 35 percent of the variation, Axis 2 an additional 36 percent, and Axis 3 an additional 17 percent. The variable with the strongest correlation to the overall data structure is flow-return interval ($r^2 = 0.37$), which is positively related to Axis 1 ($r = 0.60$) and Axis 3 ($r = 0.29$). Available water capacity also had moderately strong relationships with species composition ($r^2 > 0.28$). Cottonwood communities and sandbar willow shrublands represent a distinct set of communities associated with shorter flow-return intervals (Figure 56, lower values along Axis 1). Longer flow-return intervals are associated with mid-successional box elder and ash communities (Figure 56, higher values along Axis 1).

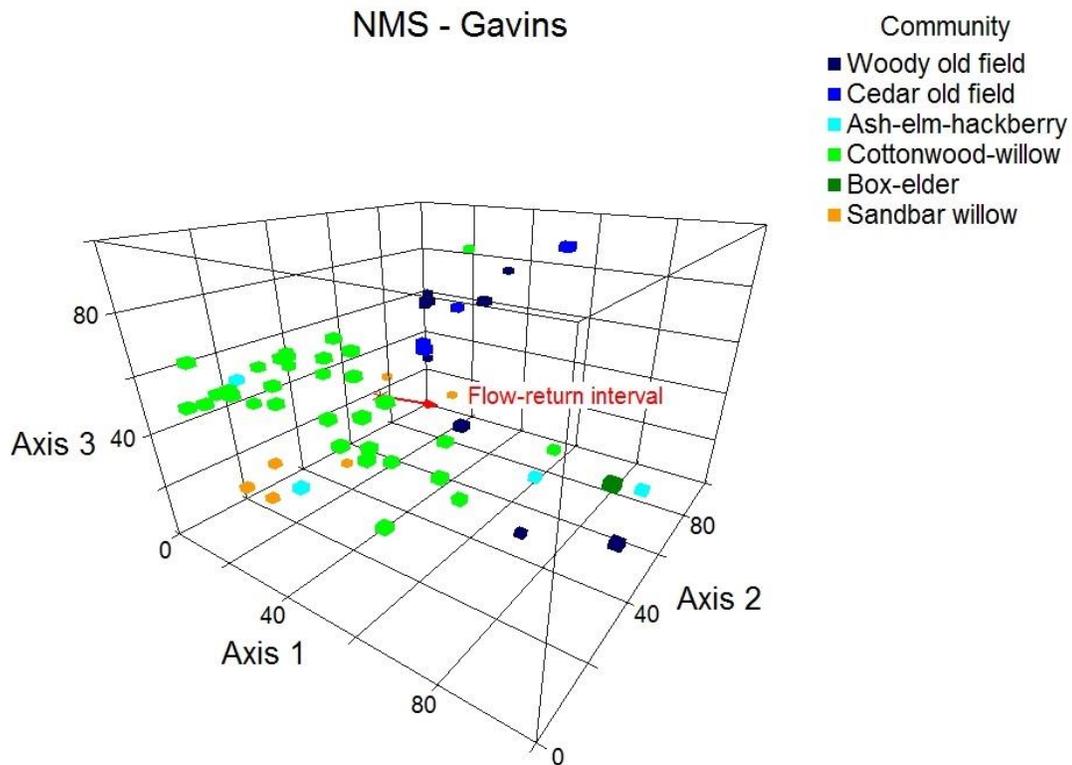


Figure 56. Graph of Non-metric Multidimensional Scaling for plots in the Gavins sampling site showing separation of cottonwood and sandbar willow communities (left) from other communities along a flow-frequency gradient.

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Platte

Results of NMS from the Platte site are similar to those from the Gavins site (3 dimensional solution; final stress of 11.4; axes 1, 2, and 3 explain 34, 36, and 17 percent of the variation). The environmental variables with the highest correlation to community composition are AWC to all depths ($r^2 > 0.40$), distance to the nearest levee ($r^2 = 0.26$), and flow-return interval ($r^2 = 0.25$). The latter metric is negatively correlated with Axis 2 ($r = -0.50$). Flow-return interval separates cottonwood-black willow forests on sites with short intervals from bur oak, ash and box-elder communities on longer flow-return intervals (Figure 57). Sandbar willow shrublands are distinct from all other sites in their association with sites having low AWC.

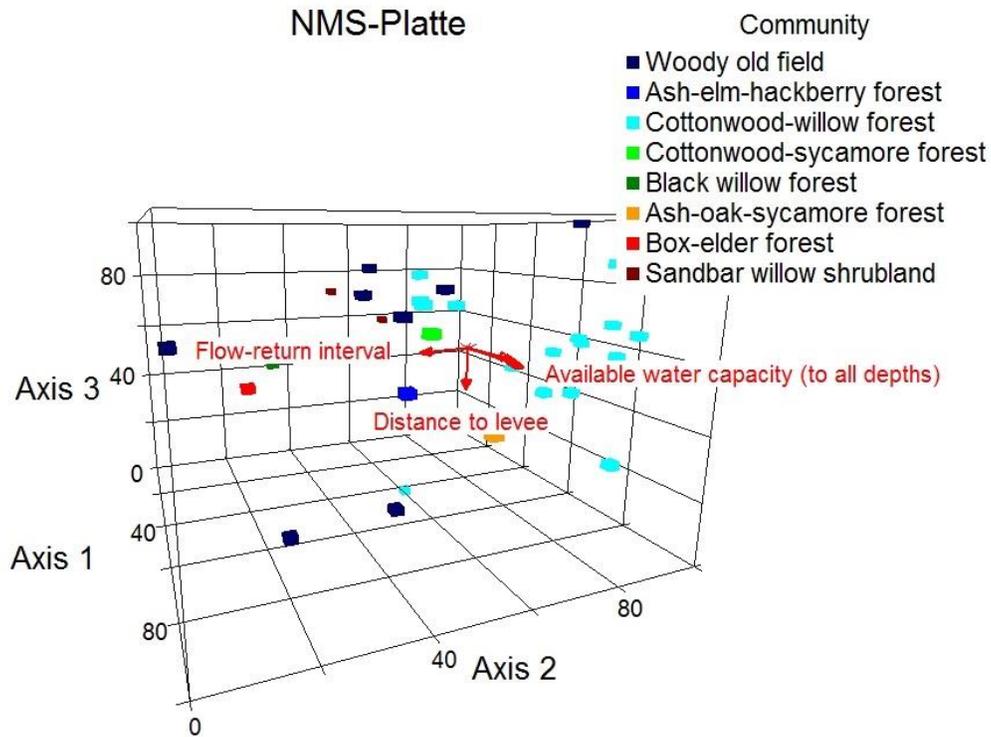


Figure 57. Graph of Non-metric Multidimensional Scaling results for plots in the Platte sampling site showing separation of cottonwood-willow forests (right) from other communities (left) along a flow-frequency gradient and from sandbar willow communities (rear) along an available water capacity gradient.

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Squaw Creek

At Squaw Creek, NMS analysis yielded a 3 dimensional solution with a final stress of 7.3; axes 1, 2, and 3 explain 61 percent, 8 percent, and 16 percent of the variation in community composition. The variables that most correlated with community composition are AWC, flow-return interval, and soil drainage ($r^2 > 0.25$). Longer flow-return intervals, better drained soils, and higher AWC favor cottonwood forests over black willow forests and ephemeral ponds (Figure 58, foreground); the same variables separate ash forests from silver maple forests (Figure 58, background). Available water capacity has the strongest relationship to Axis 1; cottonwood and willow communities (foreground) are associated with lower AWC than ash and silver maple communities (background).

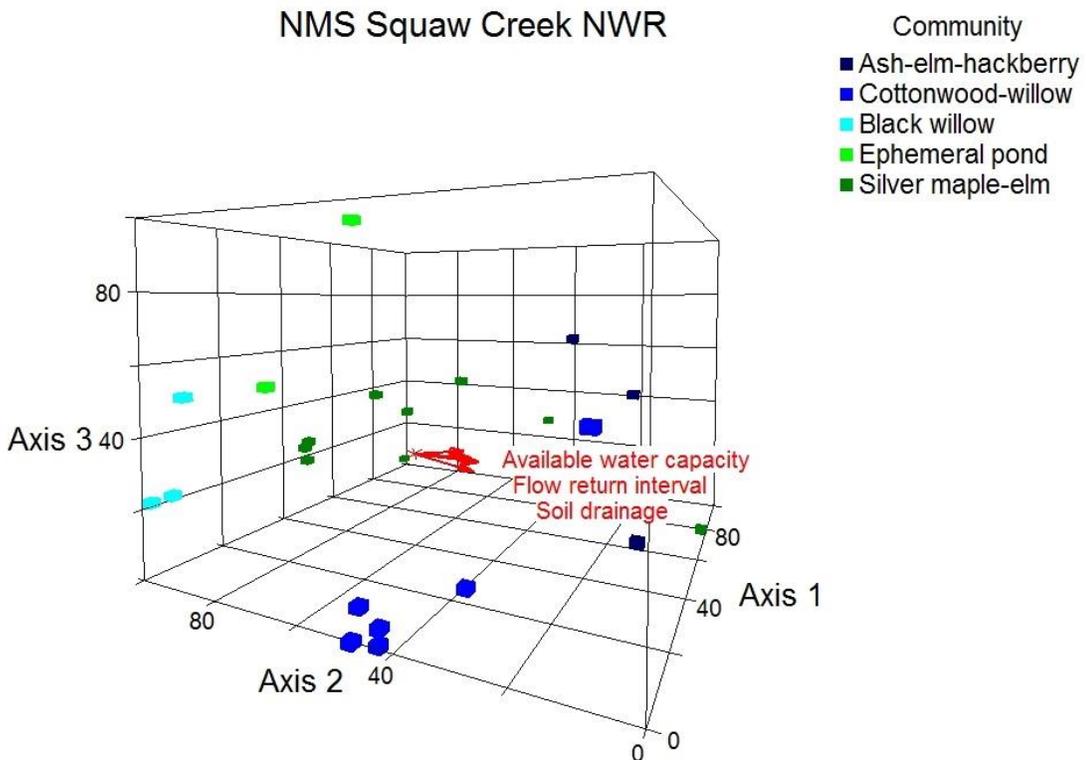


Figure 58. Graph of Non-metric Multidimensional Scaling results for plots in the Squaw Creek NWR sampling site showing black willow, pond, and silver maple communities with poor soil drainage, short flow-return intervals, and low available water capacity (left of graph).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Fort Leavenworth

Ordination of data from Ft. Leavenworth yielded a two dimensional solution with a final stress of 11.7. Axis 1 explains 60 percent of the variance, and Axis 2 explains an additional 27 percent. Variables most closely correlated with the data structure are distance to the river ($r^2 = 0.25$) and distance to the nearest road ($r^2 = 0.14$). For both variables, nearly all of that correlation is due to association with Axis 1; river distance is negatively related ($r = -0.50$) and road distance is positively related ($r = 0.37$). Axis 1 appears to be driven by a shift from cottonwood at lower axis values toward box elder and elm at upper values (r values for these species are -0.703 , 0.66 , and 0.60 , respectively; Figure 59). The decreasing abundance of cottonwood forests closer to the river is somewhat contrary to the results of Thogmartin et al. (2009).

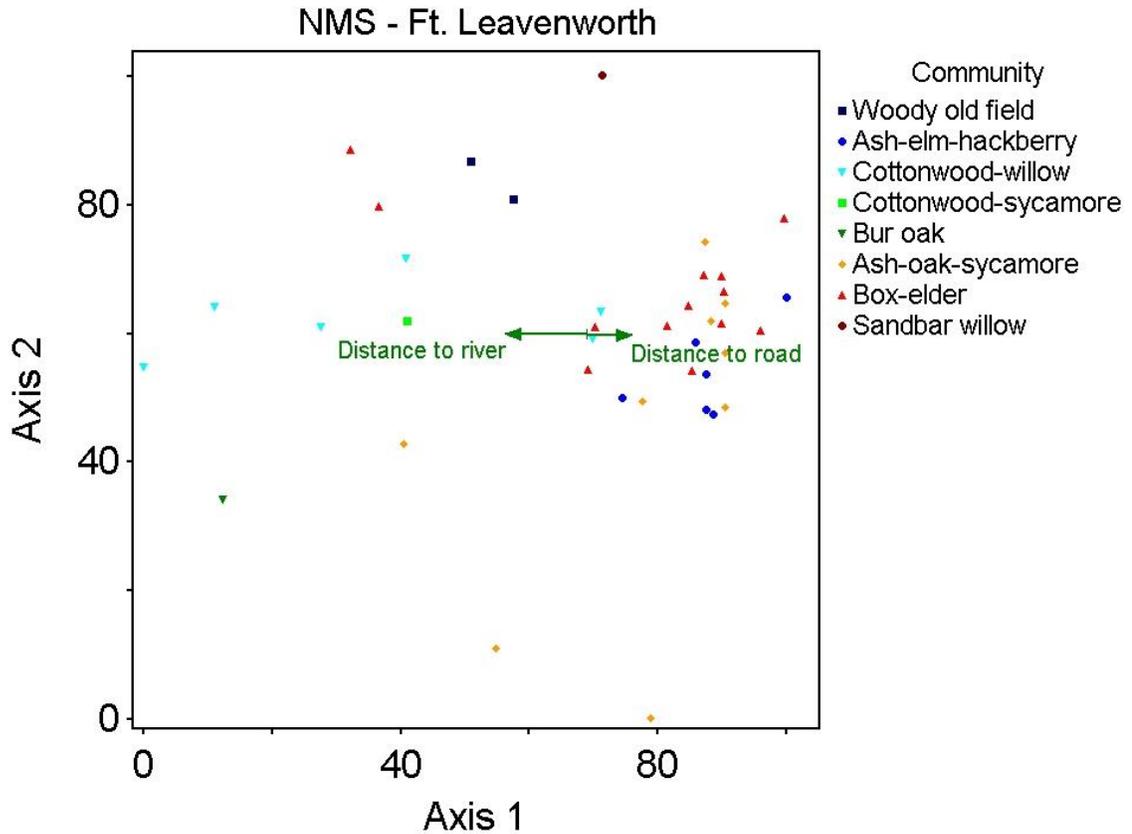


Figure 59. Graph of Non-metric Multidimensional Scaling results for plots in the Ft. Leavenworth sampling site showing a shift from cottonwood communities to box-elder and elm forests as one moves closer to the river and further from roads (left to right along Axis 1).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Lisbon Bottom

Lisbon Bottom ordination analysis yielded a 2 dimensional solution with a final stress of 16.1. Axis 1 explains 64 percent of the variation in composition; Axis 2 explains only 4 percent. Soil drainage and flow-return interval show the highest correlation to the overall community composition ($r^2 = 0.09$ and $r^2 = 0.06$), although these relationships are weak. Nearly all of the plots at both sites are classified as cottonwood-willow forests; therefore, the ordination graph includes the location of woody species indicated by species codes (U.S. Department of Agriculture-Natural Resource Conservation Service, 2014) in addition to plots (symbols color-coded by community type) (Figure 60). The species with the highest correlation to the community composition are cottonwood, box-elder, sycamore, and sandbar willow. These and all other woody species are aggregated toward the left of the graph, indicating that woody species are more abundant on better drained soils. The high final stress value and the low correlation values for environmental variables reflect the lack of vegetative variation throughout the site; all but one plot represented cottonwood dominated communities.

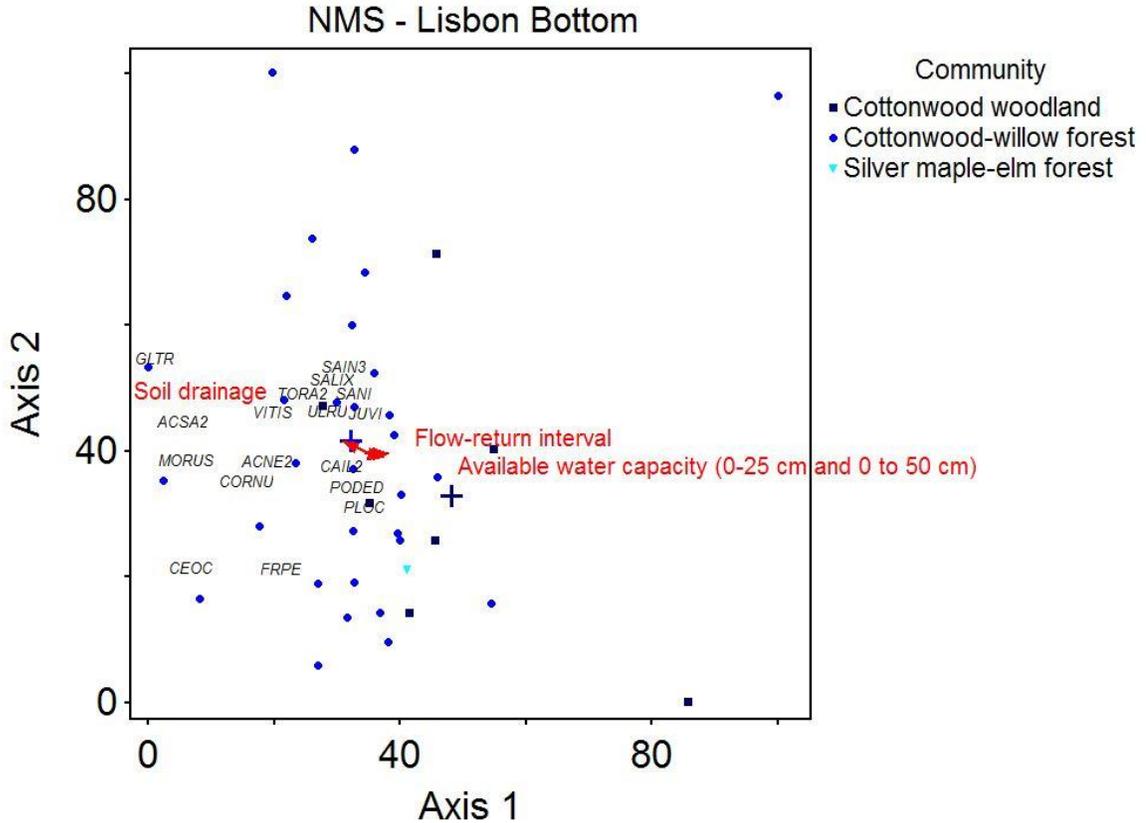


Figure 60. Graph of Non-metric Multidimensional Scaling results for species at Lisbon Bottom showing that cottonwood-willow forests and all woody species are less dominant at locations with poorer soil drainage (lower right of graph).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution. Labels—USDA PLANTS Database codes (U.S. Department of Agriculture-Natural Resource Conservation Service, 2014)—indicate locations of woody species in ordination space.

Jameson Island

Analysis using NMS at Jameson Island yielded a 3-dimensional solution with a final stress of 15.9. All but 6 plots were classified as the Midwestern Cottonwood – Black Willow Forest type). Within this narrow expression of communities, soil drainage ($r^2 = 0.17$), AWC in the upper 0.5 meters of soil ($r^2 = 0.1$), and flow-return interval (0.08) were the variables most correlated with ordination results. These variables were positively related to each other. Cottonwood forests dominate the central portion of the graph, reflecting the dominance of that community type; other communities are scattered around the perimeter of the ordination graph for the site (Figure 61). Sand flat communities appear to occupy locations with better soil drainage, consistent with the inclusion of the “sand” modifier in the community name;

however, the sample size is too small to draw any firm conclusions. As at Lisbon Bottom (which is directly across the river from Jameson Island), the high stress and generally low correlation between environmental variables and the ordination solution are probably due to lack of variation in composition between plots.

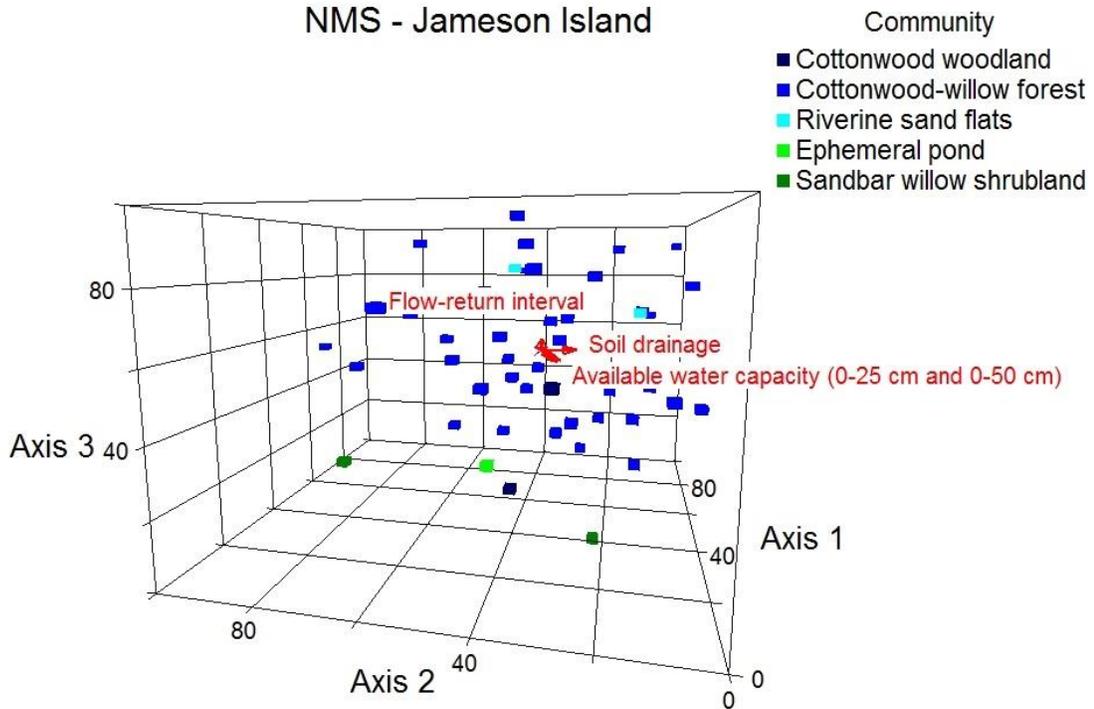


Figure 61. Graph of Non-metric Multidimensional Scaling results for Jameson Island showing dominance by cottonwood-willow forests and direction of increase for those variables most correlated with ordination results (soil drainage and available water capacity in the top 50 cm of soil).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Overton North

Overton North data was best resolved using a 3-dimensional NMS solution with a final stress of 14.9. Axes 1, 2, and 3 explain 37, 18 and 15 percent of the variation in species distribution, respectively. Soil drainage is most correlated with the ordination results ($r^2 = 0.35$), followed by AWC to 100 cm and distance to the river ($r^2 = 0.28$). These variables have r values of -0.58, -0.52, and -0.52 relative to Axis 1. Sites with better drained soils close to the river are dominated by cottonwood and willow communities; ephemeral ponds are most abundant far from the river on poorly drained soil (Figure 62).

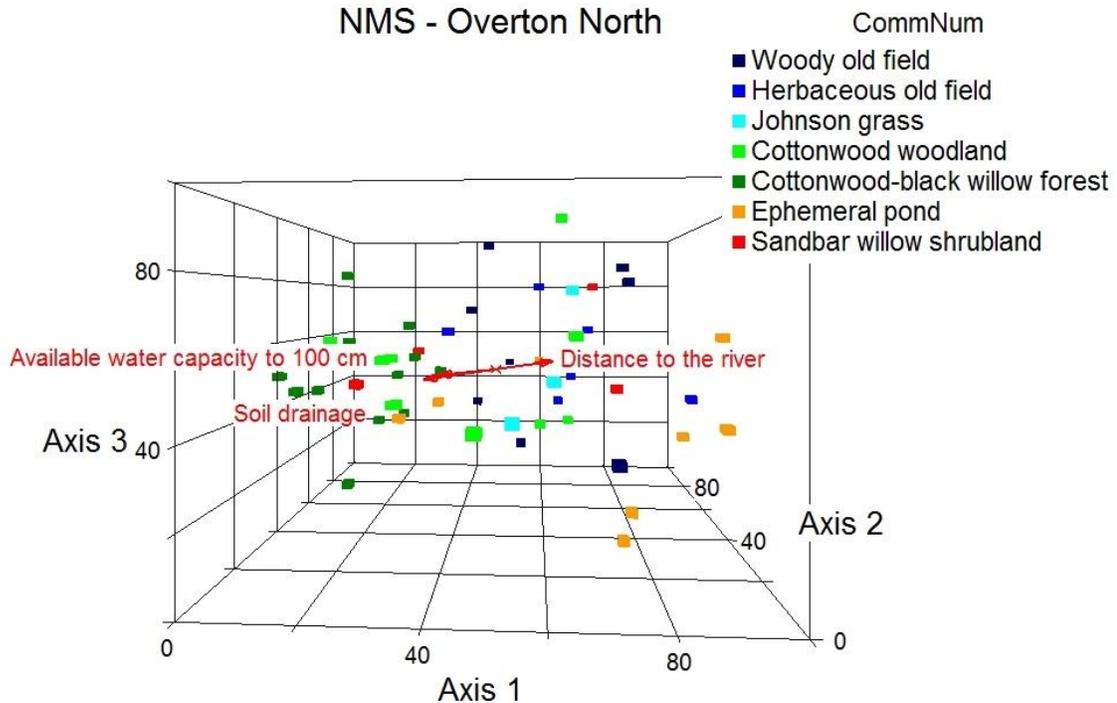


Figure 62. Graph of Non-metric Multidimensional Scaling results for plots at Overton North showing that better drained soils closer to the river (left of the ordination origin) are dominated by cottonwood and willow communities.

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Overton South

Data from Overton South yielded a 3-dimensional solution with a final stress of 15.4. Axis 1 explains 32 percent of the variation in data, Axis 2 explains 31 percent, and Axis 3 explains 10 percent. Soil drainage ($r^2 = 0.25$) and flow-return interval ($r^2 = 0.16$) are most correlated with the distribution of species in ordination space. The continuous elevation variable and distance to the river are correlated to the data nearly as well as flow-return interval ($r^2 > 0.15$). As at Lisbon Bottom and Jameson Island, cottonwood-willow forests and more open-canopied cottonwood woodlands represent nearly all of the sampling points (Figure 63). Despite this lack of diversity, results indicate that cottonwood communities are associated with better drained soils with less frequent flooding. Willow dominated communities tend to occur in more frequently flooded sites with poorer drainage, consistent with a tolerance for anoxic conditions (Schaff et al., 2003; Shin and Nakamura, 2005) and mechanically-induced damage due to flooding (Karrenberg et al., 2002). These analytical results are also consistent with observations made

during mapping in 2011 that repeated and prolonged flooding in low lying areas was inducing mortality in cottonwoods more than in other species, thereby increasing dominance by species such as black-willow.

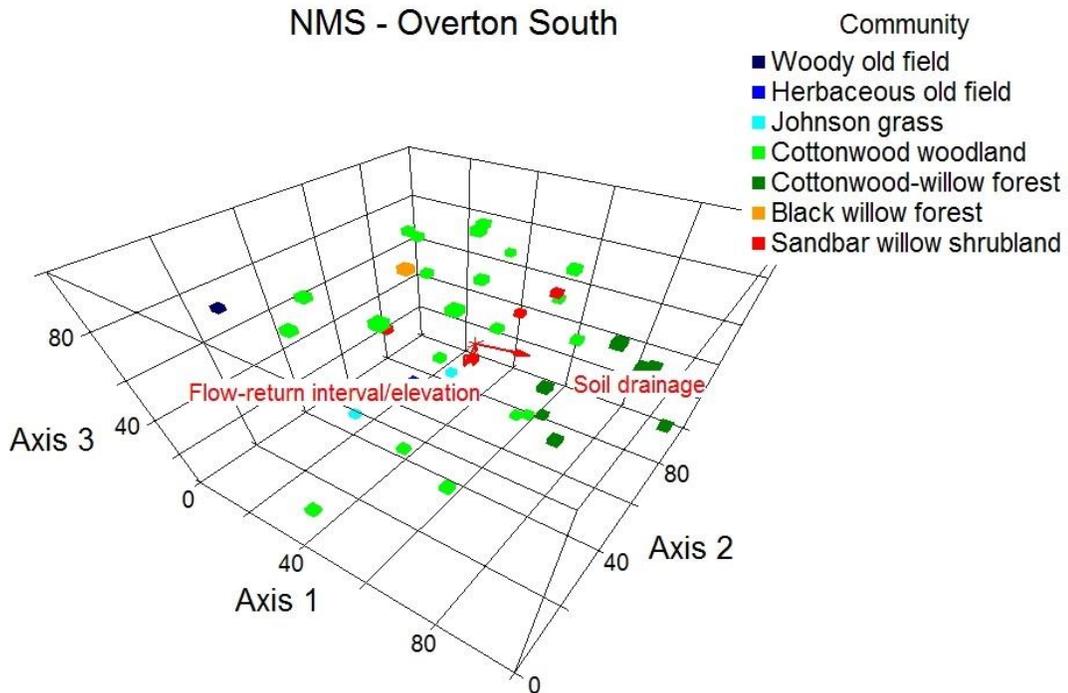


Figure 63. Graph of Non-metric Multidimensional Scaling results for plots at Overton South showing that better drained soils closer with less frequent flooding are dominated by cottonwood communities.

Arrows indicate the direction and magnitude (length) of increase for the variables with the strongest relationship to the distribution of species.

Eagle Bluffs

Analysis of data from Eagle Bluffs Conservation Area yielded a 2 dimensional solution with a final stress of 11.1. Axis 1 explains 64 percent of the variation in the data structure and Axis 2 explains an addition 18 percent. The variables most strongly correlated with the distribution of species are available water content ($r^2 > 0.74$ for all soil layers), which is positively correlated with Axis 1 ($r > 0.86$ for all soil layers; Figure 64). The next most correlated variables are distance to the nearest road ($r^2 = 0.27$) and distance to the river ($r^2 = 0.24$); both are negatively related to Axis 1. Cottonwood-willow forests dominate the left half of Figure 64, indicating that they occur on soils with lower AWC. Lower AWC can reflect coarser soil textures that are sometimes associated with better drainage; however, soil drainage is only weakly related to the data structure ($r^2 = 0.10$). Cottonwood communities also tend to occur farther from the

river and roads than other communities, contrary to results from other research (Thogmartin et al., 2009). Early-successional willows and cottonwood are associated with better drained soils farther from the river (Figure 65, left), and mid-successional woody species are more abundant on poorly drained soils near the river (Figure 65, right).

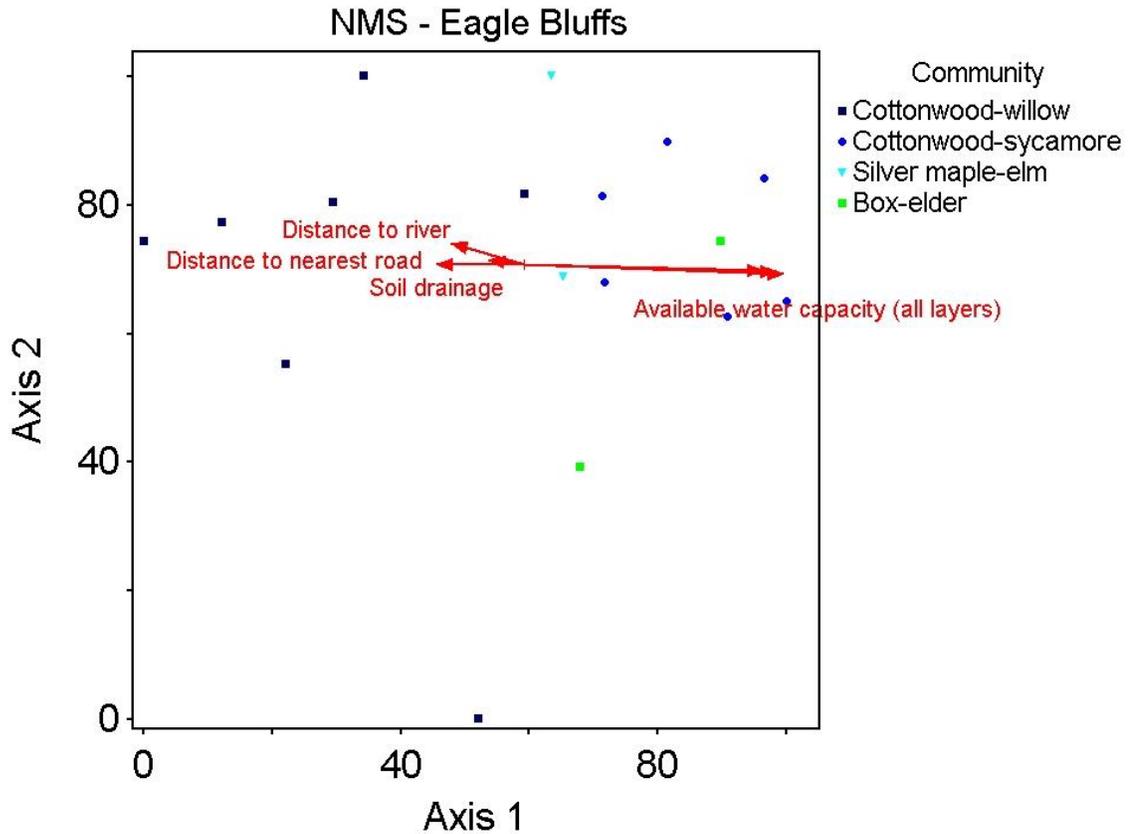


Figure 64. Graph of Non-metric Multidimensional Scaling results for plots at Eagle Bluffs Conservation Area, Missouri, showing cottonwood-willow forests on soils with lower available water capacity farther from the river than other communities.

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

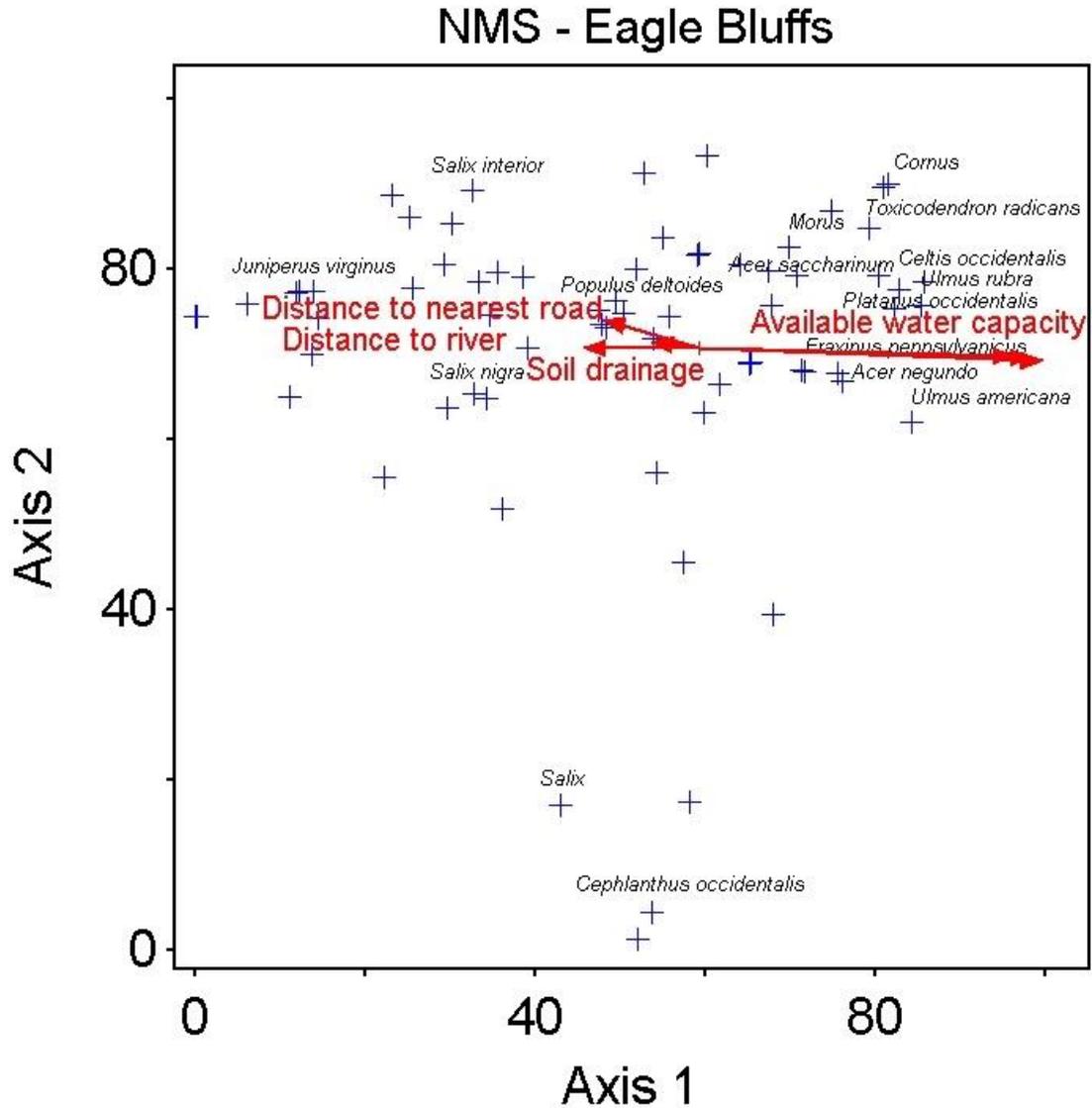


Figure 65. Graph of Non-metric Multidimensional Scaling results for species at Eagle Bluffs Conservation Area, Missouri, showing the affinity of willows (*Salix* spp.) and cottonwood (*Populus deltoides*) for soils with lower available water capacity (left of origin) and of nearly all other woody species for soils with higher available water capacity (right of origin). Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

St. Aubert Island

The optimal ordination solution for data from St. Aubert Island was 2 dimensional with a final stress of 9.6. Axis 1 explains 62 percent of the variation; Axis 2 explains 13 percent. Flow-return interval is the variable most correlated with the data structure ($r^2 = 0.30$) and is positively related to Axis 1 ($r = 0.55$).

Distance to the nearest road is negatively related to Axis 1 ($r = -0.44$), and is moderately related to the species distribution ($r^2 = 0.19$). Transition from short to long flow-return intervals is associated with a progression from ephemeral ponds, to cottonwood communities, to box-elder forests (Figure 66).

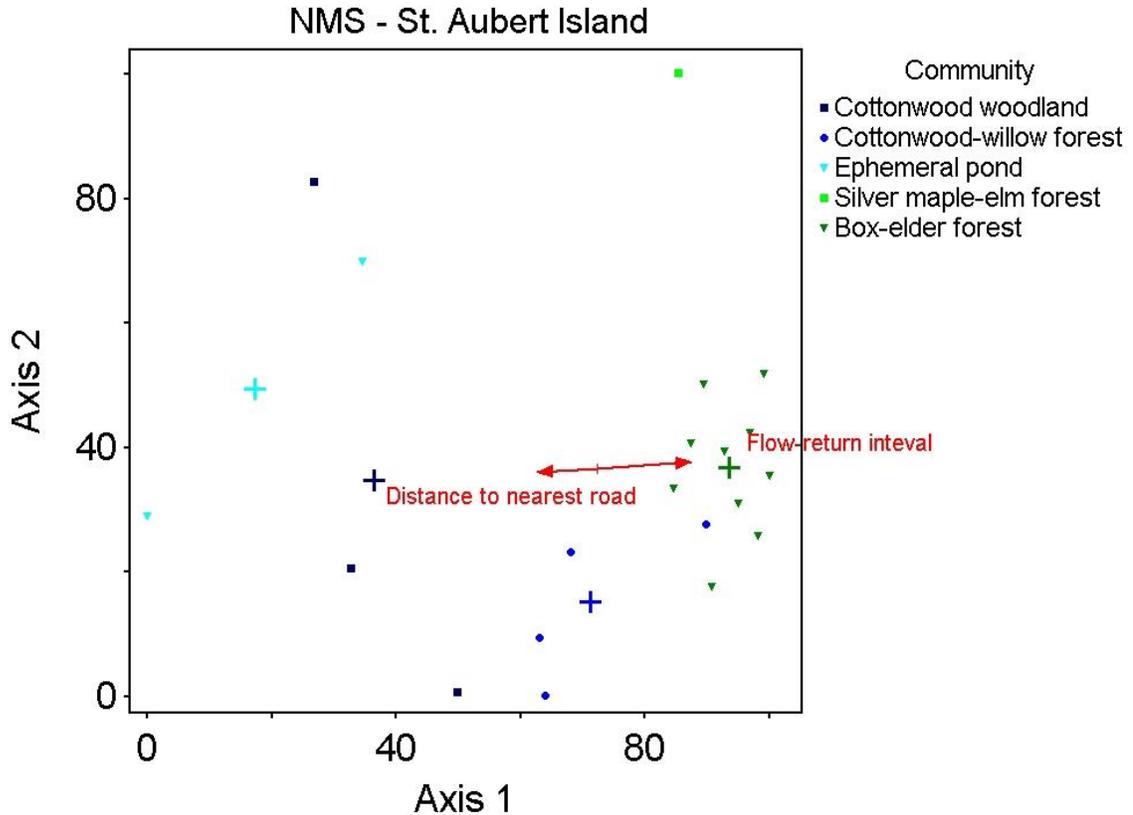


Figure 66. Graph of Non-metric Multidimensional Scaling results for plots at St. Aubert Island showing a transition from ephemeral pond through cottonwood communities to box elder communities as flow-return interval increases (crosses indicate centroid for community type with matching color).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Howell Island

Howell island data yielded a 3-dimensional solution with a final stress of 12.4. Variation in the data explained by Axis 1, Axis 2, and Axis 3, is 47 percent, 20 percent, and 9 percent, respectively. All variables exhibited relatively high r-square values ($r^2 > 0.16$). The variable with the highest correlation to species' distributions is distance to the river ($r^2 = 0.47$), which is negatively correlated with Axis 2. Elevation had the second highest r-square value (0.34) and distance to the nearest road had the third highest (0.32). (Distance to roads and distance to rive are inversely related, because the roads are generally located

on the central portion of the site.) Soil drainage ($r^2 = 0.28$) and flow-return interval ($r^2 = 0.24$) rank behind most other variables in terms of their ability to explain variation in species distribution. Sampled locations in close proximity to the river at Howell Island tend to support cottonwood and silver maple communities, while those further from the river support box elder and ash forests (Figure 67).

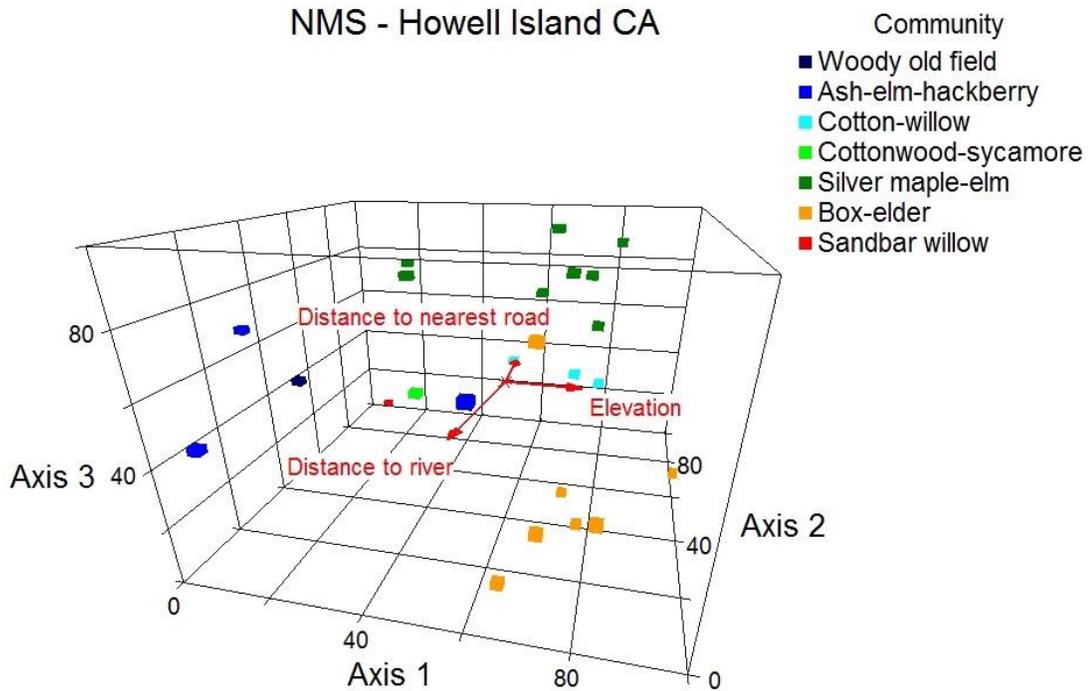


Figure 67. Graph of Non-metric Multidimensional Scaling results for plots at Howell Island Conservation Area, Missouri, showing higher elevations occupied by box elder and cottonwood-willow forests. Additionally, distance from the river separates box-elder and ash communities (farther from river) from silver maple communities (closer to river).

Arrows point in the direction of increasing value, with length indicating the relative strength of the variable's relationship to the ordination solution.

Summary of NMS results

The analyses above indicate that the relationships between the distribution of species and environmental variables—including flow-return interval and soil drainage—vary depending on site (Table 15). In most cases, flow-return interval is more strongly correlated with ordination results than is the continuous elevation variable; Howell Island and Fort Leavenworth are exceptions to this rule. Only at Overton North, Eagle Bluffs, Ft Leavenworth, and Howell Island is flow-return interval excluded from

those variables most correlated with the data structure; at the latter two sites, elevation is still an important variable. Soil drainage is less often included among variables with the strongest relationship to the ordination solutions; however, at 4 of the 5 sites where it is included, it had the strongest correlation with the solution. These four sites (Lisbon Bottom, Jameson Island, Overton North and Overton South) are in close proximity to one another in the Grand segment of the river downstream of the transition from the prairie province to the forest province. Only the analyses for Howell Island, Eagle Bluffs, and Ft Leavenworth excluded both flow-return interval and soil drainage from the variables with the best correlation to the ordinations results (elevation was included at Howell island and Ft. Leavenworth).

The NMS results reveal the disconnect between available water content and soil drainage. Where soil texture is the dominant factor determining both AWC and soil drainage, we would expect them to be related negatively to one another (Soil Survey Staff, 1993; Brady and Weil, 2008; Schoeneberger et al., 2012). However, the variable relationship between available water capacity and soil drainage is reflected in the inconsistent relationship between these variables within the NMS analyses. At Squaw Creek and Jameson Island, for example, soil drainage and AWC are positively related; at Eagle Bluffs, they are negatively related. Previous research has shown that these variables are important determinants of the distribution of cottonwoods and willows (Hosner, 1960; Hosner and Minckler, 1963; Friedman et al., 1996; Shafroth et al., 1998).

Table 15. Summary of Non-metric Multidimensional Scaling (NMS) results by site.

Axis	Axis r^2 increment	Variable(s) with strongest relationship(s) to NMS solution	Variable multiple r^2
All plots (number of dimensions = 3; stress = 16.5)			
1	0.35	River section or sample site	> 0.30
2	0.18	Distance to nearest levee	0.18
3	0.15	Flow-return interval	0.13
Gavins (number of dimensions = 3; stress = 11.7)			
1	0.35	Flow-return interval	0.37
2	0.36	Available water capacity (to all depths)	> 0.28
3	0.17	Distance to water	0.22
Platte (number of dimensions = 3 ; stress = 11.4)			
1	0.34	Available water capacity (to all depths)	> 0.40
2	0.36	Distance to nearest levee	0.26
3	0.17	Flow-return interval	0.25
Squaw Creek NWR (number of dimensions = 3; stress = 7.3)			
1	0.61	Flow-return interval	0.30
2	0.08	Available water capacity (to all depths)	> 0.28
3	0.16	Soil drainage	0.25
Fort Leavenworth (number of dimensions = 2; stress = 11.7)			
1	0.64	Distance to river	0.25
2	0.18	Distance to nearest road Elevation	0.14 0.13
Lisbon Bottom (number of dimensions = 2; stress = 16.1)			
1	0.64	Soil drainage	0.09
2	0.04	Flow-return interval Available water capacity (0-25 cm and 0-50 cm)	0.06 0.05
Jameson Island (number of dimensions = 3; stress = 15.9)			
1	0.40	Soil drainage	0.17
2	0.16	Available water capacity (0-25 cm and 0-50 cm)	0.10
3	0.19	Flow-return interval	0.08
Overton North (number of dimensions =3 ; stress = 14.9)			
1	0.37	Soil drainage	0.35
2	0.18	Distance to river	0.28
3	0.15	Available water capacity (to 100 cm)	0.28
Overton South (number of dimensions =3 ; stress = 15.4)			
1	0.32	Soil drainage	0.25
2	0.31	Flow-return interval /elevation	0.16
3	0.10	Distance to river	0.15
Eagle Bluffs Conservation Area (number of dimensions = 2; stress = 11.1)			
1	0.64	Available water capacity (to all depths)	> 0.74
2	0.18	Distance to nearest road Distance to river	0.27 0.24
St. Aubert Island (number of dimensions = 2; stress = 9.6)			
1	0.61	Flow-return interval	0.30
2	0.13	Distance to nearest road Elevation	0.19 0.15
Howell Island Conservation Area (number of dimensions = 3; stress = 12.4)			
1	0.47	Distance to river	0.47
2	0.20	Elevation	0.34
3	0.09	Distance to road	0.32

Species frequency and abundance analyses

In the analyses that follow, differences between LCPI flow-return intervals and soil drainage classes in the abundance of species, species groups, and communities are quantified using data related to naturally occurring vegetation in a post-agricultural setting. The goal is not to predict in a spatially explicit manner the likelihood of a particular species occurring on a given site, but rather to identify broad categories of LCPI classes that may support desired species and communities or that may be more or less susceptible to invasion by exotic species are more likely to support desired species and communities.

Exotic species

Frequency by flow-return interval

Lands with short flow-return intervals (less than 10 years) were far more intensively sampled than were floodplains with long flow-return intervals; approximately 2 percent of sampled locations were on lands with flow-recurrence intervals greater than 100 years (Table 16). Garlic mustard, velvet leaf, and sweet clover distributions were the least similar to the sampling distribution, all having similarity scores less than 80 percent; the other species had similarity scores above 90 percent. All species frequency distributions showed significant deviations from the distribution of sampling locations among flow classes (Chi-square test, $\alpha = 0.05$; $p < 0.001$). Johnson grass and garlic mustard slightly exceed their expected frequency on infrequently flooded land; reed canary grass, sweet clover, and velvetleaf exceed their expected frequency on frequently flooded land (Figure 68). Japanese hops are more abundant in the 5 to 10 and 10 to 20 year flow classes that would be expected, indicating that it thrives at moderate flood frequencies.

The likelihood that garlic mustard and Johnson grass will occur increases as flow-return interval increases, such that the probability of occurrence on intervals greater than 20 years is from 2 to 3 times greater than on flow intervals less than 5 years (Figure 69). Reed canary grass, sweet clover and velvetleaf exhibit a low likelihood of occurrence on lands with flow-return intervals exceeding 10 years compared to shorter flow-return intervals (Figure 69). The likelihood of encountering Japanese hops is highest on flow-return intervals between 5 and 50 years, with moderate reductions toward the extremes of the flow-return interval spectrum (Figure 69).

Table 16. Distribution of sampling points and exotic species occurrences among LCPI flow-return intervals.

All species showed significant deviation from the expected frequency based on sampling point distribution (Chi-square test, $\alpha = 0.05$; $p < 0.001$; flow-return intervals greater than 50 years were combined into a single class in order to improve approximations of p).

Sample points	Flow-return interval (years)									Total	Similarity to sampling distribution
	0-2	2-5	5-10	10-20	20-50	50-100	100-200	200-500	>500		
	1,169	1,752	553	286	138	29	10	10	30	3,977	--
<i>Alliaria petiolata</i>	23	95	73	54	17	1	2	2	8	275	69.1%
<i>Humulus japonicus</i>	291	586	177	129	70	14	5	6	8	1,286	93.0%
<i>Phalaris arundinacea</i>	204	332	150	69	36	7	3		2	803	92.5%
<i>Sorghum halepense</i>	180	249	88	24	9		1		3	554	94.0%
<i>Melilotus officinalis</i>	82	94	3	2	1		2	1		185	77.2%
<i>Abutilon theophrasti</i>	65	37	6	1						109	68.8%

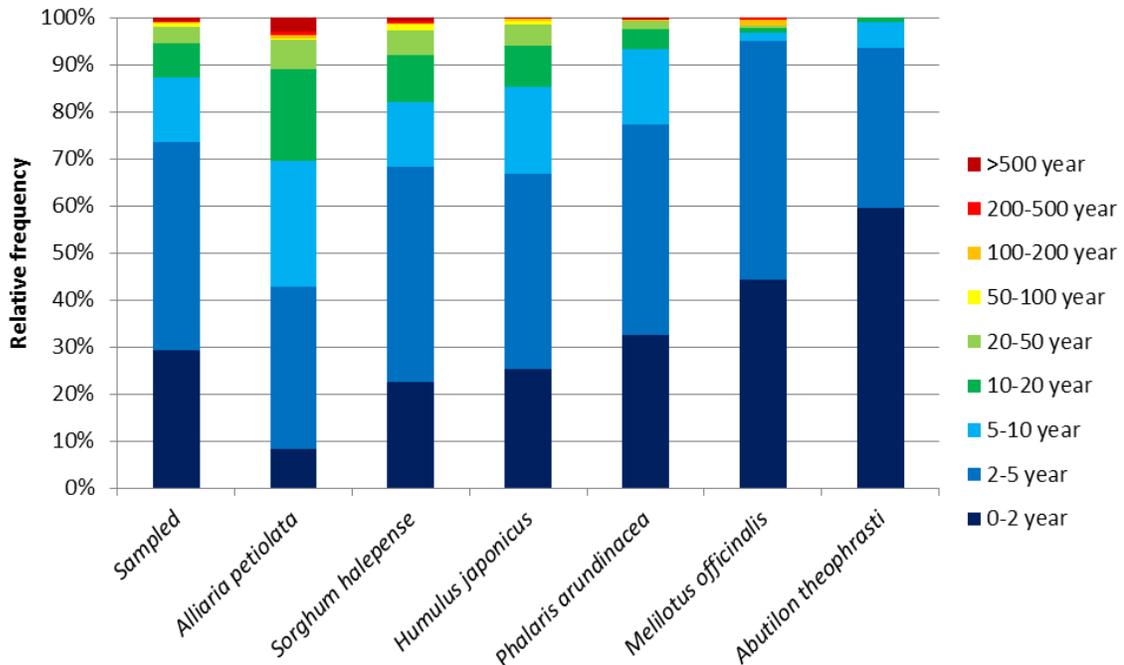


Figure 68. Relative frequency of exotic species sampling points and exotic species occurrences amongst flow-return intervals.

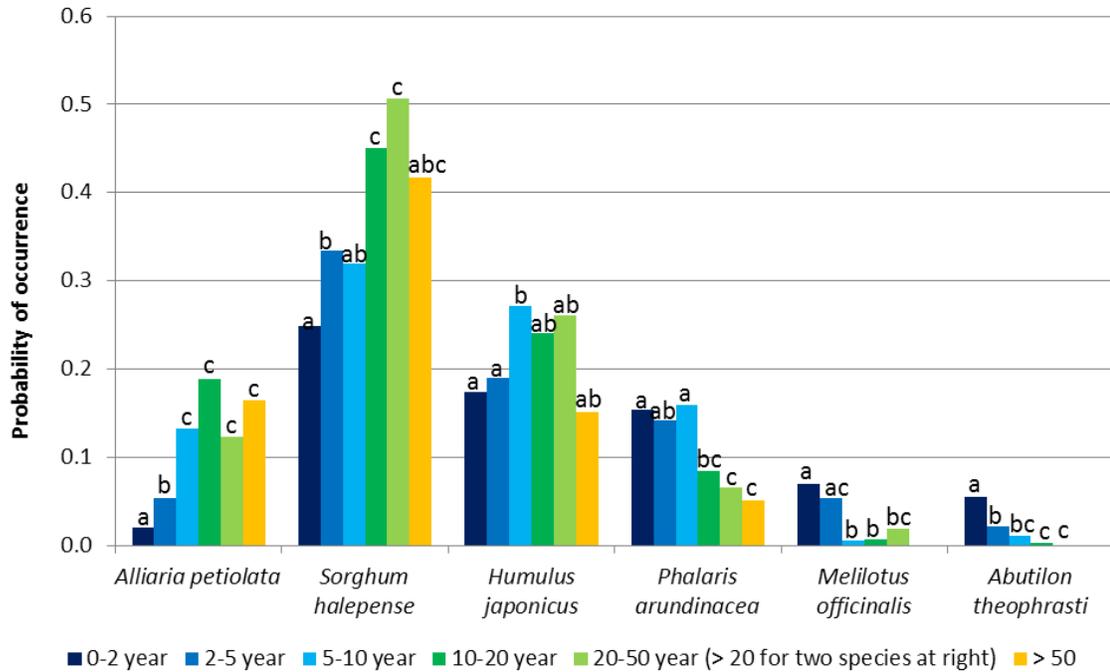


Figure 69. Probability that the indicated exotic species will occupy land with a given flow-return interval.

For each species, flow-return intervals that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$).

Lands with flow-return intervals exceeding 10 years are more abundant and represent a greater proportion of the sampled area in the Prairie Parkland (Temperate) Province than in the Central Interior Broadleaf Forest Province (data not shown; Cleland et al. 2007). The probability that garlic mustard will occur on flow-return intervals less than 10 years is approximately the same in both provinces; however, it is more likely in the forest province to occur on lands with flow-return intervals between 10 and 50 years and less likely to occur on flow-return intervals exceeding 50 years (Figure 70). Velvet leaf shows a consistently higher likelihood of occurring on frequently flooded sites in both provinces (Figure 70). Nearly all of the variation in the distribution of hops and reed canary grass (Figure 69) is due to differences observable in the prairie province (Figure 70). The prairie province accounts for all of the sweet clover occurrences on infrequently flooded sites, but the forest province accounts for most of the occurrences in frequently flooded sites (Figure 70).

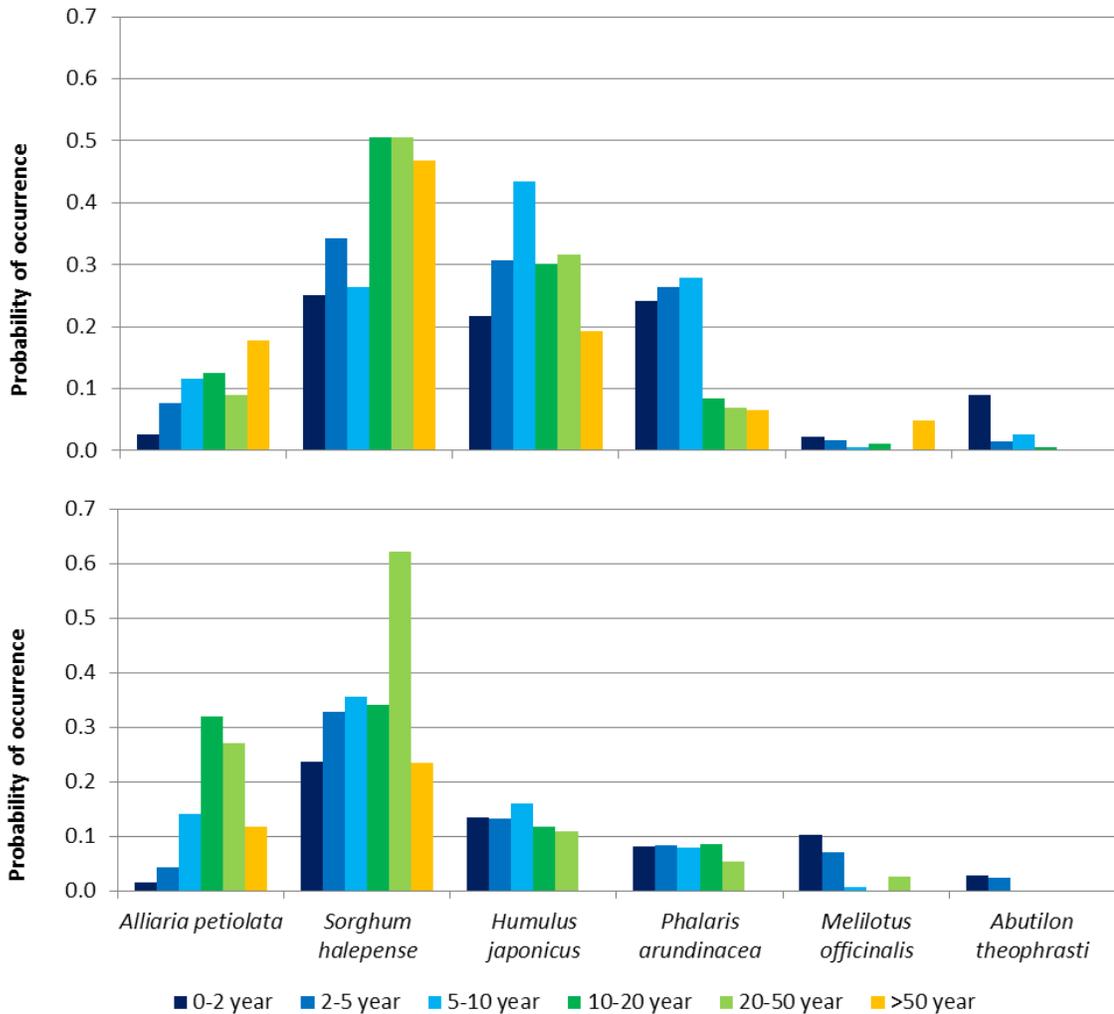


Figure 70. Probability that the exotic species will occupy land with the given flow-return interval in the Prairie Parkland (Temperate) Province (top) and the Central Interior Broadleaf Forest Province (bottom).

Probabilities were not tested for statistical differences between flow-return intervals or regions.

Cover by flow-return interval

Johnson grass mean percent cover values exhibit the clearest relationship with flow-return interval, increasing with the length of the flow-return interval (Figure 71). Reed canary grass and sweet clover mean cover values are highest in frequently flooded locations; these species are virtually absent from infrequently flooded locations. Japanese hops also exhibit a trend toward greater mean cover on more frequently flooded sites. Garlic mustard cover exhibits no trend associated with flow-return interval. Velvetleaf was only encountered on frequently flooded sites (less than 20 year flow-return interval), but no clear trend in cover could be identified.

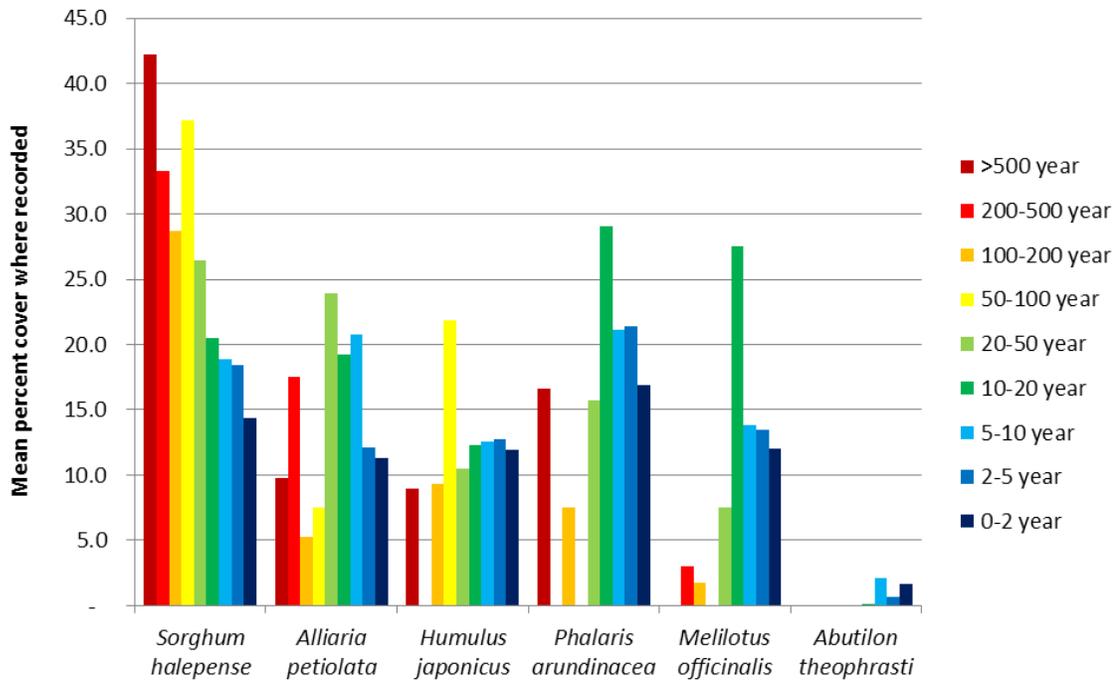


Figure 71. Bar graph of mean cover for six exotic species by flow-return interval class.

As a general rule, the lowest quantile limits were encountered on sites with flow-return intervals less than two years, indicating that the examined species do not tend to become abundant when they establish on these sites (Figure 72). Analysis of variance indicates significant differences in the distribution of cover values between flow-return interval for garlic mustard and Johnson grass; however, pairwise comparisons between intervals for garlic mustard were not significantly different ($\alpha = 0.05$). Garlic mustard tended to have the highest upper quantile values on sites with flow-return intervals between 5 and 50 years (Table 17, Figure 72). On sites with flow-return intervals greater than 20 years, the median equals that from the 5 to 10 and 10 to 20 year classes; however, differences in distribution are evident in a reduction in the number of records with low cover values (indicated by an increase in the lower quantile limits) and an absence of high cover values (indicated by a reduction in the upper quantile limit). Only for Johnson grass did pairwise comparisons identify statistically significant differences between flow classes (Table 17, Figure 72). Infrequently flooded classes had higher quantile values than frequently flooded classes, consistent with the trend of greater mean cover with increasing flow-return interval.

Table 17. Results of Kruskal-Wallis analysis of variance on ranks with Dunn's multiple comparison tests comparing exotic species cover between flow-return intervals.

Classes not sharing a letter have significantly different distributions for the indicated species ($\alpha = 0.05$).

Flow-return interval	N	25%	Median	75%
<i>Abutilon theophrasti</i> (H = 1.623; 5 df; P = 0.444)				
0-2 year	65	0.01	0.05	3
2-5 year	37	0.01	0.01	0.584
> 5 Year	7	0.01	0.05	3
<i>Alliaria petiolata</i> (H = 16.071; 5 df; P = 0.007)				
0-2 year	23	3	7.5	7.5
2-5 year	95	0.5	3	17.5
5-10 year	73	3	7.5	37.5
10-20 year	54	3	7.5	37.5
20-50 year	17	5.25	7.5	50
>50 year	13	5.25	7.5	17.5
<i>Humulus japonicus</i> (H = 4.426; 5 df; P = 0.490)				
0-2 year	204	1.594	7.5	17.5
2-5 year	332	0.5	7.5	17.5
5-10 year	150	3	7.5	17.5
10-20 year	69	3	7.5	17.5
20-50 year	36	0.5	3	17.5
>50 year	12	4.125	12.5	17.5
<i>Melilotus officinalis</i> (H = 3.314; 4 df; P = 0.507)				
0-2 year	82	0.5	7.5	17.5
2-5 year	94	0.656	7.5	17.5
5-10 year	3	0.01	4	37.5
10-50 YEAR	3	7.5	17.5	37.5
>50 year	3	0.5	3	3
<i>Phalaris arundinacea</i> (H = 5.313; 5 df; P = 0.379)				
0-2 year	206	0.5	3.1	20.5
2-5 year	257	0.5	7.5	37.5
5-10 year	90	2.52	7.65	37.5
10-20 year	24	0.5	27.5	46
20-50 year	9	0.5	7.5	37.5
>50 year	4	5.53	7.5	30
<i>Sorghum halepense</i> (H = 46.177; 5 df; P = <0.001)				
0-2 year ^a	291	0.5	7.5	17.5
2-5 year ^{ab}	587	3	7.5	37.5
5-10 year ^{abc}	177	3	7.5	37.5
10-20 year ^{bcd}	129	3	17.5	37.5
20-50 year ^{cd}	70	7.5	17.5	37.5
>50 year ^d	33	17.5	37.5	62.5

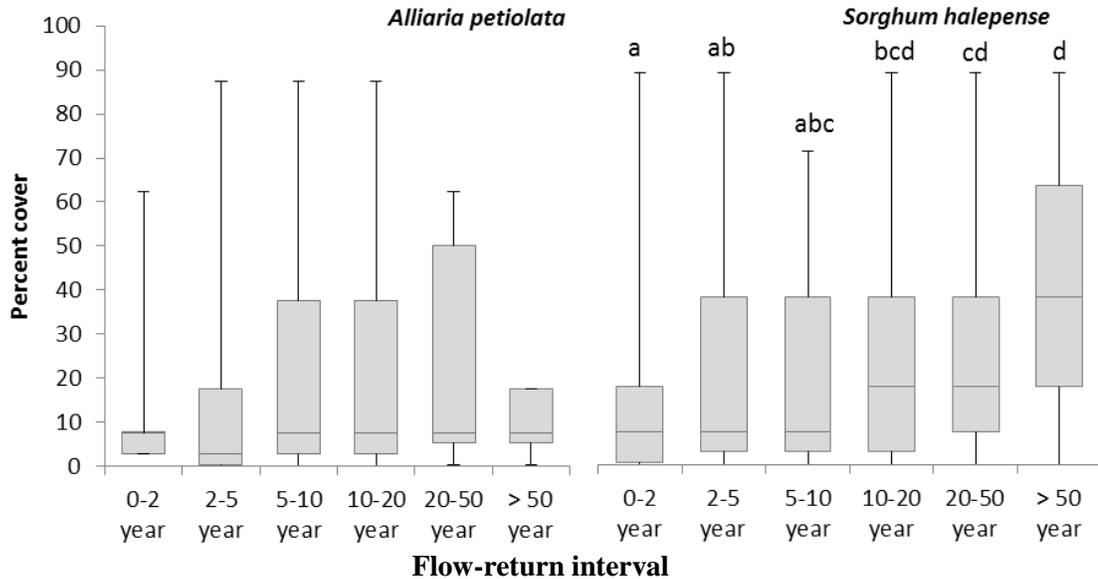


Figure 72. Quantile distribution for species with significant differences in the distribution of cover values between flow-return intervals.

Upper and lower whiskers represent 4th and 1st quantiles; upper and lower boxes represent 3rd and 2nd quantiles, with the median at the dividing line. Intervals that do not share a letter have significantly different distributions (Kruskal-Wallis analysis of variance on ranks with *post-hoc* Dunn's test; $\alpha = 0.05$). Pairwise comparisons for *Alliaria petiolata* were not significant.

Sites on which garlic mustard is most likely to become abundant (cover exceeding 15 percent) are those with flow-return intervals between 5 and 20 years (Figure 73). Compared to its likelihood of occurrence (Figure 69), garlic mustard is even less likely to exceed 15 percent cover on sites with a flow-return interval below 5 years. Johnson grass shows a trend toward greater likelihood of becoming abundant as flow-return interval increases (Figure 73), consistent with its likelihood of occurrence (Figure 69) and with the strong positive response in mean cover shows to increasing flow interval (Figure 71). Sites with moderate flow-return intervals are most at risk for Japanese hops exceeding 15 percent (Figure 73), but differences between flow classes are slight. The risk of reed canary grass and sweet clover becoming abundant decreases as flow-return interval increases; the only two instances in which velvetleaf exceeded 15 percent cover were recorded on the 0 to 2 year flow-return interval (Figure 73).

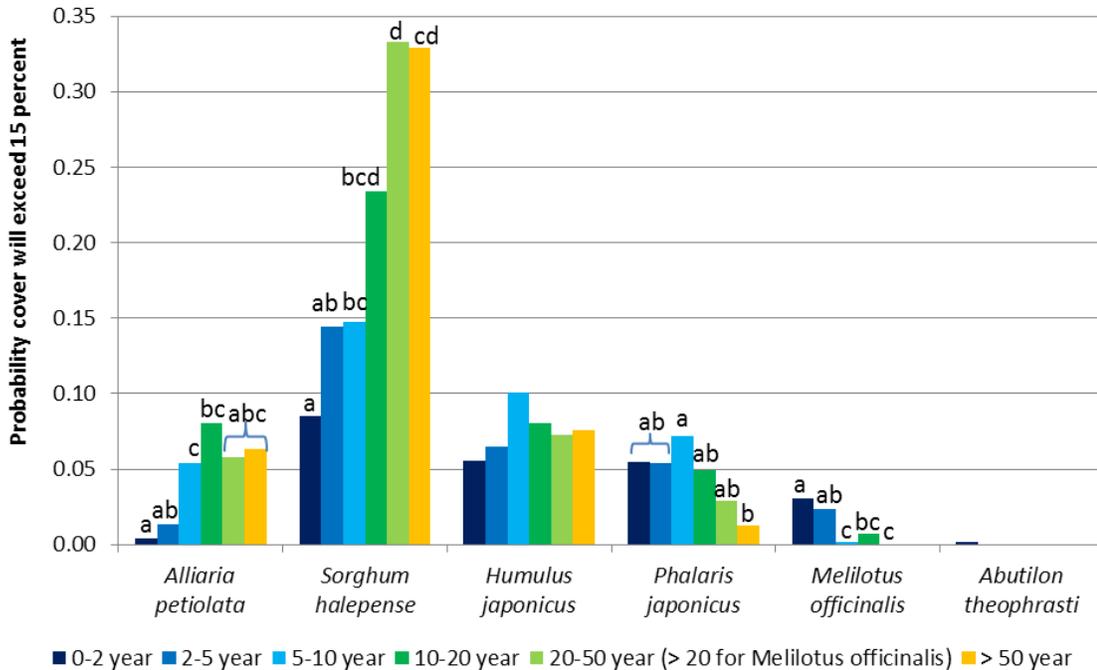


Figure 73. Probability cover for the indicated exotic species will exceed 15 percent on the flow-return interval.

For each species, flow-return intervals that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). *Humulus japonicus* did not demonstrate significant differences between classes; *Abutilon theophrasti* was not analyzed due to small sample size.

Frequency by soil drainage class

Approximately 36 percent of exotic species sample points were in the poorly drained soil classes, 43 percent in well drained classes, and 21 percent in excessively drained classes (Table 18, Figure 74). All species showed statistically significant deviations from the distribution that would be expected based upon the sampling point distribution among the various soil drainage classes (Chi-square test, $p < 0.001$). Garlic mustard showed the greatest deviation from the expected distribution, having only 71 percent similarity. Excessively drained soils accounted for 40 percent of garlic mustard occurrences, even though that drainage class represented less than 20 percent of the sampling points. Similarly, somewhat poorly drained soils represent only 16 percent of garlic mustard detections, compared to 30 percent of the sampled points. Along with Japanese hops, garlic mustard is virtually absent from the most poorly drained classes (these species were detected only 5 times at 273 sample locations on poorly drained soils). Sweet clover and velvetleaf occur less frequently on excessively drained soils than would be expected. The former occurs disproportionately more often on well drained soils and the latter occurs disproportionately more often on

somewhat poorly drained soils. Sweet clover had the second lowest percent similarity with the sampling distribution among of the six exotic species analyzed.

Table 18. Distribution of exotic species sampling points and exotic species occurrences among LCPI soil drainage classes.

All species showed significant deviation from the expected frequency based on sampling point distribution (Chi-square test, $\alpha = 0.05$; $p < 0.001$).

	Very poorly drained	Poorly drained	Somewhat poorly drained	Moderately well drained	Well drained	Somewhat excessively drained	Excessively drained	Total	Percent similarity to sampling distribution
Sample points	167	89	1,170	307	1,423	56	752	3,964	--
<i>Alliaria petiolata</i>	1	0	36	3	111	4	120	275	70.8%
<i>Humulus japonicus</i>	0	4	249	79	249	15	199	795	89.5%
<i>Phalaris arundinacea</i>	1	42	210	42	166	12	114	551	87.7%
<i>Sorghum halepense</i>	63	7	335	136	499	31	215	1,286	92.5%
<i>Melilotus officinalis</i>	9	3	56	7	95	0	15	185	83.1%
<i>Abutilon theophrasti</i>	13	0	46	9	37	1	3	109	79.1%

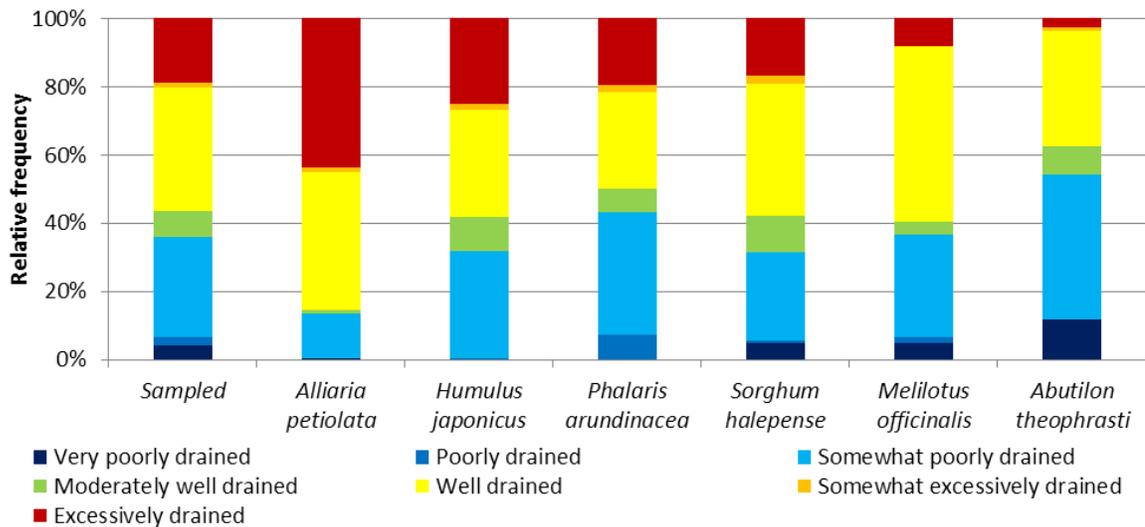


Figure 74. Relative frequency of exotic species sampling points and exotic species occurrences amongst soil drainage classes.

The probability that garlic mustard will be found on a site increases from 3 percent on poorly drained soils to more than 15 percent on excessively drained soils, with significant differences between soil drainage groups (Figure 75). Japanese hops are approximately 50 percent more likely to occur on excessively drained soils than on other soil types (Figure 75). Excessively drained soils appear to provide

poor habitat for sweet clover and velvetleaf; both species are significantly less likely to occur there than on poorly drained or well drained soils (Figure 75). Johnson grass is significantly more likely to occur on soils with moderate drainage capacity (Figure 75). Reed canary grass is least likely to occur on well drained soils, significantly less than on poorly drained soils(Figure 75).

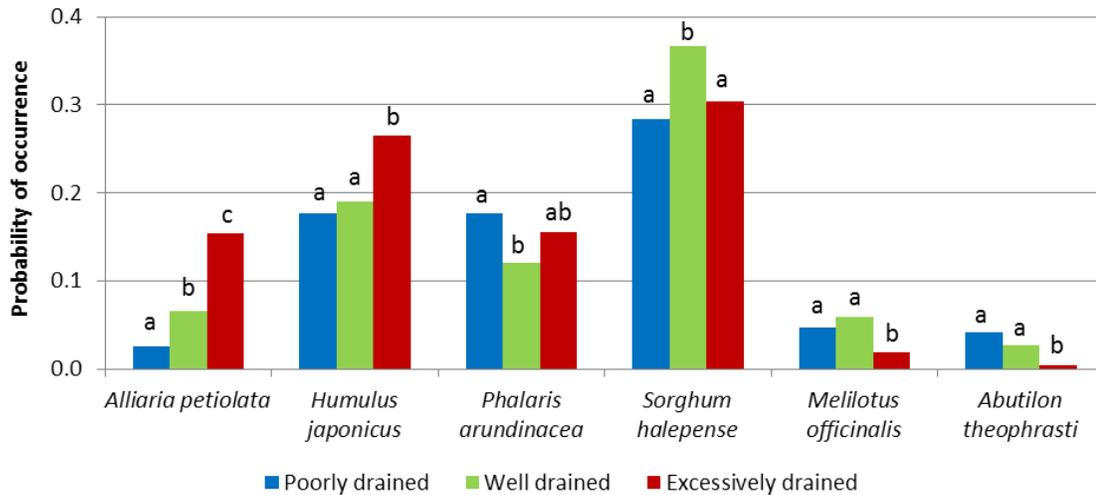


Figure 75. Probability that exotic species will occupy land with the indicated soil drainage group. For each species group, drainage classes that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$).

Examination of the distribution of exotic species among soil drainage classes at the ecological province indicates a few important differences between provinces. First, the “somewhat excessively drained” and “moderately well drained” soil designations are more frequently applied in the Prairie Parkland Province than in the Central Interior Broadleaf Forest Province (data not shown). Second, the very poorly drained soil class is not represented among sample points in the prairie province and the poorly drained class is not represented among sample points in the forest province. These differences may reflect real differences in the abundance of the classes; however, dramatic shifts in class abundance associated with state and county boundaries suggest these differences may be due to variable mapping standards used in the two regions. Excessively drained soils represent a larger proportion of the prairie province than the forest province. Collectively, lands classified as somewhat poorly, poorly, or very poorly drained represent nearly the same proportion in each region (about 36 percent)

Within this context, comparison of occurrence probabilities between ecological provinces indicates that ecological setting affects the distribution of species. Regardless of ecological province, the

likelihood that garlic mustard and Japanese hops will be found on a site increases with soil drainage (Figure 76). For hops, this trend is somewhat stronger in the forest province; for garlic mustard, it is somewhat stronger in the prairie province (Figure 76). Velvetleaf is least likely to be found on excessively drained soils in both provinces (Figure 76). The data indicate that the differences in likelihood in occurrence for sweet clover are driven entirely by data from the forest province; only slight differences between soil drainage classes are evident in the prairie province (Figure 76). Well drained soils are at greater risk of invasion by reed canary grass in the forest province, but are less likely to be invaded by that species in the prairie province (Figure 76). The likelihood that Johnson grass will occupy well and excessively drained soils decreases from the prairie province to the forest province; poorly drained soils are more likely to be occupied by Johnson grass in the forest province than in the prairie province (Figure 76).

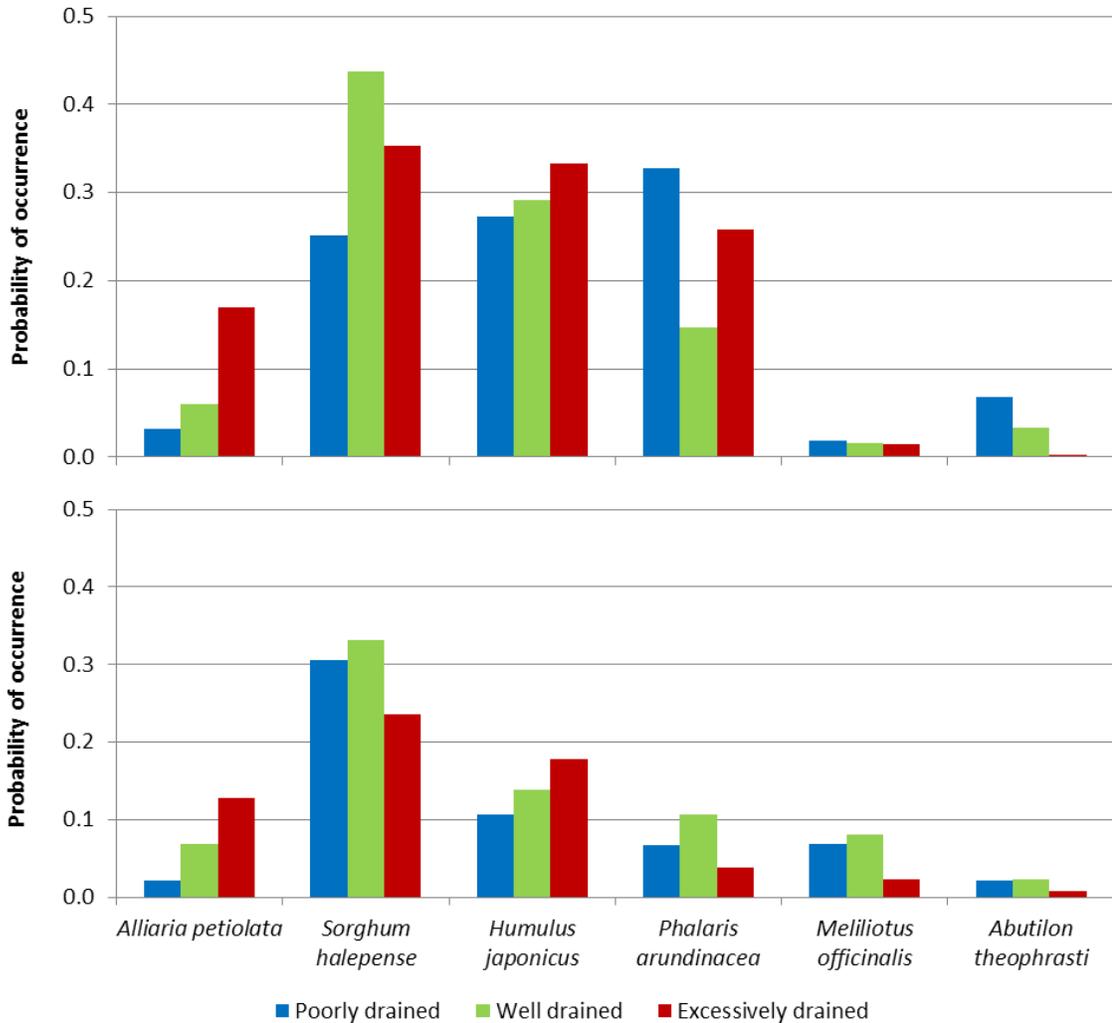


Figure 76. Probability that exotic species will occupy land with the indicated soil drainage group in the Prairie Parkland (Temperate) Province (top) and the Central Interior Broadleaf Forest Province (bottom).

Probabilities were not tested for statistical differences between soil-drainage classes or regions.

Cover by soil drainage class

The relationships between exotic species cover and LCPI soil drainage classes varied with species. Japanese hops mean cover exhibits the clearest relationship with soil drainage classes, having a steady increase in mean cover as soil drainage capacity diminishes (Figure 77). Reed canary grass also has greater cover on very poorly drained soils, but garlic mustard has greater cover on well drained soils. Sweet clover and velvetleaf have their greatest mean cover on moderately drained soils. Johnson grass has a uniformly high mean cover value across soil drainages classes.

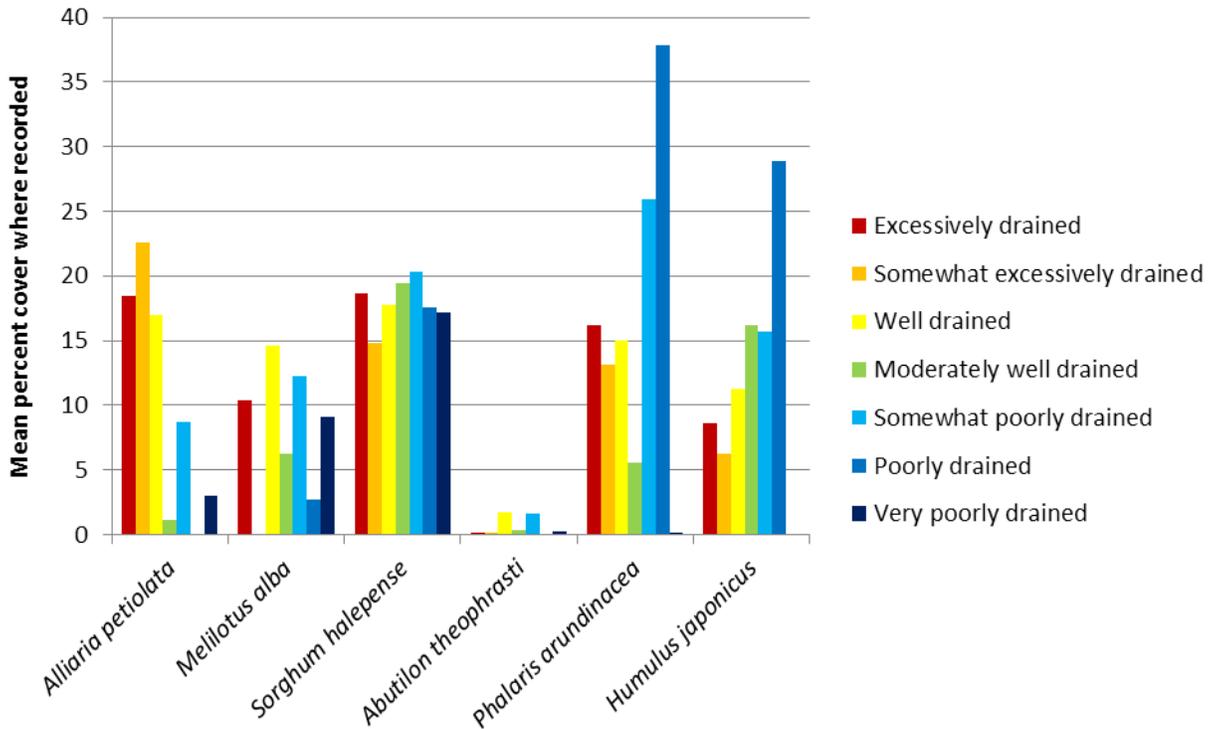


Figure 77. Bar graph of mean cover for six exotic species by LCPI soil drainage class in order of increasing abundance as soil drainage capacity decreases.

Analysis of variance on ranks indicates that Japanese hops and reed canary grass have significantly different distributions between aggregated soil drainage classes (Table 19). For Japanese hops, poorly drained soils have a higher 25th percentile value (3 percent) than both well drained and excessively drained soils (0.5 percent), indicating that hops occur at lower cover values relatively less frequently on poorly drained sites (Figure 78). Cover on excessively drained soils never exceeded 62.5 percent; but reached 87.5 percent on poorly and well drained soils. All quantile values for reed canary grass were highest in poorly drained soils, indicating a greater abundance on those soil types than on well or excessively drained soils (Table 19).

Table 19. Results of Kruskal-Wallis analysis of variance on ranks with Dunn's multiple comparison tests comparing exotic species cover between soil drainage classes.

Classes not sharing a letter have significantly different distributions for the indicated species ($\alpha = 0.05$).

Aggregated drainage class	N	25th percentile	Median	75th percentile
<i>Abutilon theophrasti</i> (H = 4.265; 2 df; P = 0.119)				
Poorly drained	59	0.01	0.5	3.0
Well drained	46	0.01	0.05	1.04
Excessively drained	4	0.01	0.01	0.04
<i>Alliaria petiolata</i> (H = 1.679; 2 df; P = 0.432)				
Poorly drained	37	2.5	7.5	7.5
Well drained	114	3.0	7.5	17.5
Excessively drained	124	3.0	7.5	37.5
<i>Humulus japonicus</i> (H = 27.848; 2 df; P < 0.001)				
Poorly drained ^a	253	3.0	7.5	17.5
Well drained ^b	328	0.5	7.5	17.5
Excessively drained ^b	214	0.5	3.0	17.5
<i>Melilotus officinalis</i> (H = 5.820; 2 df; P = 0.054)				
Poorly drained	68	0.5	3.0	17.5
Well drained	102	3.0	17.5	17.5
Excessively drained	15	3.0	7.5	17.5
<i>Phalaris arundinacea</i> (H = 32.074; 2 df; P < 0.001)				
Poorly drained ^a	217	3.0	10	37.5
Well drained ^b	208	0.5	3.0	10.5
Excessively drained ^b	126	0.5	4.0	17.5
<i>Sorghum halepense</i> (H = 0.221; 2 df; P = 0.895)				
Poorly drained	405	3.0	7.5	37.5
Well drained	635	3.0	7.5	37.5
Excessively drained	246	3.0	7.5	37.5

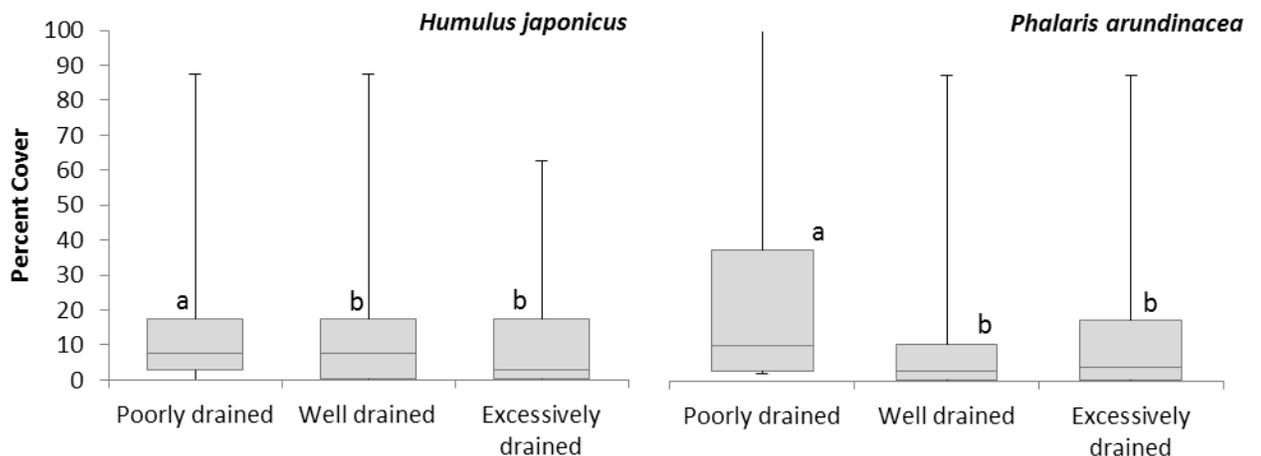


Figure 78. Quantile distribution for two species with significant differences in the distribution of cover values between soil drainage classes.

Upper and lower whiskers represent 4th and 1st quantiles; upper and lower boxes represent 3rd and 2nd quantiles, with the median at the dividing line. Intervals that do not share a letter have significantly different distributions (Kruskal-Wallis analysis of variance with *post-hoc* Dunn's test; $\alpha = 0.05$).

Table 20. Distribution of sample points and locations where exotic species cover exceeded 15 percent.

	Very poorly drained	Poorly drained	Somewhat poorly drained	Moderately well drained	Well drained	Somewhat excessively drained	Excessively drained
Sample points	167	89	1,171	307	1,423	56	752
<i>Alliaria petiolata</i>			6		43	2	44
<i>Humulus japonicus</i>		3	104	34	79	3	52
<i>Phalaris arundinacea</i>		14	101	5	45	2	36
<i>Sorghum halepense</i>	26	3	160	68	212	13	95
<i>Melilotus officinalis</i>	3		22	2	50		5
<i>Abutilon theophrasti</i>			1		1		

Garlic mustard shows a clear and significant trend of increasing likelihood of becoming abundant (cover greater than 15 percent) as soil drainage improves (Figure 79). Although Japanese hops are more likely to occur on excessively drained soils, the likelihood of it becoming abundant is nearly equal across soil drainage types. Reed canary grass is 2 to 3 times more likely to become invasive on poorly drained soils than other soil types (Figure 79); it is also more likely to occur on poorly drained soils (Figure 75). The likelihood that Johnson grass will become invasive on the various soil drainage types is nearly identical to the likelihood that it will occur at all (Figure 75, Figure 79), consistent with the assessment of mean cover by soil drainage class (above). Sweetclover is significantly less likely to become abundant on excessively drained soils. Velvetleaf is unlikely to become abundant on any soil type (Figure 79).

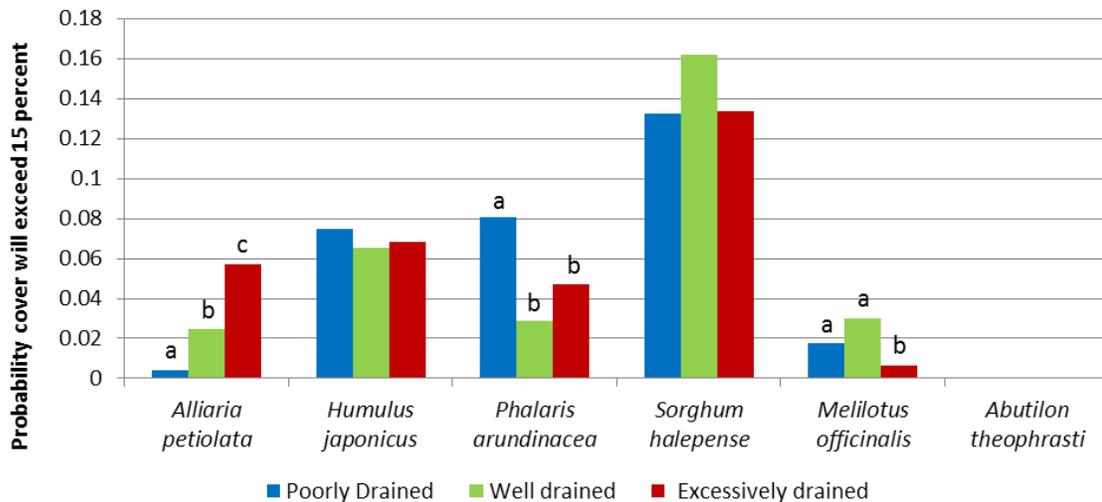


Figure 79. Probability that exotic species will occupy land with the indicated soil drainage. For each species group, drainage classes that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Groups without letters did not demonstrate significant differences between classes.

Native species

Plot data and data relating to dominant species identified at mapping points during 2012 sampling were used to identify relationships between native species or species groups and LCPI classes. The probability of a species group occurring on a particular drainage or flow class was calculated solely from plot data; the probability that species would become abundant (cover exceeding 15 percent) was calculated from both plot and community classification point data. The species groups of interest include cottonwood (*Populus deltoides*), willows (*Salix* spp.), late-successional woody species (Table 5), and sedges (*Carex* spp. and *Cyperus* spp.) and smartweeds (*Polygonum* spp.) indicative of herbaceous wetlands. Soils were aggregated into “Poorly Drained”, “Well Drained” and “Excessively Drained” groups as for exotic species; flow-return intervals great than 100 years were aggregated into a single class, and those between 20 and 100 years were aggregated into another.

Flow-return interval

Smartweeds and sedges occur infrequently on lands with long flow-return intervals; fewer than one percent of the occurrences of these species are on land with flow-return intervals exceeding 20 years, despite the fact that those flow classes represent more than 10 percent of the sampling locations (Table 21; Figure 80). Willows also occur at on sites with long flow-return intervals less frequently than would be expected based on the distribution of plots. Cottonwood is ubiquitous within Big Muddy and at other sites in the Kansas, Grand, and Osage sections, within which most of the plots are distributed. Consequently, the cottonwood frequency distribution is nearly identical to that of the plots (95 percent similarity; Chi-square test, $p = 0.65$; Table 21). Only late-successional species exhibited a tendency to occur more often on infrequently flooded lands.

Table 21. Distribution of sampling plots and species group occurrences among LCPI flow-return intervals.

All species groups excluding cottonwood showed significant deviation from the expected frequency based on sampling point distribution (Chi-square test, $\alpha = 0.05$; $p < 0.001$; flow-return intervals greater than 50 years were combined into a single class in order to improve approximations of p).

	Flow-return interval (years)								Total	Similarity to sampling distribution	
	0-2	2-5	5-10	10-20	20-50	50-100	100-200	200-500			>500
Plots	121	182	48	19	4	3		4	29	410	--
Sedges	77	122	23	4	0	0	0	0	2	228	86.6%
Smartweeds	98	245	50	8	1	1	0	0	1	404	83.1%
Willows	89	234	59	27	1	5	0	1	8	424	84.8%
Cottonwood	79	139	42	17	3	3	0	4	24	311	95.9%
Late-successional species (Table 5)	193	188	55	15	9	12	0	13	117	602	82.1%

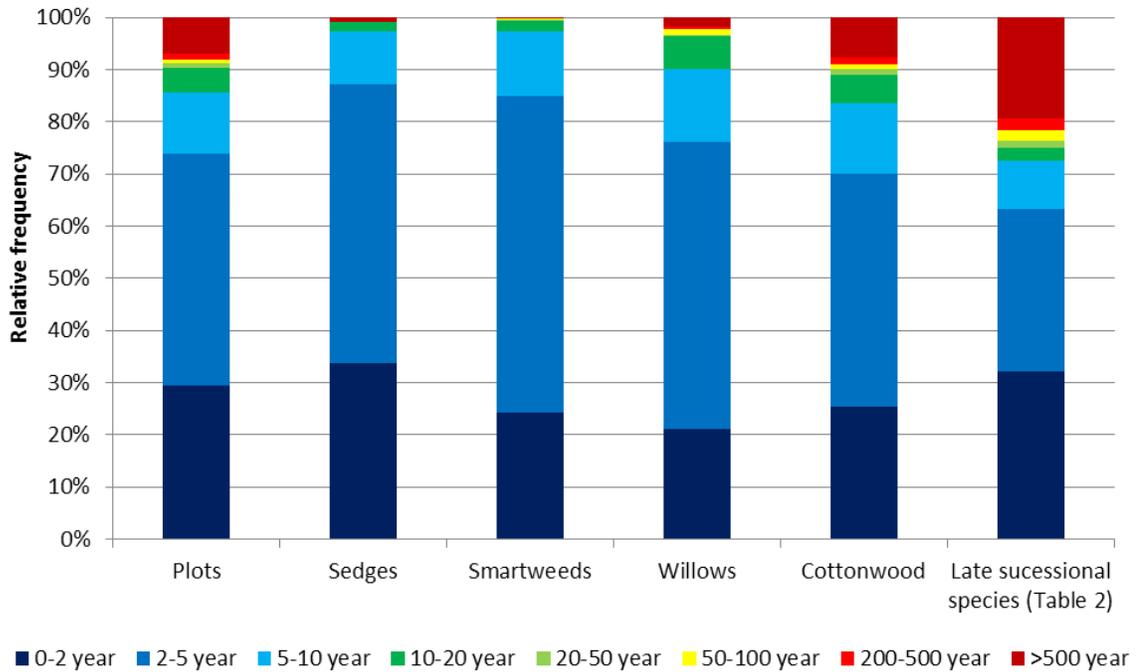


Figure 80. Relative frequency of sampling points and species group occurrences amongst flow-return intervals.

Sedges and smartweeds are more likely to occur at frequently flooded sites than at infrequently flooded sites (Figure 81). Willows (*Salix* spp.) are least likely to occur at the extremes of the flow-return interval spectrum (Figure 81). Cottonwood shows little difference between flow classes, but peak likelihood of occurrence is on flow-return intervals between 5 and 20 years, and it is slightly less likely to occur on frequently flooded sites (Figure 81). Occurrence of late-successional species is 30 to 100 percent more likely on lands with flow intervals exceeding 20 years than anywhere else (Figure 81).

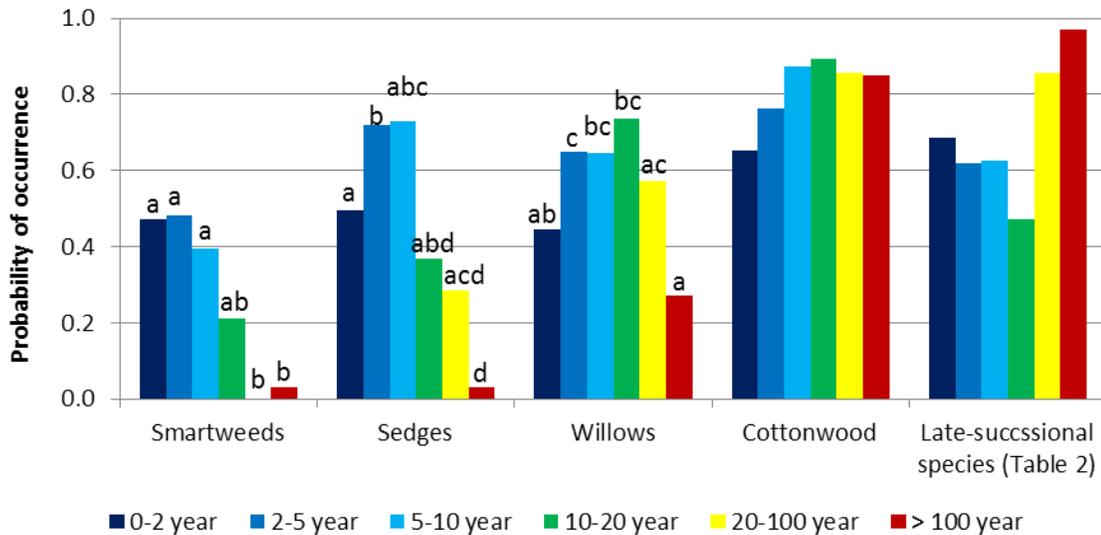


Figure 81. Probability that select species groups will occupy land with the indicated flow-return interval.

For each species group, flow-return intervals that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Species groups without letters did not demonstrate significant differences between classes.

The 15 percent cover criterion used to identify locations where exotic species are likely to become invasive also was used to identify locations in which the species groups of interest were a major component of the floral composition. Smartweeds are most likely to become abundant where flow-return intervals are less than 2 years, and they show a decreasing likelihood of becoming abundant as flow-return interval increases (Figure 82). Sedges show a similar pattern, but differences between flow-return intervals are smaller (Figure 82). The likelihood of willows becoming abundant is highest where flow-return intervals are between 2 and 20 years, with much reduced abundance at longer intervals (Figure 82). The likelihood of cottonwood exceeding 15 percent cover is highest where the flow-return interval is between 10 and 20 years; that likelihood decreases toward the extremes of the flow spectrum (Figure 82). The likelihood of

late-successional species being a significant floral component is relatively low where flow-return intervals are less than 10 years, but increases dramatically with increasing on intervals beyond that threshold (Figure 82).

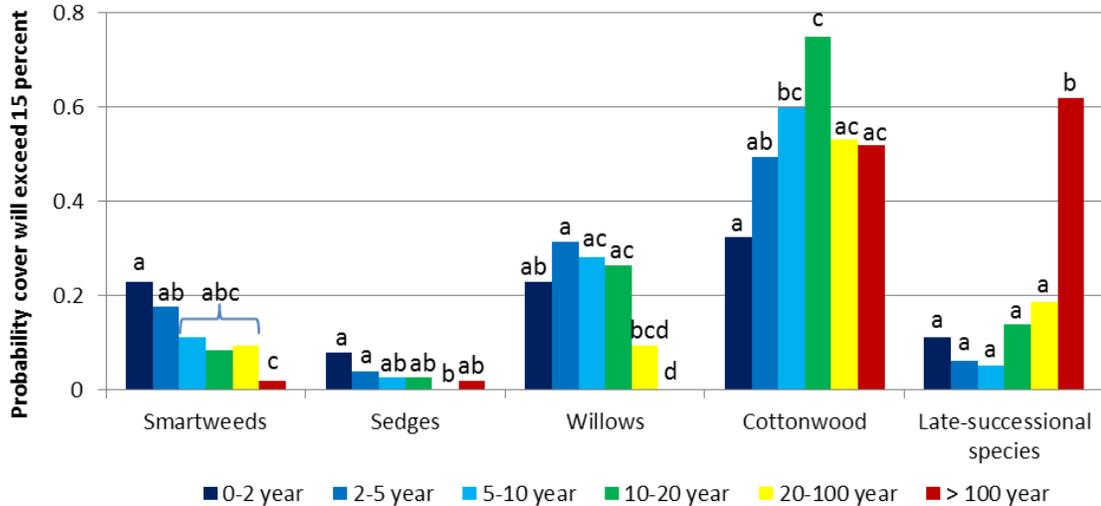


Figure 82. Probability that the cover of select species groups will exceed 15 percent on land with the indicated flow-return interval.

For each species group, flow-return intervals that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$).

Soil drainage

The distributions of species groups examined deviate far less from sampling point distribution among soil drainage classes than among flow-return intervals. Only the willow distribution has less than 90 percent similarity to the distribution of sampling points (Table 22). Relative to the frequency distribution of plots, sedges and smartweeds show a slight shift away from the extremes of the soil drainage spectrum; willows, cottonwood, and late-successional species show a slight shift toward better drained soils (Figure 83). The largest deviation from plot distribution is the reduced frequency of willows on somewhat poorly drained soils (Figure 83).

The shift away from drainage extremes for sedges and smartweeds is evident in the slightly higher probability of occurrence on well drained soils than on poorly or excessively drained soils (Figure 84). The other species groups are least likely to occur on poorly drained soils than on other drainage types, although only willow exhibited significant differences between soil drainage classes (Figure 84). Late-successional

species show the clearest trend of increasing likelihood of occurrence with better soil drainage, although this relationship is not significant (Figure 84).

Table 22. Distribution of sampling points and species group occurrences among LCPI soil drainage classes.

All species showed significant deviation from the expected frequency based on sampling point distribution (Chi-square test, $\alpha = 0.05$; $p < 0.001$).

Sample points	Very poorly drained	Poorly drained	Somewhat poorly drained	Moderately well drained	Well drained	Somewhat excessively drained	Excessively drained	Total	Similarity to sampling distribution
Smartweeds	15	1	166	48	126		45	401	91.9 %
Sedges	6	1	103	18	70		26	224	90.7 %
Willows	26	11	118	57	124		71	407	87.1 %
Cottonwood	15	7	108	31	89	1	50	301	93.1 %
Late-successional species (Table 5)	23	23	241	48	140	5	106	586	94.4 %

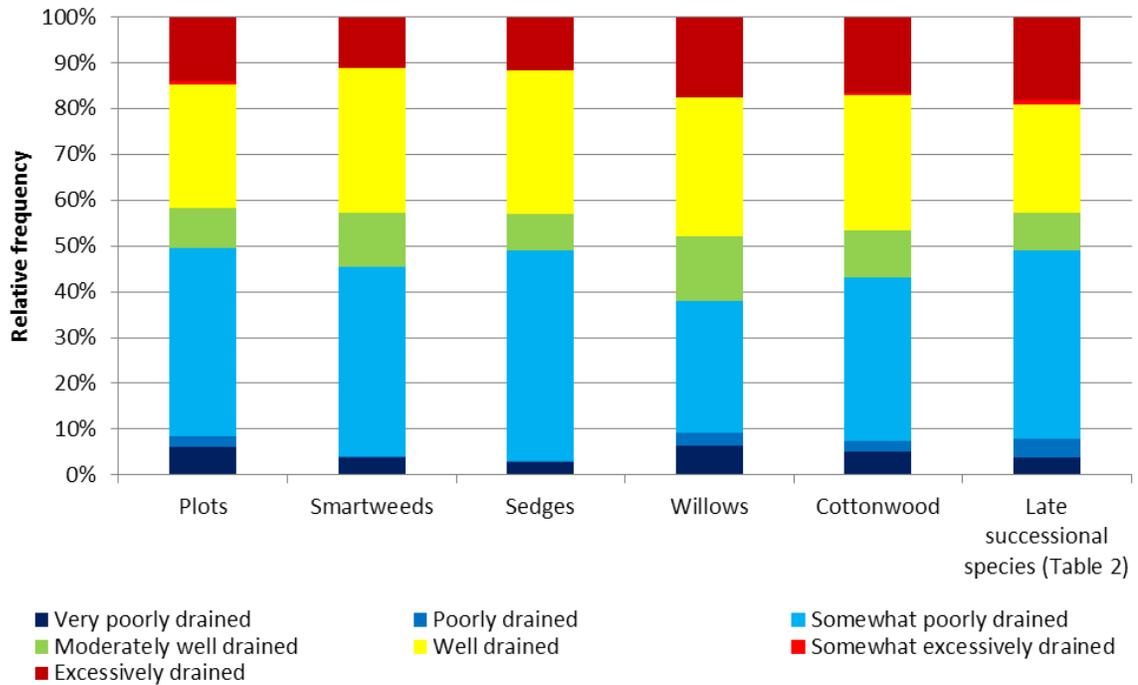


Figure 83. Relative frequency of sampling points and species group occurrences amongst soil drainage classes.

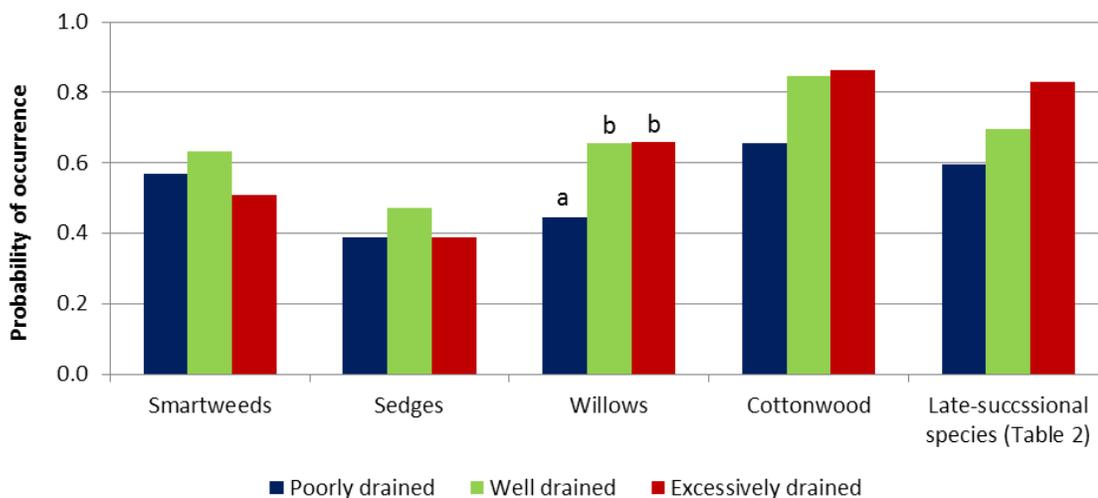


Figure 84 Probability that select species groups will occupy land with the indicated soil drainage. For each species group, drainage classes that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Species groups without letters did not demonstrate significant differences between soil classes.

Although smartweeds show little variation in the likelihood of occurrence across drainage classes (Figure 84), they are much more likely to become abundant on poorly drained soils and show a trend of decreasing likelihood with improved soil drainage (Figure 85). Sedges show a similar trend, but with much smaller, non-significant differences between soil drainage types (Figure 85). Willows and cottonwood exhibit a clear trend of increasing likelihood of becoming abundant with better soil drainage; cottonwood is significantly less likely to become abundant on poorly drained soils than elsewhere (Figure 85). Although late-successional species are more likely to occur on better drained soils (Figure 84), the likelihood of them becoming abundant is approximately equal across soil drainage classes (Figure 85).

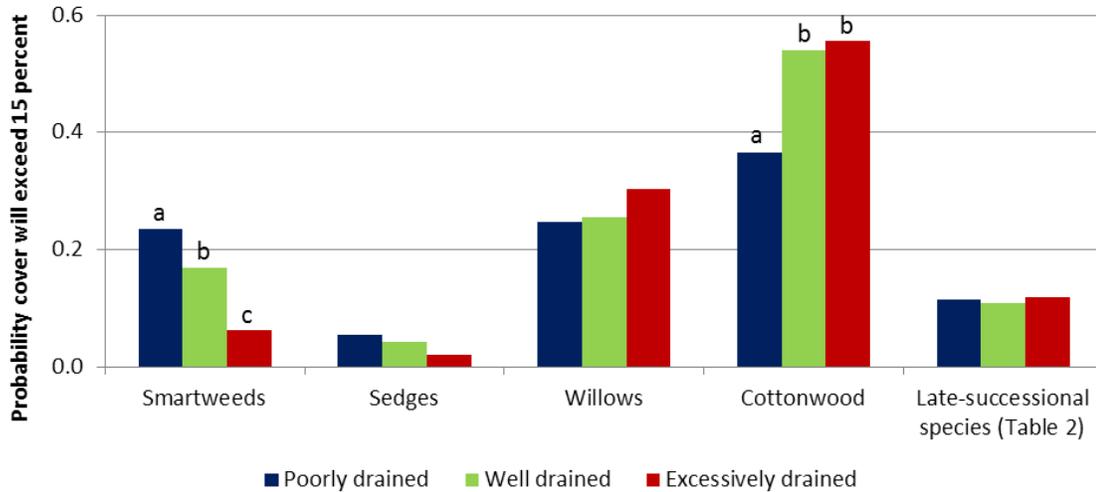


Figure 85. Probability that the cover of select species groups will exceed 15 percent on land with the indicated soil drainage.

For each species group, drainage classes that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Species groups without letters did not demonstrate significant differences between soil classes.

Community frequency and abundance analyses

The most abundant mapped community types at Big Muddy National Fish and Wildlife refuge are cottonwood and willow dominated communities, herbaceous old fields representing early-successional communities that have not yet differentiated into recognized community types, and herbaceous communities dominated by smartweeds (*Polygonum* spp.) and sedges (*Carex* and *Cyperus* spp.) (Table 23). The least abundant communities are forests in which abundant ash is diagnostic. The ash – oak – sycamore forest was limited to the mouths of upland drains entering the floodplain at Baltimore Bend, and the ash – elm – hackberry forest was recorded only at Jackass Bend (Struckhoff, 2013). Given their small sample size and restricted geographic and ecological distribution, these communities are excluded from the statistical analyses that follow.

Flow-return interval within Big Muddy

Longer flow-return intervals are extremely uncommon; accordingly, flow-return intervals greater than 50 years were aggregated into a single class for statistical analysis for most communities. For Riverine

Sand Flats, Johnson grass communities, and Cottonwood – Sycamore Forests, intervals above 20 years were aggregated; for the Central Midwest Sedge Meadow intervals above 10 years were aggregated.

Table 23. Distribution of mapped vegetation communities among LCPI flow-return intervals

Vegetation community*	Flow-return interval									Total	Percent similarity to sampling distribution
	0-2 year	2-5 year	5-10 year	10-20 year	20-50 year	50-100 year	100-200 year	200-500 year	>500 year		
Midwest Ephemeral Pond	172	182	49	8	7					418	73.7%
Cottonwood - Sycamore Forest	20	25	9	2	1	1				58	80.5%
Sandbar Willow Shrubland	255	279	126	42	31	3	2			738	86.1%
Herbaceous Old Field	217	278	95	45	33	4	1	1	3	677	85.3%
Central Midwest Sedge Meadow	11	10	5	4	2					32	89.8%
Black Willow Riparian Forest	74	90	48	17	15	1		1	2	248	92.1%
Silver Maple - Elm Forest	58	58	42	22	12	3	1	1	1	198	95.9%
Cottonwood Floodplain Woodland	230	316	227	111	60	4	3	6	13	970	96.3%
Riverine Sand Flats	56	20	23	16	10	5	2		1	133	78.2%
Box-elder Floodplain Forest	69	75	49	24	22	6	4		4	253	93.5%
Bottomland Woody Old Field	50	81	40	24	20	3	2	4	4	228	92.1%
Midwestern Cottonwood - Black Willow Forest	429	645	609	369	196	57	20	5	13	2,343	87.2%
Johnson Grass	16	41	40	15	8	2	1			123	86.2%
Ash - Oak - Sycamore Mesic Bottomland Forest**	3	3	3						5	14	64.8%
Ash - Elm - Hackberry Forest**	1	1	4	1	3		2			12	53.3%
Total mapped polygons	1,661	2,104	1,369	700	420	89	38	18	46	6,445	

* (Struckhoff et al., 2011; Struckhoff, 2013)

**Not analyzed due to low overall frequency

Figure 86 displays the relative frequency of LCPI flow-return interval polygons by total mapped area and by individual communities arranged in order from those communities mapped most often on frequently flooded areas to those mapped more often on infrequently flooded lands. The extremes of the graph and the riverine sand flats community include those communities whose distributions are least similar to the sampling point distribution. The two ash-dominated communities on the extreme right

represent mid- and late-successional communities (NatureServe, 2014), and they are more abundant on infrequently flooded sites.

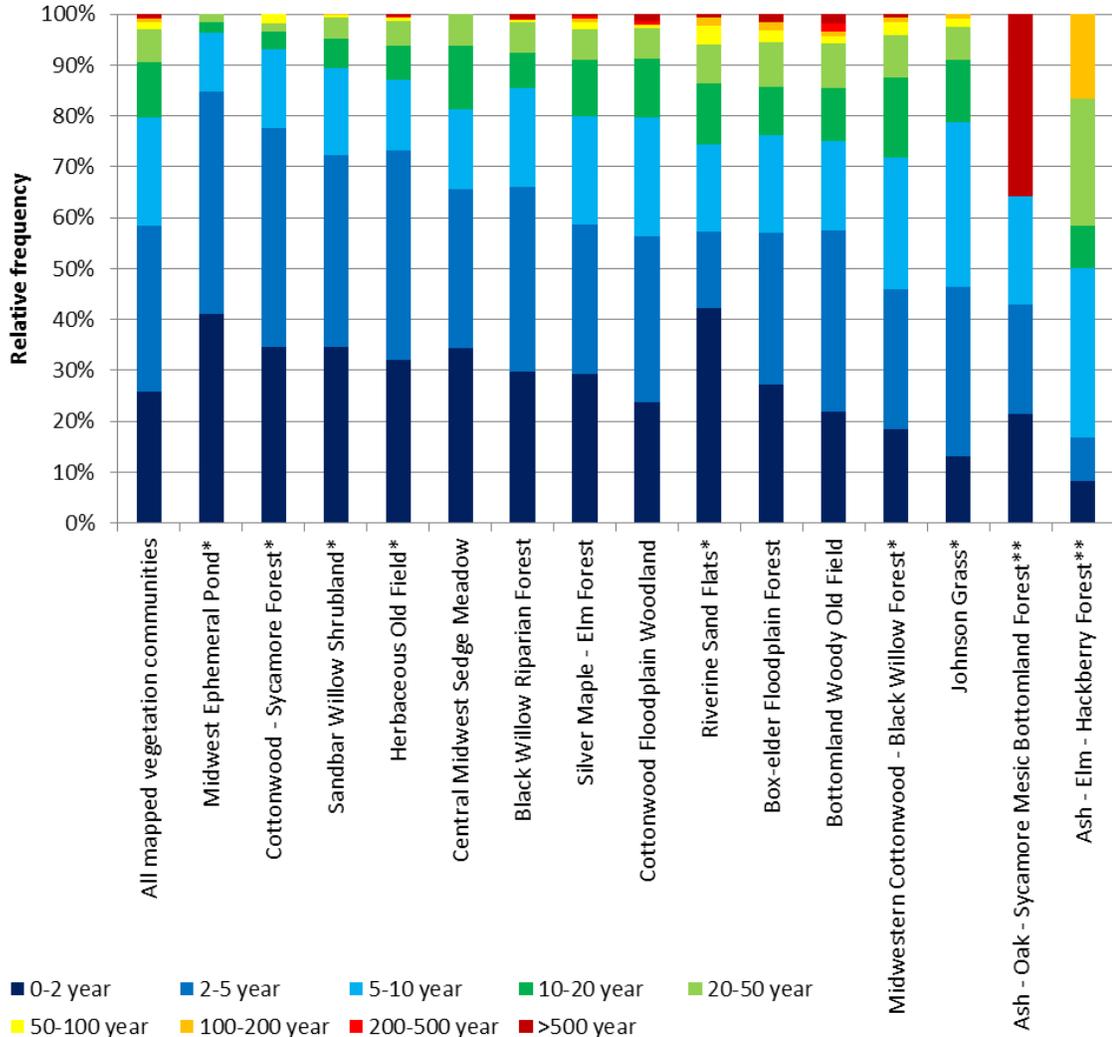


Figure 86. Relative frequency of mapped polygons and vegetation communities across LCPI flow-return intervals for Big Muddy National Fish and Wildlife Refuge.

* Significantly different (Chi-square, $\alpha = 0.05$) from distribution of flow-return intervals across the total mapped area. (Struckhoff et al., 2011; Struckhoff, 2013).

** Not analyzed due to low overall frequency

Cottonwood and willow dominated communities are broadly distributed across the flow frequency spectrum represented in Figure 86. The Midwestern Cottonwood – Willow Forest toward the right end of the graph is by far the most abundantly mapped community, consisting primarily of forests that had established following historic floods in the 1990s (Struckhoff et al., 2011; Struckhoff, 2013). The three

other forest and woodland types with abundant cottonwood—the Cottonwood Floodplain Woodland, the Black Willow Riparian Forest, and the Cottonwood – Sycamore Forest—are progressively more frequent with increasing flow frequency.

An examination of the relative abundance of communities by flow-return interval reveals patterns in community distribution related to flow-return interval. Cottonwood-dominated communities reach their maximum relative frequency on sites that have flow-return intervals between 5 and 100 years, and tend to decrease towards the ends of the flow-return interval spectrum (Figure 87). Analysis of variance indicates that the 10-20 year class has significantly greater mean relative area in the cottonwood – black willow forest community than do the 0 to 2 and 2- to 5 year classes. (When cottonwood-dominated communities are examined collectively, the 10-20 year class is significantly greater than only the 2 to 5 year interval.) This is evident in the quantile distribution graph for the community, which indicates that in polygons mapped in the 10 to 20 year flow class, the relative area exceeds 80 percent the polygon more than 75 percent of the time (Figure 88).

Sedge meadows and ephemeral ponds are most abundant in areas with short flow-return intervals, and they give way to riverine sand flats at higher elevations with longer flow-return intervals (Figure 87). Similarly, the sandbar willow shrubland is mapped more often on and occupies a larger percentage of frequently flooded lands than infrequently flooded lands. Relative frequency and area decrease from 15 and 11 percent on the 0 to 2 year flow class to 0 on lands with flow intervals greater than 200 years. Analysis of variance indicates significant differences in the relative abundance of this community between flow classes, but pairwise analysis did not identify significantly different pairs.

A reduction in the relative frequency of herbaceous old fields with increasing flow-return intervals is mirrored by an increase in the frequency of the woody old field community (Figure 87). This trend is even more evident when the metric of comparison is relative area. Herbaceous old fields decrease from more than 24 percent of the 0 to 2 year flow interval area to less than 1 percent of lands with flow-return intervals greater than 200 years; woody old fields increase from 1 to 26 percent over the same range. Analysis of variance indicates that lands with flows-return intervals greater than 50 years have a significantly greater relative abundance of woody old fields than sites with flow intervals below 2 years; quantile limits tend to increase with flow-return interval (Figure 88). Box-elder forests are more uniformly

distribution across the landscape. Relative frequency ranges from 4 percent on frequently flooded lands to 11 percent at higher locations; relative area ranges from less than 1 percent to 9 percent (Figure 87). Analysis of variance indicates significant differences in distribution between classes, but was unable to identify significant pairwise differences (Figure 88).

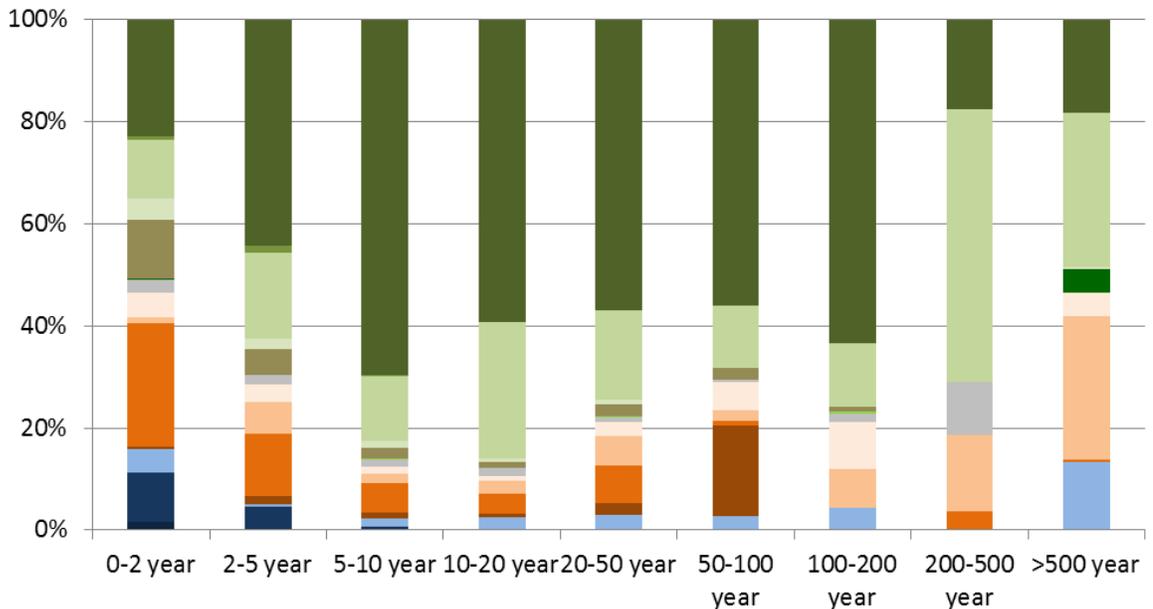
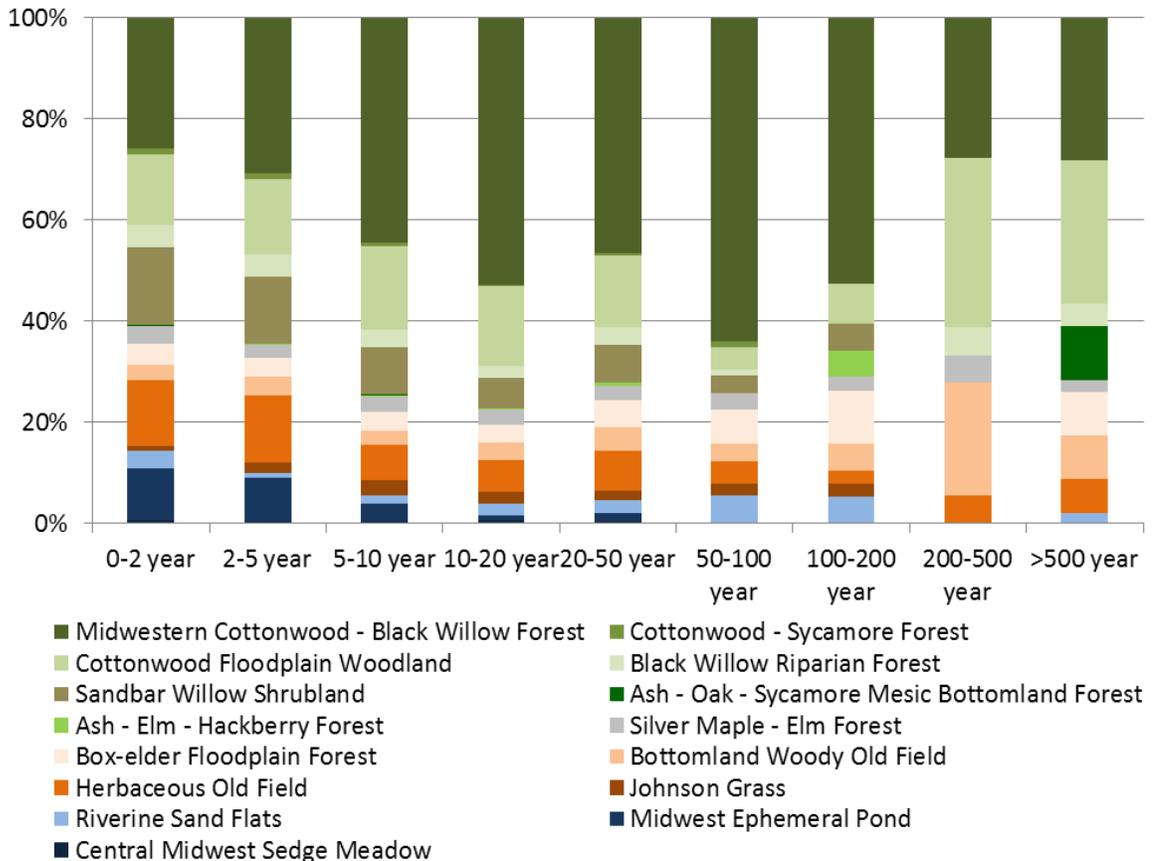


Figure 87. Relative frequency (top) and relative area (bottom) of natural communities within LCPI flow-return intervals based on intersection of LCPI model and map of vegetation communities at Big Muddy National Fish and Wildlife Refuge.

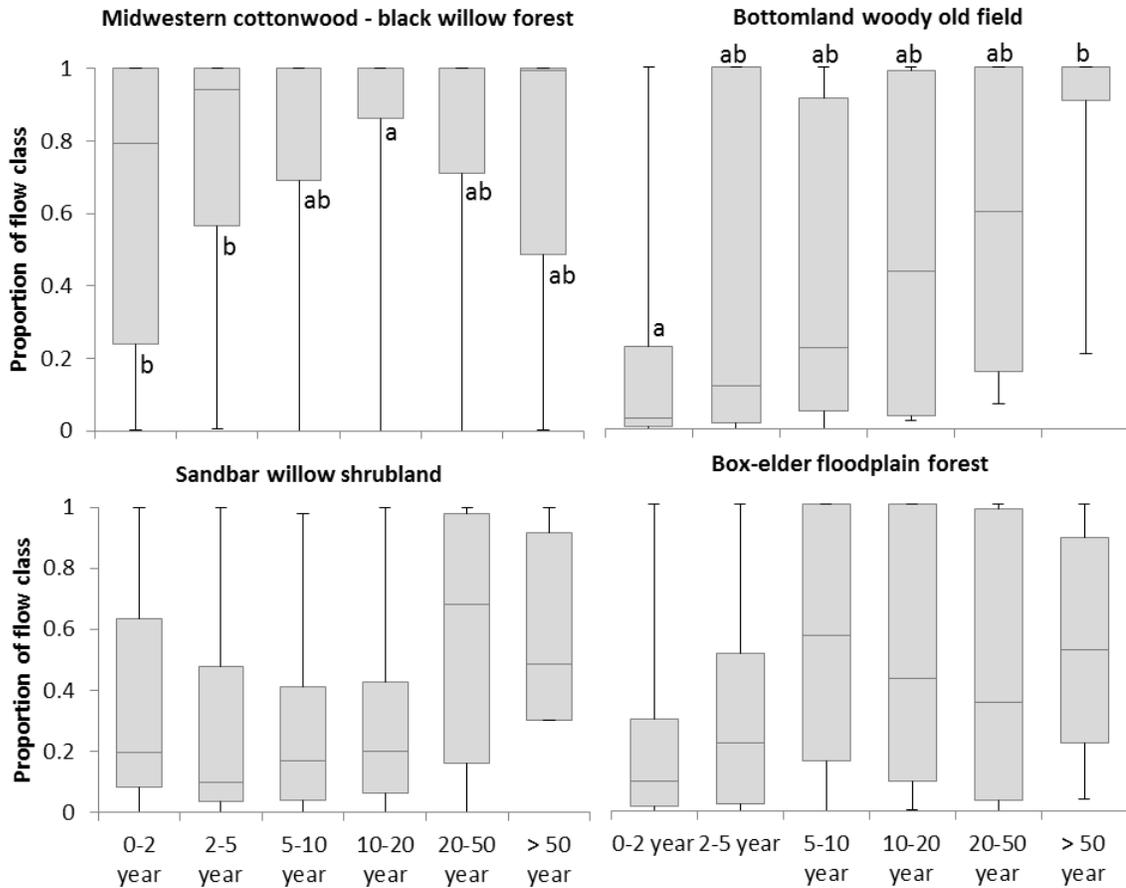


Figure 88. Quantile distribution for vegetation communities with significant differences in the relative mapped area between flow-return intervals.

Upper and lower whiskers represent 4th and 1st quantiles; upper and lower boxes represent 3rd and 2nd quantiles, with the median at the dividing line. Intervals that do not share a letter have significantly different distributions (Kruskal-Wallis analysis of variance on ranks with *post-hoc* Dunn's test; $\alpha = 0.05$). Pairwise comparisons for sandbar willow shrublands and box-elder floodplain forests were not significant.

The distribution of some communities is strongly related to flow frequency. Ephemeral ponds, herbaceous old fields, sandbar willow shrublands, black willow forests and cottonwood-sycamore forests all show a clear trend of decreasing likelihood of occurrence as flow-return interval increases (Figure 89). In contrast, the likelihood of occurrence increases with flow-return interval for woody old fields, box-elder forests, ash forests, and cottonwood forests. (Figure 89). Sedge meadows, sand flats, silver maple forests, and Johnson grass communities show no clear trend in relation to flow-return interval (Figure 89).

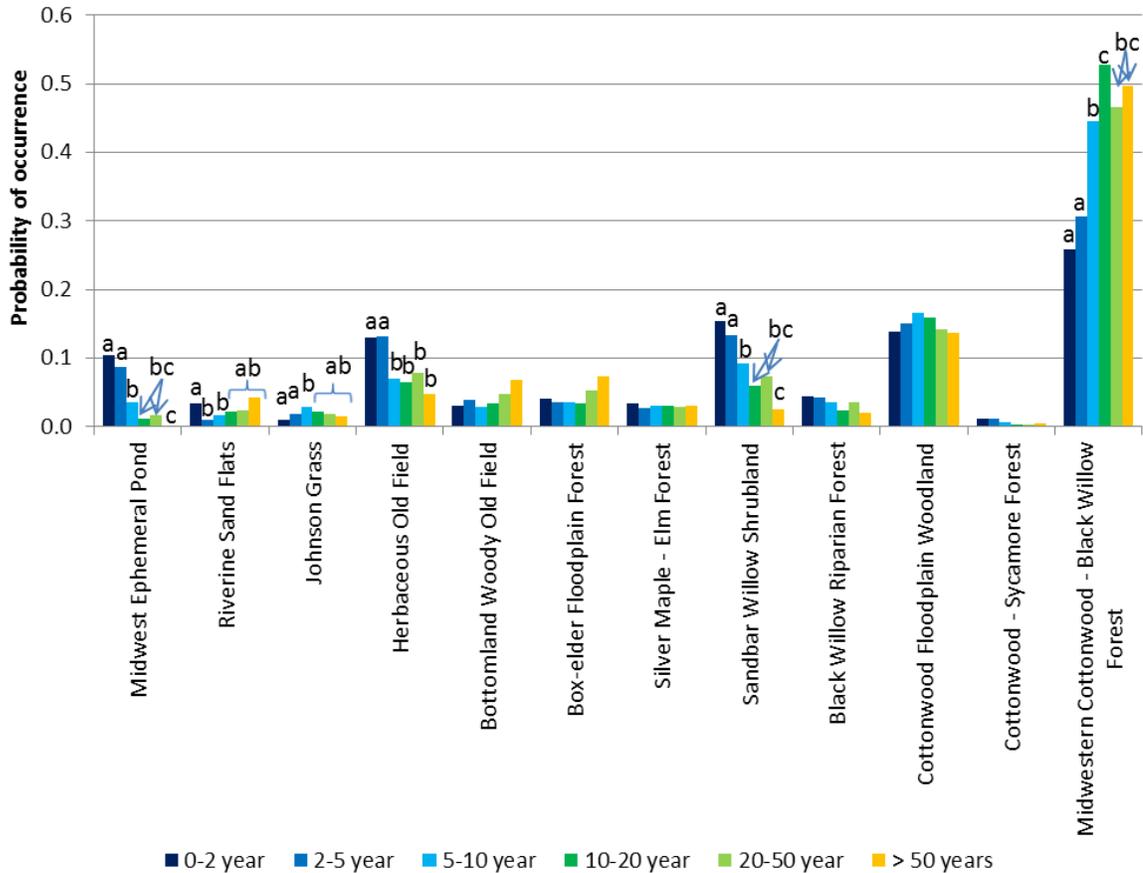


Figure 89. Probability of community occurrence across flow-return intervals.

For each community, flow-return intervals that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Communities without letters did not demonstrate significant differences between flow-return intervals.

Flow-return interval and plots outside of Big Muddy

The distribution of sampling and communities outside of mapped area of Big Muddy is quite different from that inside the refuge, although trends detected in the mapped area are still evident. Regarding sampling distribution, flow-return intervals greater than 500 years represent a larger portion of the sampled area outside of the mapped area (9.4 percent) than in the mapped area (0.7 percent); correspondingly, intermediate flow-return intervals (between 10 and 500 years) drop from 20 percent to approximately 5 percent (Figure 86, Figure 90). This reflects the inclusion of points in the Gavins and Platte sections, where severe incision of the river has increased the abundance of lands with longer flow-return intervals (see section on the distribution of LCPI classes). Given the small sample size within many flow classes, statistical comparisons between the mapped area and plots outside of the mapped area were

not appropriate; the comparisons made below are intended to illustrate variation in the distribution of communities between the two areas.

Outside of Big Muddy, only four communities (box-elder forests, ash-elm-hackberry forests, cottonwood forests, and woody old fields) were recorded on lands with flow-return intervals greater than 10 years (Figure 90). All of these communities except for the box-elder forest were more often encountered on infrequently flooded lands than would be expected based on sampling effort, consistent with the pattern observed on mapped areas of Big Muddy. Also consistent with patterns on the refuge, the ephemeral pond, sandbar willow, cottonwood-sycamore, and black willow forest communities were more abundant on frequently flooded lands than would be expected. Other than the fact that it is absent from infrequently flooded location, the distribution of the silver maple forest approximates the distribution of sampling locations, as it did within the mapped area. The Ash – Oak –Sycamore Forest is notable in that outside of the refuge it was only recorded on the most frequently flooded locations, whereas within the refuge it tended to occur on less frequently flooded lands. The reed canary grass community was not recorded within the refuge, but its distribution is consistent with that species' greater ability to thrive on frequently flooded lands (Figure 68).

As on the refuge, the cottonwood-black willow forest is least likely to be encountered on frequently flooded sites, and reaches maximum likelihood of occurrence on flow-return intervals between 10 and 50 years (Figure 89, Figure 91). Woody old fields are slightly more likely to occur on longer flow-return intervals on the refuge (Figure 89); this pattern appears somewhat more pronounced outside of the refuge (Figure 91). Silver maple forests and box-elder forests appear minimally responsive to flow frequency based on the refuge map (Figure 89), but both communities were limited to the most frequently flooded locations outside of the refuge (Figure 91). Ephemeral ponds, black willow forests, and cottonwood-sycamore forests were infrequently sampled ($n < 10$), but all occurrences were limited to infrequently flooded locations (Figure 91), consistent with their greater likelihood of occurrence on such sites within the refuge (Figure 89).

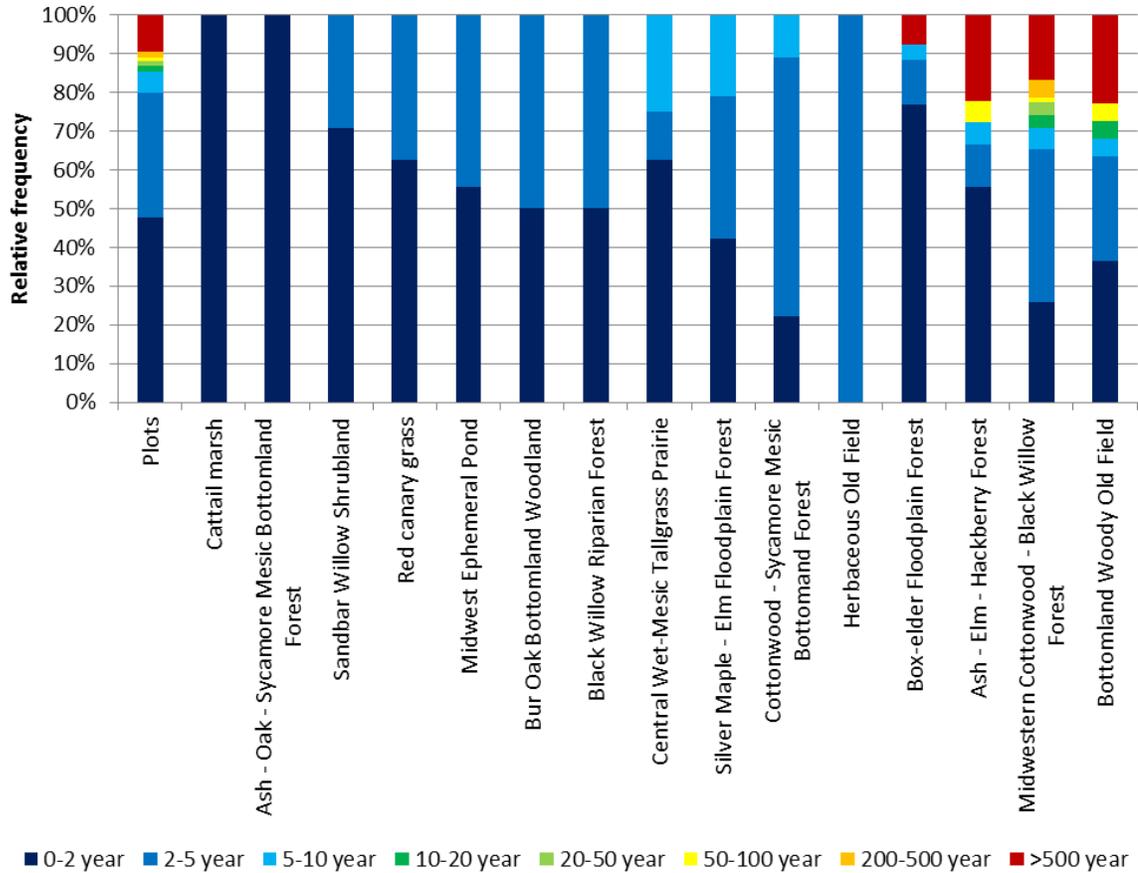


Figure 90. Relative frequency of sampling points and associated vegetation communities among LCPI flow-return intervals based on plot data for locations outside of Big Muddy National Fish and Wildlife Refuge.

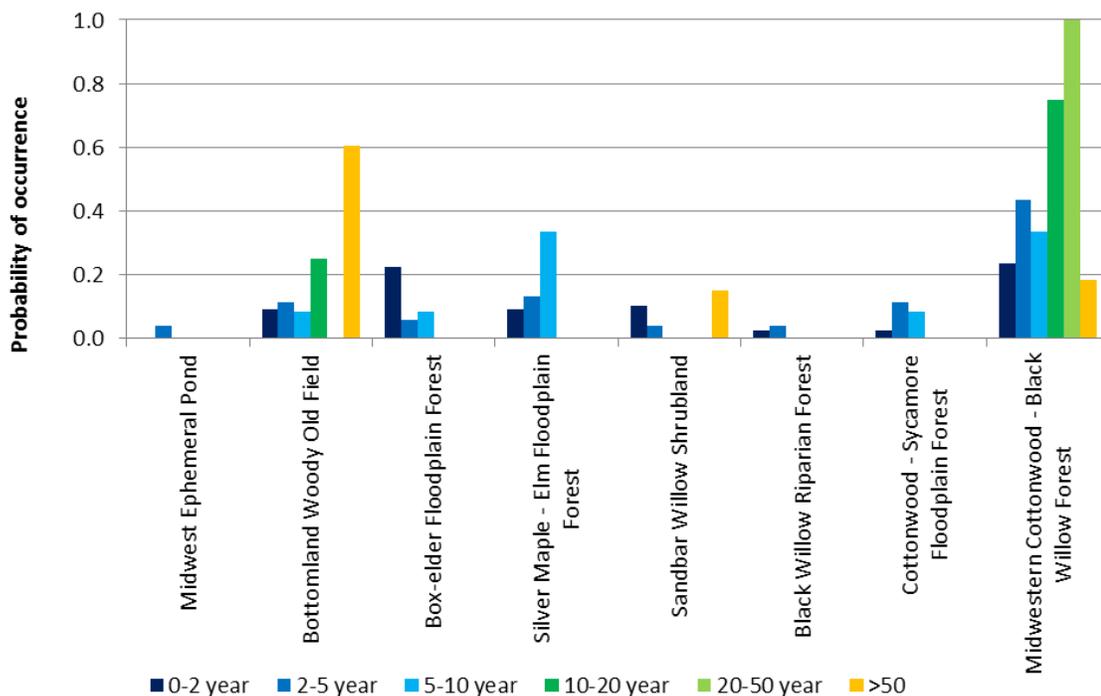


Figure 91. Probability of community occurrence across flow-return intervals for plots outside of mapped portions of Big Muddy National Fish and Wildlife Refuge, Missouri.

Soil drainage within Big Muddy

Within the mapped area, 29 percent of lands were classified as somewhat poorly, poorly, or very poorly drained, 52 percent as well or moderately well drained, and 19 percent as excessively or somewhat excessively drained (Table 24). Communities that deviate most (less than 80 percent similarity) from the sampling distribution toward poorly drained soils included ephemeral ponds and black willow forests; those that deviate most toward excessively drained soils included ash dominated mid- and late-successional communities and sedge meadows. The cottonwood – sycamore forest type also was less than 80 percent similar to its expected distribution; this was driven by greater frequency than expected in both poorly drained soils and excessively drained soils, suggesting that its constituent species cannot thrive on those soil types (Figure 92). Sandbar willow shrublands are slightly more abundant on better drained soil classes; herbaceous and woody old fields are slightly more abundant in poorly drained soil classes (Figure 92).

Table 24. Distribution of mapped vegetation communities among LCPI soil drainage classes

Vegetation community*	Drainage class							Total	Percent similarity to sampling distribution
	Very poorly drained	Poorly drained	Somewhat poorly drained	Moderately well drained	Well drained	Somewhat excessively drained	Excessively drained		
Midwest Ephemeral Pond	39	7	174	37	123	5	30	415	75.0%
Bottomland Woody Old Field	32		72	20	62	2	34	222	80.6%
Black Willow Riparian Forest		6	95	5	68	3	59	236	75.7%
Herbaceous Old Field	31	8	231	83	229	19	73	674	83.0%
Cottonwood - Sycamore Forest		2	17	10	12	4	13	58	73.3%
Sandbar Willow Shrubland	14	2	204	51	310	5	133	719	96.2%
Cottonwood Floodplain Woodland	39	3	255	51	415	4	191	958	95.3%
Johnson Grass	4		29	7	61		22	123	93.9%
Box-elder Floodplain Forest	1		61	12	99	7	55	235	91.9%
Silver Maple - Elm Forest	2		35	23	75	7	40	182	87.9%
Midwestern Cottonwood - Black Willow Forest	18	3	419	189	1,256	23	389	2,297	89.4%
Riverine Sand Flats			21	4	56		35	116	83.3%
Central Midwest Sedge Meadow			5		20			25	64.5%
Ash - Oak - Sycamore Mesic Bottomland Forest**			2		12			14	58.8%
Ash - Elm - Hackberry Forest**					1		11	12	25.6%
Total mapped polygons	180	31	1,620	492	2,799	79	1,085	6,286	

* (Struckhoff et al., 2011; Struckhoff, 2013); Naming conventions follow the National Vegetation Classification System as maintained by NatureServe (2014).

**Not analyzed due to low overall frequency

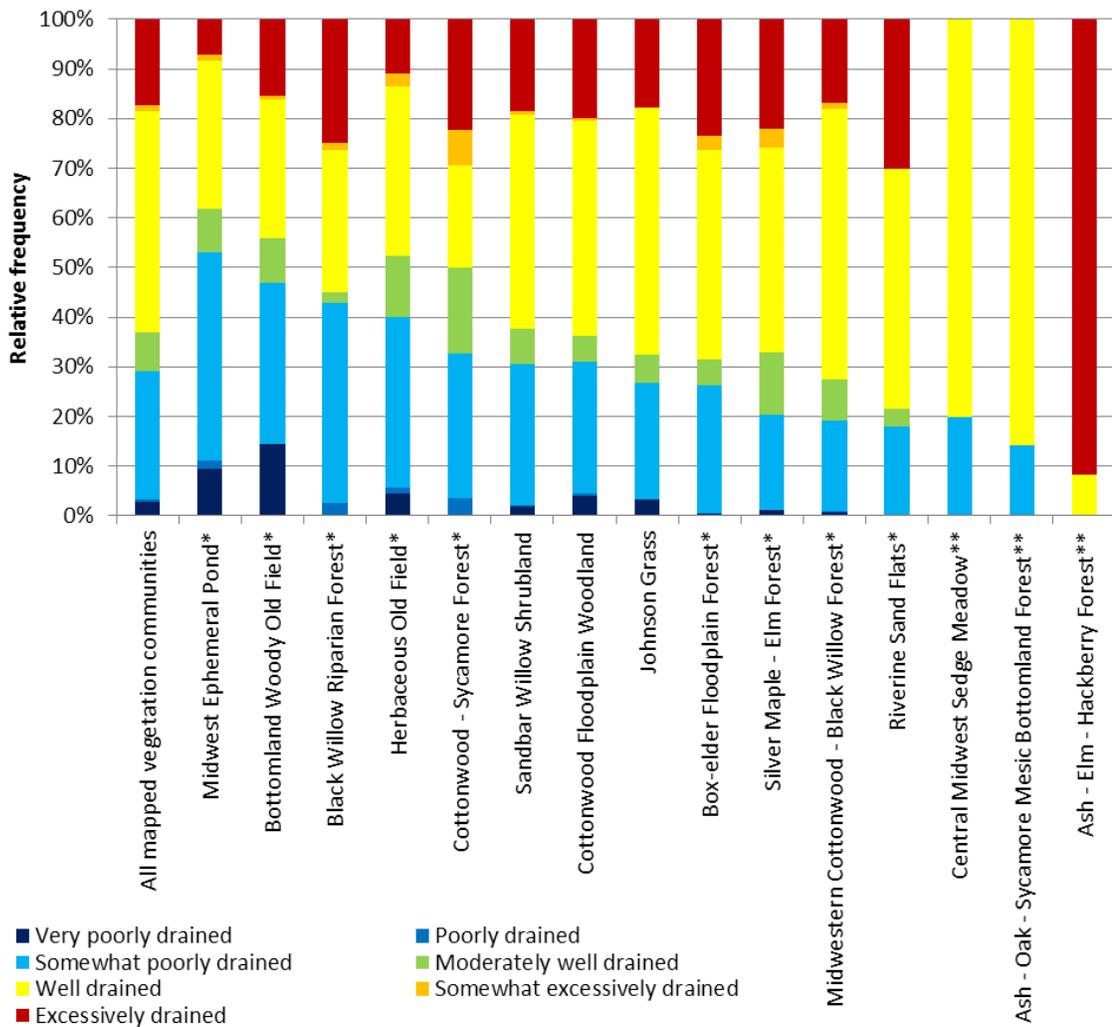


Figure 92. Relative frequency of vegetation community mapped polygons across LCPI soil drainage classes on Big Muddy National Fish and Wildlife Refuge.

* Significantly different (Chi-square test, $\alpha = 0.05$) from distribution of drainage classes across the total mapped area (Struckhoff et al., 2011; Struckhoff, 2013).

** Not analyzed due to low overall frequency

Collectively, communities dominated by cottonwood are mapped more frequently on and occupy a much larger percentage of soils that are well drained or better than soils that are poorly drained (Figure 93). Only about 31 percent of the polygons and about 25 percent of the area classified as very poorly drained soil polygons include communities classified as one of the cottonwood types; by contrast, the relative frequency of these communities doubles to 62 percent and the relative area more than triples to greater than 80 percent on well drained soils (Figure 93). Analysis of variance indicates significantly different relative area distributions between drainage classes for the Midwest Cottonwood – Black Willow

Forest, with all quantile limits being higher on well drained soils than on poorly drained or excessively drained types, although individual pairwise comparisons were not significant (Figure 94).

The only other community with significant differences in the distribution of relative area values is the ephemeral pond community. The community has its highest relative frequency and highest relative area values on soils classified as either very poorly drained or poorly drained, and there is a clear trend of reducing abundance as soil drainage improves (Figure 93). Analysis of variance indicates that the aggregated excessively drained soil group has significantly less relative area occupied by the ephemeral pond community than either the poorly or well drained groups (Figure 94).

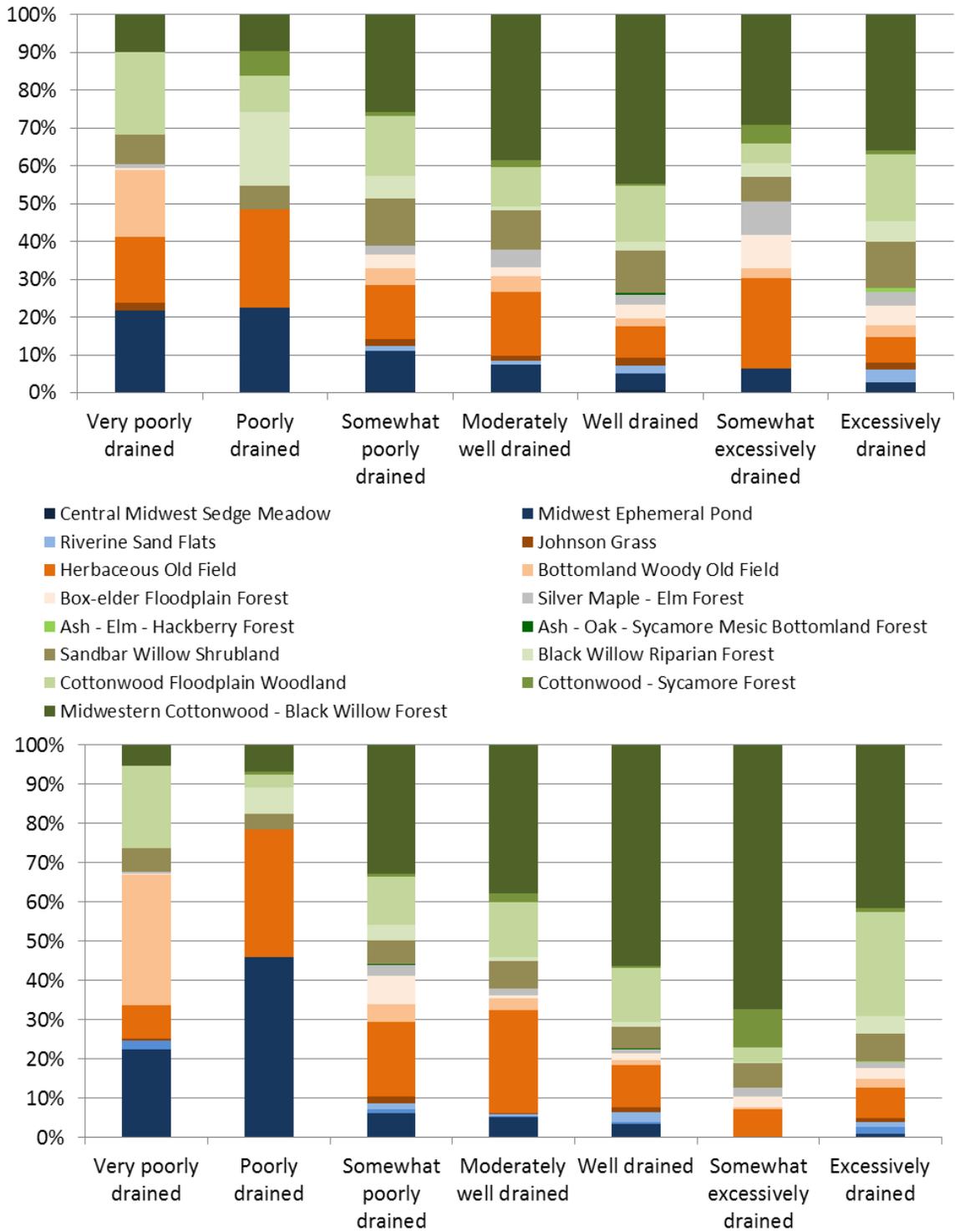


Figure 93. Relative frequency (top) and relative area (bottom) of natural communities within LCPI soil drainage classes based on intersection of LCPI model and map of vegetation communities at Big Muddy National Fish and Wildlife Refuge.

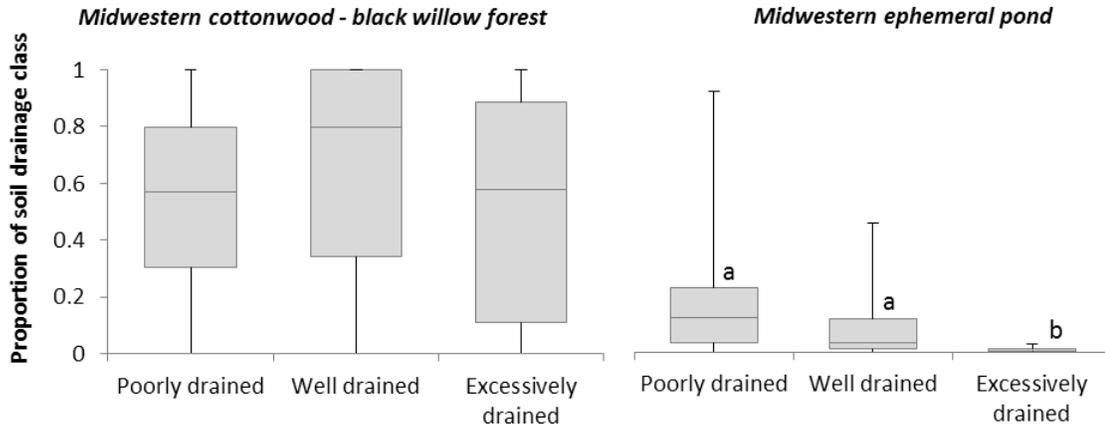


Figure 94. Quantile distribution for vegetation communities with significant differences in relative mapped area between soil drainage classes.

Upper and lower whiskers represent 4th and 1st quantiles; upper and lower boxes represent 3rd and 2nd quantiles, with the median at the dividing line. Intervals that do not share a letter have significantly different distributions (Kruskal-Wallis analysis of variance on ranks with *post-hoc* Dunn's test; $\alpha = 0.05$). Pairwise comparisons for the cottonwood-willow forest were not significant.

Fewer community types exhibit variation in abundance associated with soil drainage class than with flow frequency. Midwest ephemeral ponds and old field communities are significantly more likely to occur on poorly drained soils than on other soil types (Figure 95). Sand flats, box-elder forests, silver maple forests, and cottonwood forests with or without sycamore are significantly less likely to occur on poorly drained soils; these communities are from 50 to 100 percent more likely to occur on excessively drained soils than on other soil types (Figure 95). The slightly lower frequency of sandbar willow shrublands, black willow forests, cottonwood-sycamore forests, and cottonwood woodlands on well drained soils is mirrored by an increase on that soil type in the cottonwood-willow forest, with which they are closely allied.

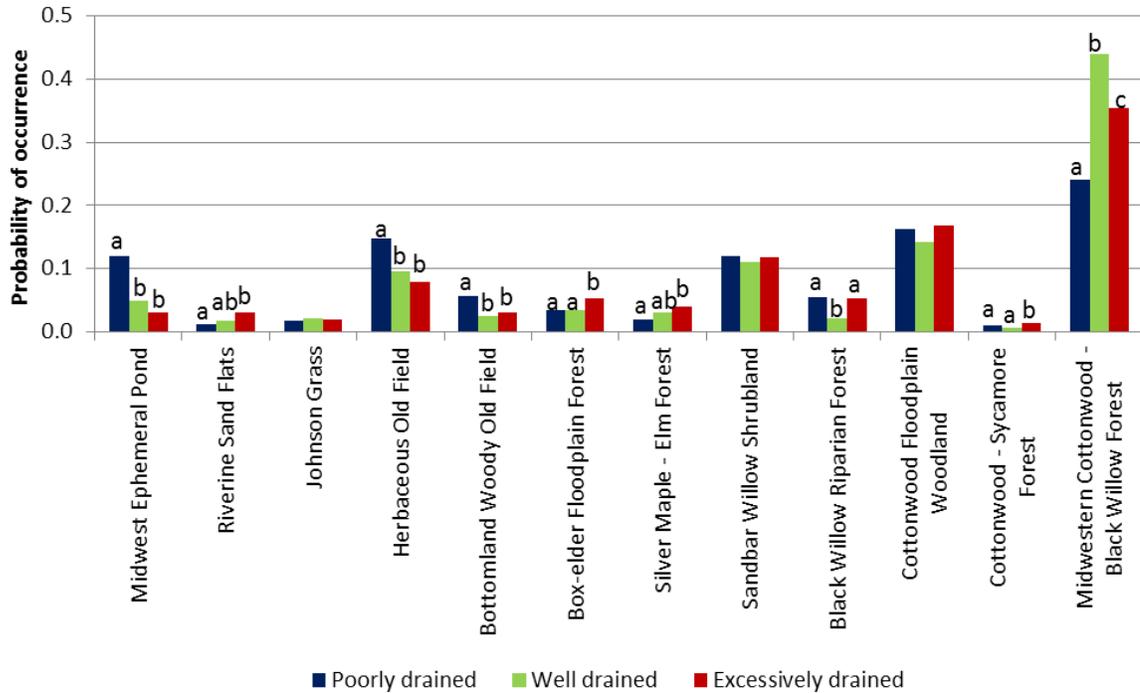


Figure 95. Probability that the given community will occupy land with the indicated flow-return interval.

For each community, drainage classes that do not share a letter are significantly different (Chi-square test with *post hoc* Marascuilo multiple comparison procedure; $\alpha = 0.05$). Species groups without letters did not demonstrate significant differences between soil classes.

Soil drainage outside of Big Muddy

Of the plots outside of Big Muddy, approximately 60 percent occurred on soils that are poorly drained or worse (Figure 96), a much greater percentage than polygons within similar soils on the refuge. Most of this increase in poorly drained soil relative to the refuge is mirrored by a reduction in well or moderately well drained soils. Approximately 18 percent of the plots off the refuge were on soils that are excessively or somewhat excessively drained, about equal to the area on these soils within the refuge (Figure 96). As with flow-return interval, the distribution of communities outside of the refuge does not allow statistical comparison between the two areas; the comparisons that follow are for illustrative purposes only.

There are some similarities in the distribution of communities between the mapped area and the plots outside of the refuge. Consistent with the mapped area, ephemeral ponds and black willow forests tend to occur more frequently on poorly drained soil types. The reed canary grass community found on

poorly drained soils among the plots was not mapped at Big Muddy; however, the quantile distribution graph for the species indicates that it is much more likely to be dominant on poorly drained soils within the refuge (Figure 78). Woody old fields, cottonwood forests, and sandbar willow shrublands are more frequent on soils with better drainage than would be expected based on the distribution of plots. For cottonwood forests, this is consistent with the relationships in the mapped area; for the other two communities it represents a shift toward better drained soils relative to the mapped area.

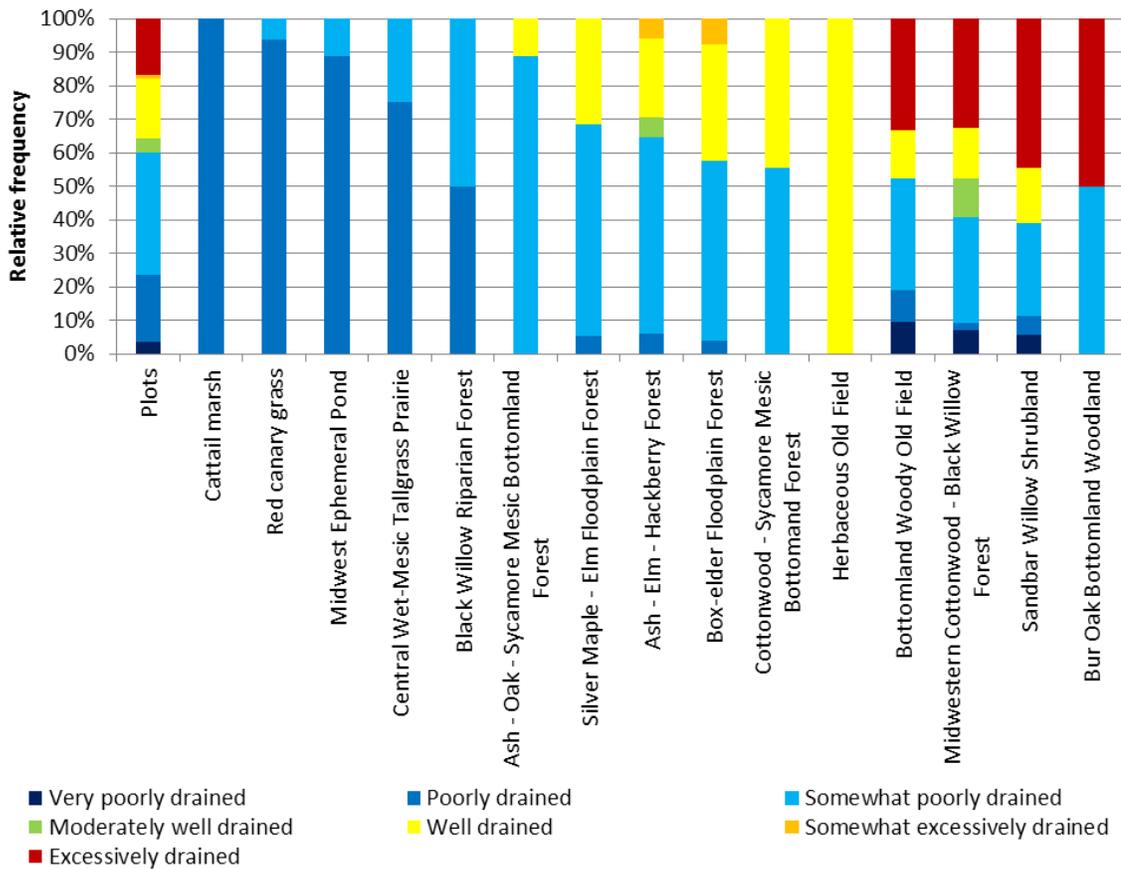


Figure 96. Relative frequency of sampling points and associated vegetation communities among LCPI soil drainage classes based on plot data for locations outside of Big Muddy National Fish and Wildlife Refuge.

As on the refuge, cottonwood-black willow forests are least likely to occur on poorly drained soils (Figure 97). In contrast to the distribution of this type on the refuge however, it is more likely to be encountered on excessively drained soils than on well drained soils among the plots outside of the refuge (Figure 97). Woody old fields occur most frequently on excessively drained soils outside of the refuge

(Figure 97), but most frequently on poorly drained soils within the mapped area (Figure 95). Box-elder forests are more likely to be encountered on excessively drained soils within the refuge (Figure 95), but are more likely to occur on well drained soils outside of the mapped area (Figure 97). The two ephemeral ponds that were sampled outside of the refuge were found on poorly drained soils (Figure 97), consistent with their greater tendency to occur on such sites within the refuge (Figure 95).

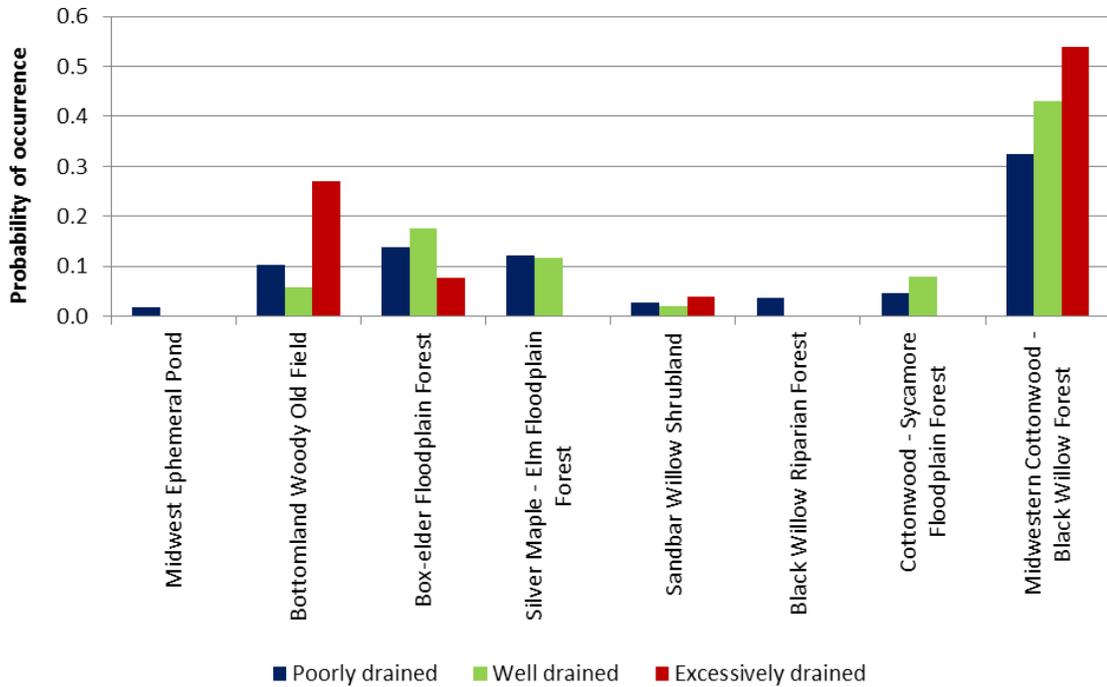


Figure 97. Probability that the given community will occupy land with the indicated soil drainage for plots outside of mapped areas of Big Muddy National Fish and Wildlife Refuge.

Chapter IV:

Discussion

Current distribution of LCPI classes

Earlier in this thesis, four questions were posited regarding the current distribution of LCPI classes:

1. Are there differences in the abundance of LCPI classes between ecological Provinces?
2. Are there differences in the abundance of LCPI classes between hydrogeomorphic sections?
3. Are tributaries associated with shifts in LCPI class abundance?
4. Are there trends in changing LCPI class abundance associated with tributaries draining different ecological regions (do tributaries from a given region share a hydrogeomorphic signature?)

The results of the research presented here indicate that all four answers can be answered affirmatively.

Ecological provinces

The differences in LCPI class abundance between provinces are not unexpected, given the well-documented and geographically extensive effects of the Gavins Point Dam on stream flow and sediment regime (Jacobson et al., 2009). In particular, that system has induced incision that lowers the stream bed relative to the floodplain (Jacobson et al., 2009), increasing the abundance of infrequently flooded lands for hundreds of miles downstream from the Gavins Point Dam. The prairie province also has a greater abundance of poorly drained soils, but there is not a clear trend attributable to the effects of the reservoir system. The magnitude of effects of the reservoir system makes it difficult to discern differences that may be due to the geologic, upland soil, and land-use characteristics that differentiate the provinces.

On the other hand, the transition point between the two provinces is marked by a local spike in the abundance of longer flow-return intervals and better drained soils. The transition point marks a shift into an incising section of the river (Jacobson et al., 2009), and a lower stream bed necessarily increases the discharge required for overland flow for a particular recurrence interval. Indirectly, it also may be

responsible for the increased abundance of better drained soils through and downstream of this transition area; reduced groundwater elevation associated with an incising stream would expose fewer sites to prolonged periods of free water in the upper soil strata upon which drainage classifications are based. This causative link between incision and soil drainage assumes that drainage classification reflects soil development under the modern flow-regime. Such an assumption may be true for recently accreted lands and recently deposited surface soils, but is probably not appropriate for older surface soils on the floodplain (Soil Survey Staff, 1993; Brady and Weil, 2008; Schoeneberger et al., 2012). Downstream of the transition, the abundances of long flow-return intervals and better drained soils diminishes, but remain elevated relative to conditions upstream. The results suggest that geologic inflection points and hydrologic features induce shifts in class abundance.

Hydrogeomorphic sections

The relative abundance of lands with short flow return intervals tends to increase as the river enters into and move through stable and aggrading sections, and decrease as the river enters and moves through incising sections. This is a direct result of the relationship between elevation and flow-return interval, because channel bed incision increases the discharge required to raise water elevation sufficient to induce overland flow.

The reasons for the decrease in abundance in poorly drained soils through stable and aggrading section of the stream is more difficult to identify. If soil drainage class has been determined in part by the modern flow and sediment regimes, poorly drained soils should increase in abundance through such sections, because the aggrading stream bed would raise groundwater elevation and increase the likelihood of flooding, thereby exposing the upper soil strata upon which drainage classifications are based to more frequent and prolonged free water in the soil profile (Soil Survey Staff, 1993; Brady and Weil, 2008; Schoeneberger et al., 2012). The fact that soil drainage does not follow the expected pattern may be an indication that current soil classification does not reflect the modern hydrologic and sediment regimes, and that the system has not yet attained equilibrium following the closure of the dams.

Disequilibrium is more generally supported by the fact that differences between hydrogeomorphic sections reflect the diminishing effects of the Gavins Points Dam with greater distance downstream. Despite the fact that the river is incising through the Gavins and Ponca sections, those sections are

characterized by increasing relative abundance of short flow return intervals. This trend reflects attenuation of the effects of the Gavins Points Dam as first the Big Sioux River enters the river valley (between Incising zones 1a and 1b), then the Big Sioux River and Floyd River join the Missouri River (between the Ponca and Sioux segments), and finally the Little Sioux River joins the Missouri River (in Incising zone 1b). Below the Platte River, the valley is dominated by lands with flow return intervals less than 20 years. Below this point, management for communities that require a long-term absence of flooding may be difficult, although the incising section of the Kansas segment may provide more opportunities. Regional planning may benefit from a better understanding of how incision and aggradation affect class abundance over broad scales.

Tributaries

Tributaries are associated with local shifts in LCPI class abundance and there are broad trends among ecological regions. Local decreases in soil drainage capacity near the Big Sioux, Little Sioux, Grand and Chariton River may be due to elevated water tables associated with tributary inflows. The increase in relative area occupied by lands with better soil drainage at the Platte river are likely due to the coarse sediment load of that stream (Simon et al., 2004). Although the mouth of the Big Sioux is associated with longer flow return intervals, this drying effect of the Big Sioux is somewhat misleading, because these changes in flow-return interval abundance return them to their amounts upstream of the point where the Big Sioux enters the river valley (Figure 22, Figure 23, Figure 24). Thus, the Big Sioux River is associated with an increase in frequently flooded lands where it enters the valley until the mouth of the river, below which lands with longer flow-return intervals return to their previous abundances. This localized shift probably reflects the combined effects of an elevated water table associated with the Big Sioux and erosion creating low areas near the channel of the Big Sioux. The increase in flow return intervals less than 5 years below the Platte river likely reflect the effects of channel aggradation through this river segment.

In both ecological provinces, flow-return intervals tend to increase near the mouths of tributaries (Figure 41). This is likely due to the presence of alluvial fans that are elevated relative to the rest of the floodplain (Brady and Weil, 2008). In the prairie province, the drier conditions associated with longer flow-return intervals may be offset by the generally poorer soil drainage associated with the mouths of tributaries draining that region; by contrast, in the forest province, soil drainage shows a very slight improvement near

tributary mouths. In both provinces, tributary mouths are associated with increased flow-return intervals (Figure 41). In either case, tributaries induce local shifts in LCPI class abundance that may provide opportunities to manage for species that thrive on landforms that are otherwise locally scarce.

Urban areas

Urban areas are generally associated with increases in flow-return intervals and a greater abundance of better drained soils. Longer flow-return intervals are evident at Omaha, (mile 646), St. Joseph (mile 454-444), Kansas City (mile 369-356), Jefferson City (mile 150-135), and the St. Louis metropolitan area (beginning at mile 50), and likely reflect management actions to reduce flood risk, including raising the elevation of the floodplain. Similarly, better soil drainage below the mouth of the Kansas likely reflect valley narrowing and channel incision associated with urban development (Jacobson et al., 2009), which would lower the water table and reduce potential exposure to free water in the upper soil strata.

The analysis of LCPI class distribution demonstrates that there are broad differences between ecological regions and geomorphological sections of the river. It also provides evidence that geologic inflection points, tributaries, and urban areas induce local changes in LCPI class abundance that sometimes extend many miles downstream. Such sites may provide opportunities to incorporate otherwise poorly represented flow and drainage classes into the conservation portfolio. Regional planners can explore the LCPI model in conjunction with geology and hydrologic maps in order to identify where such points are likely to occur, and whether management for particular species or communities is indicated by abiotic conditions modeled in the LCPI.

There are a couple of caveats relevant to the application of the LCPI in this manner. First, for both wetness indices, the numeric values assigned to the various classes are arbitrary. Therefore, it is difficult to determine what changes of the magnitude identified here would represent in an ecological context. Nevertheless, the values convey relative increases or decreases in potential wetness that may be used as a coarse guide to the capacity of lands to support desired communities or species based on their wetness requirements. Second, users should also be aware of shifts in mapping standards that within SSURGO database that can affect the abundance of soil drainage classes. One such example occurs near mile 553, where clear shifts in classification patterns are evident at the state boundary (Soil Survey Staff, 2012).

Potential future LCPI class abundance

Throughout the area modeled by the LCPI, climate change is expected to increase mean monthly discharge during those months most likely to determine flow-return intervals (May and June), causing a shift toward longer flow-return intervals. The implications of these changes depend on the specific management objectives within a given area, as well the implementation of efforts to mitigate or adapt to the potential influence of climate change on flow patterns. Barring any such adaptations, a greater percentage of the study area will be experience more frequent overland flow and will have a better capacity to support species that thrive in such conditions.

Closer examination of three sections of the river illustrate that the effects of climate change-induced alteration of flow patterns vary depending on ecological setting. The Gavins section of the River, extending for 57 miles below the Gavins Point Dam, is more profoundly affected by the construction and operation of reservoir system than any other section on the Lower Missouri River (Jacobson et al., 2009). Due to intense channel incision, more than 85 percent of the floodplain currently is classified as the greater than 500 year flow-return interval. Within this section, projected climate-driven increase in area for the more frequently flooded classes is limited to the active channel (Osterkamp and Hupp, 1984) immediately adjacent to the Missouri River flowing along the south edge of the valley and Clay Creek flowing along the north edge (Figure 43). In contrast, the Grand Stable-Aggrading 2 section (Figure 44) is among the least affected by the reservoir system (Jacobson et al., 2009) and is currently dominated by LCPI classes representing short flow-return intervals. Under the discharge models reflecting climate change (Gangopadhyay et al., 2012), the increased area of the 0 to 2 year interval is accompanied by decreased area in intermediate flow classes, with very little change in area for the longest flow-return interval (Table 10) between these two extremes, the distribution of LCPI flow classes in the Sioux Stable-aggrading 1 section is more balanced (Table 10, Figure 45; however, if climate-change predictions are realized, nearly all of the increased area in the 0 to 2 year flow class is compensated for by a decrease in area representing the greater than 500 year flow class. These coarse analyses illustrate that resource managers who wish to adapt to or mitigate the effects of climate change must to examine the specifics changes anticipated in their area of interest in order to anticipate future conditions.

Here, the implications of climate-induced change in flow frequency are examined in the context of management for cottonwood forests and late-successional forests. Disruption of the historical flow regime has been cited as one cause of the decline of cottonwood forests on the Missouri River (Johnson, 1992; Dixon et al., 2010; Dixon et al., 2012a). As discussed in the literature review, Mahoney and Rood (Mahoney and Rood, 1998) developed a cottonwood “regeneration box” model that identified optimal conditions for the establishment and development of cottonwood forests. Sites suitable for cottonwoods experiences scouring floods often enough to provide bare soil for germination, are protected from late season floods that would otherwise kill new seedlings, and experience periods without flooding sufficiently long to enable recruitment into large size classes. For the Missouri River, these criteria are met in locations with intermediate flow-recurrence intervals above 9 years (Scott et al., 1997). These conclusions are supported by the research in this thesis, which shows that cottonwood abundance is maximized in the 5 to 10 year and 10 to 20 year flow classes. For the purposes of this discussion, the 5-10 and 10 to 20 year flow-return interval are assumed to provide optimal flow frequency for cottonwoods.

Based on the projected changes in the distribution of flow-return intervals, lands that are most suitable for the management for cottonwood forests will become less abundant. Currently, the greatest absolute and relative abundance of the 5 to 10 and 10 to 20 LCPI flow classes are found in the Sioux Stable-aggrading 1 and Kansas Incising 2 sections of the river; these classes cover less than 1.3 percent of the land in the Gavins and Ponca sections and less than 6 percent for the remaining sections (Table 10). If the climate change projections of are realized, the already small area with 5 to 20 year flow recurrence intervals will become even smaller. Only one section (Sioux Incising 1b) will see an increase in area represented by the 5 to 10 and 10 to 20 year flow classes (approximately 7,000 ha or 67 percent). Excluding that section, the entire river will experience a reduction of approximately 16 percent in lands representing optimal flow frequencies for cottonwood forests, further impeding efforts to manage for this community type.

Based on the increases in discharge associated with projected global climate change, (Gangopadhyay et al., 2012), lands that are best able to provide habitat for late-successional species will decrease in every river section. Reductions in these lands may have minimal impact in the upper reaches of the river (Gavins, Ponca, and Platte) where they long flow-return intervals dominate. By contrast, even

small reductions in land area with long flow- return intervals the lower reaches of the river will reduce an already scarce habitat type and make it even harder to manage for late-successional species.

While cottonwood and late-successional forest management may be impeded by climate-change driven alteration of discharge patterns, lands suitable for other community types may become more abundant. For example, the models used here indicate that there will be a greater abundance of lands that support communities that are defined by frequent (and prolonged) flooding, including sedge meadows and ephemeral pond communities. The potential effects of changes in the distribution of flow-return intervals will depend on the context. Each management agency will need to identify their particular needs and examine the potential effects of climate change-driven alteration of the flow regime at multiple scales.

The uncertainty surrounding future changes in discharge resulting from climate change are large; therefore estimates of future change in LCPI classes should be treated with caution. At most stations along the river, the 112 emission scenario/global circulation model/start value combinations used in the Climate Change Analysis for the Missouri River Basin (Gangopadhyay et al., 2012) yielded changes in discharge for May and June ranging from negative values (reductions in flow) to nearly 100 percent increases (as an example, the distribution of modeled changes in discharge for Boonville, Missouri is provided in Figure 98). For Booneville, Missouri, the second and third quartiles for May discharge change range from 9 to 31 percent; those for June range from 2 to 28 percent. The range of these quartiles nearly doubles the median estimated increase in discharge during these month (Gangopadhyay et al., 2012). Nevertheless, for all stations, the 25th percentile is positive, indicating that most climate models and emissions scenarios anticipate increases in discharge, which will yield reductions in land with longer flow-return intervals and an expansion of area suitable for wetland species that thrive in frequent inundation.

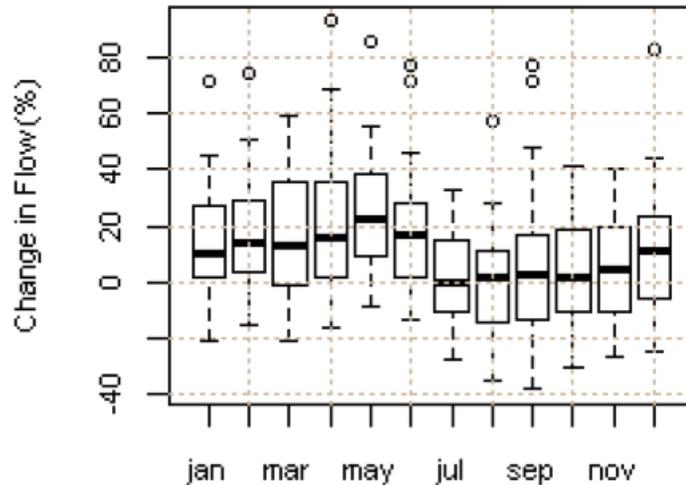


Figure 98. Distribution of change in monthly discharge values between historic period (1950 to 1999) and future conditions (2040-2069) for Boonville, Missouri from 112 simulations showing broad range of potential outcomes depending on emissions scenario, global circulation model, and initial conditions (From Figure A.1 in Gangopadhyay et al., 2012)

Variation in groundwater processes between soil drainage classes

At both Forest City and Overton North, the general trend of decreasing maximum GWRF with increasing distance from the river is consistent with GWRF simulations for other parts of the Missouri River (Table 14) (Kelly, 2000). Lag ratios increased (Figure 51) and exceedance ratios decreased (Table 12) with distance from the river, also in accordance with previous GWRF simulations (Kelly, 2000).

In terms of the magnitude of the maximum GWRF, results suggest that the Overton model is more consistent with simulated mean GWRF (Kelly, 2000) than is the Forest City model. However, those simulations assumed maximum pulse magnitude for the duration of the flow pulse simulations used to model GWRF, which would inflate modeled GWRF relative to real-world scenarios in which there is a rising and descending limb to the flow pulse; thus, the Forest City model is more consistent with the simulated data. In either case, the greater maximum GWRF values at any given distance from the river at Overton compared to Forest City suggests that the floodplain at Overton has a higher overall transmissivity than at Forest City, consistent with the greater relative abundance of soils with better drainage at Overton (compare Figure 6 and Figure 7).

Data for individual wells indicate that maximum GWRF increases as soil drainage improves. At both sites, soil with better drainage had higher mean maximum GWRF than the site-specific models

indicated for each well's given distance from the river. Additionally, the majority of groundwater responses for wells in better drained soils were higher than the site specific models; in contrast poorly drained soils had the majority of response below what site models predict. Contradictory evidence can be found at FC10, where mean maximum GWRF exceeded the predictions of the site specific model at 1,235 m from the river, despite the fact that this well is located on poorly drained soils. A similar results is evident for OV7.

With regard to lag ratios, Darcy's Law implies that, where soil drainage reflects the inherent hydraulic properties of the soil, flow through soils with higher hydraulic conductivity is faster than through soils with low conductivity (Dingman, 2002). As expected at both sites, soils with better drainage tended to have lag ratios that were less than the values predicted by the site specific models at their respective distances. This indicates that soil drainage classification is in part related to the hydraulic conductivity of the soils. Two exceptions to the above trends include FC10 and OV7, wells on poorly drained soils at which the lag time was less than the site model predicts. These are the same wells for which mean maximum GWRF values exceeded predictions for the site model, and (as with GWRF results) proximity to topographic features such as drainage ditches and scours (as opposed to the river itself) may explain these deviations from model predictions.

Results also show some evidence that SSURGO soil drainage classification affects local exceedance ratios within a given site. The higher exceedance ratios for wells on better drained soils (FC11, FC12, OV2, OV3, and OVTC) indicate that these wells experienced relatively prolonged exposure to elevated groundwater following flow pulses. By contrast, wells on soils with poorer drainage tended to have mean exceedance values and more observations below what the site model predicts. The better fit of a logarithmic rather than linear relationship at Forest City may constitute additional evidence of overall lower transmissivity of the site compared Overton; such a relationship reflects the inability of flow pulses to affect groundwater elevation at points further from the river such that with increasing distance, mean exceedance ratio approaches 0.

The comparisons between deep and shallow well drainage provide little evidence that local soil drainage characteristics are affecting vertical groundwater response to flow pulses (Figure 54). If soil drainage is a factor affecting variation in groundwater response, it should have contributed to divergence in well water elevation between shallow and deep wells within pairs and to differences in the magnitude of

that divergence between pairs, with greater divergence in poorly drained soils than in well drained soils. Instead, following well inundation and through subsequent flow pulses, GWRF values track nearly perfectly between paired short and deep wells, and the maximum range of difference between deep and shallow wells, regardless of soil drainage class, is only 8 cm. Additionally, there is virtually no difference in lag time between shallow and deep wells. The only evidence to suggest that soil drainage characteristics are affecting groundwater response is the overall greater reduction in groundwater elevation in well drained OV3 (1.69 m) relative to somewhat poorly drained OV1 (1.47 m), but this does not provide any indication that soil drainage is inducing differences in lag time between shallow and deep wells. It may be that the descending limb of the May 27 flood is overwhelming the groundwater response during subsequent flow pulses. For example, the groundwater response to flow pulses on June 11 and 23 are among the smallest recorded during the study for both OV1 and OV3; the response to the June 15 pulse was augmented by a 0.5 inch precipitation event (University of Missouri Agricultural Extension, 2014). The slow speed with which well TCS drained may be due to impoundment of water within the nearby chute (Figure 7). The slower speed with which water elevation dropped in the wells at OV3 probably is due to impounded water that gathers in the northwest corner of the formerly levee-protected area between the breach and well OVN3 during and after flooding (Figure 7).

Together, these analyses of groundwater processes in relation to the soil drainage classes do indicate that better drained soils have larger maximum GWRFs, shorter lag times, and longer exceedance ratios than do poorly drained soils. However, these conclusions should be treated with caution, given contradictory evidence from this study and the high variability associated with data presented here and from earlier simulations of GWRF (Kelly, 2000).

There are at least two potential explanations to account for the contradictory evidence within this study. First, soil drainage as classified within the SSURGO data set does not necessarily reflect hydraulic conductivity; it may instead reflect persistent water inputs due to landscape position (Schoeneberger et al.). Low lying locations are more likely to be classified as poorly drained because groundwater may be closer to the surface for longer periods of the year or because of greater precipitation-driven water input into the soil. Second, local landscape features affect hydrology. For example, the larger maximum GWRF and exceedance values and reduced lag times at wells FC10 and OV7 relative to site models may reflect

accumulation of water in a nearby drainage ditches or backflow into these ditches during flow pulses. Well OV7 is also close to the I-70 scour, in which surface water elevation is closely tied to river stage (Kelly, 2000). Functionally, closer proximity to such features reduces the distance to surface water, and Darcy's Law dictates that this will increase maximum GWRF and exceedance ratios, and decrease lag times following flow pulses. However, the spatial extent of surface water during and after flow pulses was not observed during this study, and requires additional investigation before firm conclusions can be drawn.

Additionally, misclassification of soil drainage classes may also be causing groundwater processes to deviate from what would be expected. For example, examination of the soil profile at Forest City wells 10 and 11 indicates that these wells are better drained than their SSURGO classifications of poorly and somewhat poorly drained (Soil Survey Staff, 2012). This may be reflected in the fact that the maximum GWRF for these wells approximates the value indicated by the site-specific model at their respective distances, rather than being below that value as would be expected if their classification as poorly drained or worse reflected hydraulic conductivity. A similar effect may be evident at OV2, for which the mean maximum GWRF approximates the site-model predicted value at that distance from the river, despite being classified as very poorly drained (Soil Survey Staff, 2012). A sandy texture and lack of redoximorphic features in the upper soil strata indicate better drainage than the current classification that would explain the greater than expected maximum GWRF response.

Finally, local soil drainage classification is only one factor responsible for determining the transmissivity of the floodplain. Soil drainage is determined by characteristics within the rooting zone of plants; however, vertical flow may be affected by lower soil strata that can have either higher or lower hydraulic conductivity. Also, sharp transitions between soil strata can impede flow regardless of the hydraulic conductivity of the interfacing soil strata. Additionally, flow to a site will be affected by the soil types that lie between the river and a given point of interest. As a result, local soil drainage class is an unreliable indicator of the hydraulic capacity of the broader floodplain.

Nevertheless, higher maximum GWRF values imply that for any given distance from the river, groundwater elevation rises higher in well drained soils than in poorly drained soils for a particular flow pulse. At sites where groundwater tends to be near the soil surface (lower elevation sites), better drained soils are more likely to experience free water within the root zone of the soil in response to flow pulses;

however, their classification as better drained indicates that such sites do not experience the anoxic conditions that can limit the distribution of many plant species (Teskey and Hinckley, 1977; Wharton et al., 1982; Silvertown et al., 1999). Even in sites where groundwater elevation is usually well below the soil surface (higher elevations), larger GWRF values increase the potential for capillary rise to recharge soil moisture within the root zone, even if groundwater fails to reach the upper soil strata (Merigliano, 2005). In either case (high or low elevation), in the absence of flooding, the larger groundwater response associated with better drained soils increases the likelihood of soil moisture recharge, making them less susceptible to soil moisture extremes and better able to support a broad array of species (Nilsson et al., 1989).

Contrastingly, results presented here suggest that poorly drained sites where groundwater is well below the surface are more dependent on local precipitation and flood events to recharge soil moisture. The soils moisture surplus that characterizes the study area (Koch et al., 2013) implies that, during years with average or above precipitation, there should be sufficient soil moisture for all plant species including those adapted to copious water and prolonged periods of soil anoxia to due free water at or near the soil surface. However, during droughts such as that in 2012, the evidence in this study suggests that poorly drained soils are less likely to experience soil moisture recharge resulting from groundwater elevation changes than are better drained soils, exposing the former to more severe soil moisture depletion. Such conditions are more likely to adversely affect species adapted to wet conditions than other species (Silvertown et al., 1999). Thus, during severe drought, poorly drained soils contribute to dry soil moisture conditions that most adversely affect the very species which would otherwise thrive on such soils. This implies that poorly-drained soils may experience more dynamic vegetation changes due to their greater susceptibility to soil moisture extremes.

Longer lag times associated with poorly drained soil classes are tied closely to both maximum GWRF and to the exceedance ratios. The delayed response of poorly drained soils limits maximum GWRF because low hydraulic conductivity impedes a response to flow pulse during peak river stage when the difference in pressure (hydraulic head) is greatest. Additionally, this effect reduces the probability that groundwater in poorly drained soils will exceed any particular threshold (relative to better drained soils). In this study, when the examined exceedance values are surpassed at all on poorly drained soils, the duration of exceedance is comparable to that on better drained soils (Figure 53). So, longer lag times are associated

with reduced probability that an exceedance threshold will be surpassed at all, rather than shorter durations when it is exceeded. Longer lag times also could make plant species and communities growing on them more susceptible to prolonged drought, because it reduces the likelihood of a groundwater response sufficient to provide recharge to moisture-depleted soils.

Exceedance ratio data presented here indicate that better drained soils experience longer periods during which groundwater elevation exceeds a set percentage of flow pulse magnitude. Thus, for any given flow event, vegetation on better drained soils will have access to either free water within the root zone or to bound water through capillary rise for a longer period than those sites on poorly drained soils. Longer duration of elevated groundwater also provides more time for capillary rise to affect soil water availability in soil strata above the maximum groundwater elevation (Dingman, 2002), increasing the likelihood for soil moisture recharge in the upper strata of better drained soils relative to poorly drained soil classes. However, given the classification of better drained soils as such, this greater likelihood of prolonged exposure does not appear to be associated with exposure to anoxic conditions that can limit the distribution of many species (Teskey and Hinckley, 1977; Wharton et al., 1982; Silvertown et al., 1999).

The purpose of this portion of the thesis was to relate groundwater response to changes in river stage at two sites to SSURGO soil drainage classes that have been incorporated into the LCPI. It is important to reiterate that the results presented here only suggest that better drained soil classes have larger GWRP values, shorter lag times, and longer exceedance ratios than poorly drained classes; however, the variability of the data from flow pulses of varying magnitude and duration is too great to provide any conclusive evidence. As an assessment of the utility of the LCPI in understanding hydrologic conditions and managing floodplain habitat, this study examined soil drainage classes as they are mapped within the SSURGO database (Soil Survey Staff, 2012); a hydrologic study intended to provide stronger evidence to support the above conclusions would necessarily control for variation in hydraulic conductivity at monitoring locations (individual wells). It would also control for other factors known to affect GWRP, most notably distance from the river (Kelly, 2000), distance to local features such as drainage ditches and scours that effectively reduce distance to surface water, and broader patterns of floodplain transmissivity (Dingman, 2002).

Relationships between LCPI and vegetation

The results concerning LCPI class distribution and groundwater process are only relevant to habitat management if the distribution of species and communities relates to LCPI classes. Fortunately, the analyses of relationships between floodplain vegetation and LCPI classes indicate that flow-return interval and soil drainage can be used to identify where on the floodplain plants species are more or less likely to occur and become abundant. Results of multivariate analysis (NMS) demonstrate that flow-return interval and soil drainage are critical variables related to the distribution of species on the Missouri River floodplain; LCPI classes often exhibit stronger relationships to species distributions than other factors known to influence species abundance, including distance to the river (Thogmartin et al., 2009). However, the relative ability of LCPI classes to explain variation in species abundance changes from site to site. It is posited that site variables such as land-use history, time since abandonment, and the spatial configuration of landscape features may be influencing the relative contribution that flow-return interval and soil drainage make in determining species distributions.

Non-metric Multidimensional Scaling

Within the NMS analysis at the scale of the entire river valley, community differentiation by flow-return interval is likely an artifact of the plot distribution among sites. Of the 36 plots on lands with flow-return intervals exceeding 50 years, only 2 were located outside of the Gavins section of the river (Figure 99); at sites farther downstream, plots with flow-return interval greater than 5 years become increasingly less common. This pattern in plot distribution is consistent with the scarcity of longer flow-return intervals in downstream sections that are less affected by operation of the reservoir system (Jacobson et al., 2009); however, it also exerts high leverage on the strength of the relationship between flow-return interval and species' distributions.

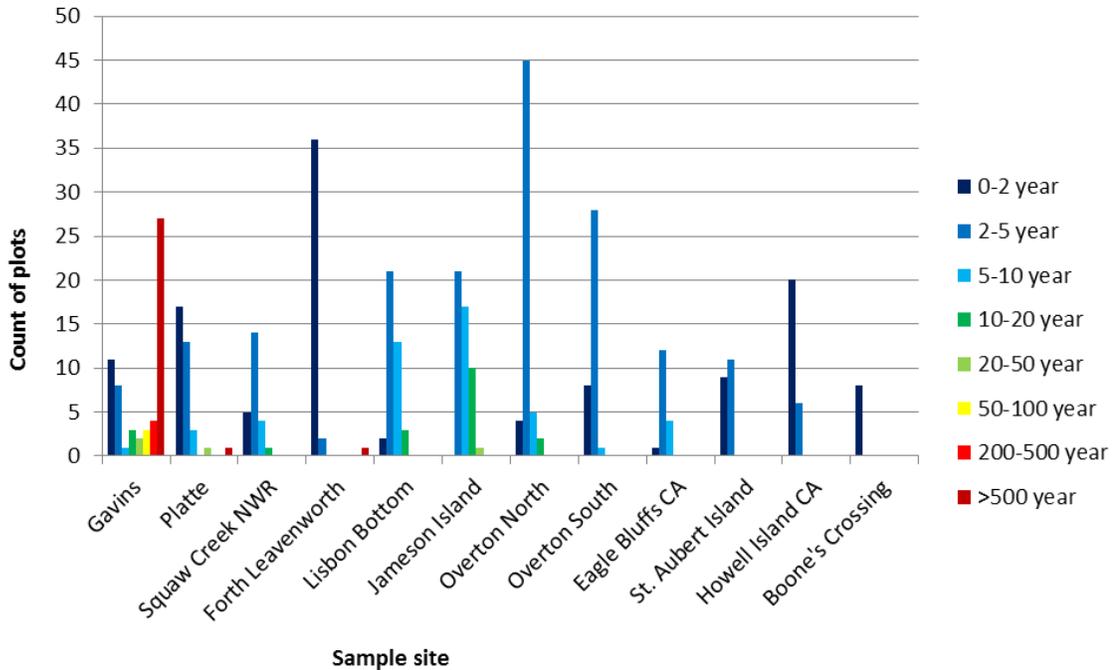


Figure 99. Distribution of plots among flow-return intervals by sample site on the Missouri River.

The differentiation of communities on a longitudinal gradient is consistent with the river continuum concept (Vannote et al., 1980), in which species and community distributions reflect a response to the changing energy of a river system as it grows and changes hydrologically downstream. In this instance, those effects may be exaggerated by the operation of the reservoir system, which exerts a particularly strong influence on the hydrologic and sediment regimes of the upper reaches of the river (Jacobson et al., 2009). Additionally, at the scale of the modeled area, changes in communities may reflect biogeographic effects as individual species respond to temperature, precipitation, and soil variation across the study area. As one example, Johnson grass is a noxious weed in many Missouri counties (Figure 100; pink), but is listed only as present in most counties bordering the upper reaches of the Missouri River (Figure 100; blue) (Kartesz 2014), suggesting there are environmental factors limiting the potential of that species to become dominant in the upstream portion of the study area. Such biogeographic realities were one reason that Brinson (1993) excluded vegetation from his hydrogeomorphic classification system, and they hint at the limitations of the LCPI as a predictor of species occurrence at large scales.

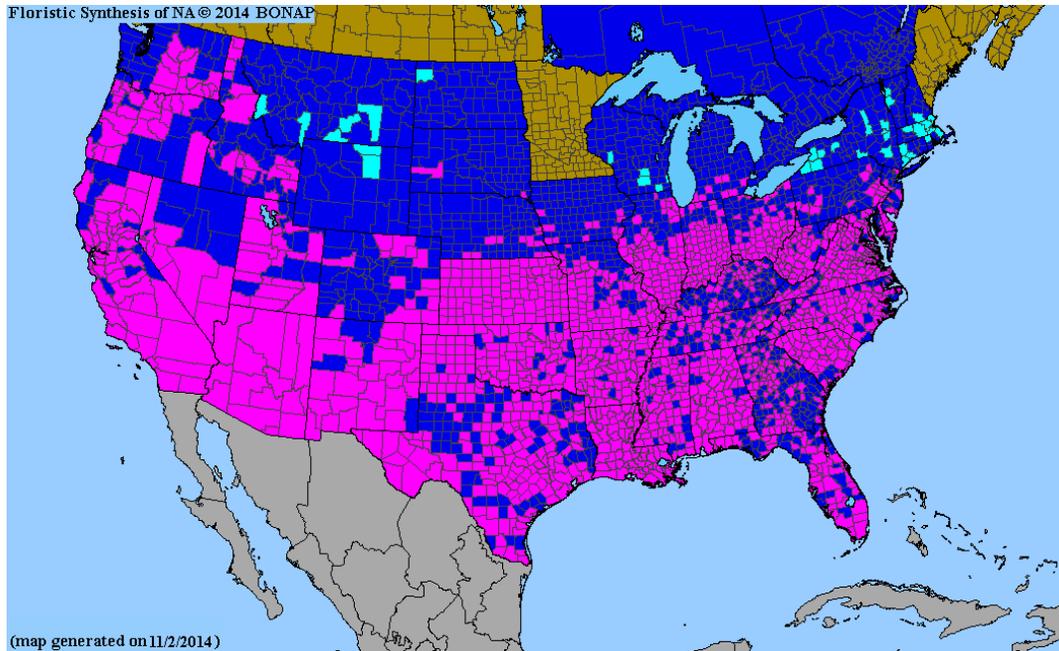


Figure 100. Distribution* of Johnson grass (*Sorghum halepense*) in the conterminous United States (Kartesz, 2014).

*pink indicates noxious, blue indicates present

The NMS analyses make it clear that the elements of the LCPI are important variables associated with the distribution of species. Ordination analyses such as those shown here are driven by species abundance patterns, and it is evident from the two NMS graphs of species that they are often sorting along gradients associated with flow-return interval and soil drainage. At Lisbon bottom, woody species occupy a distinct portion of the ordination space defined by improved soil drainage and longer flow-return intervals (Figure 60). At Eagle Bluffs, woody species are sorted from one another along the related gradients of available water capacity and soil drainage, with willow and cottonwood occupying well drained soils with low AWC (Figure 65).

The NMS results are supported by the historical distribution of species and functional groups, which can be predicted using a model that includes soil AWC and elevation (He et al., 2007). They are also consistent with the research of Thogmartin et al (2009), who demonstrated that the most parsimonious model for predicting the occurrence of forests and wet prairies was one that included flow frequency, elevation, soil drainage, and distance to the main channel. However, results differ from Thogmartin et al (2009) in that the relationship between distance from the river and the abundance of cottonwoods is variable. Among the sites above, sometimes cottonwood communities are farther from the river than other

community types, and sometimes cottonwood communities are closer; Thogmartin et al. (2009) concluded that sites in closer proximity to the river were more likely to support cottonwood communities.

The NMS analyses indicate that the relative ability of environmental variables to explain variation in ordination results changes with site. Numerous factors not measured in this study could be determining which of the environmental variables is best correlated with the data. For example, site history, including time since abandonment and previous land use can affect the relative importance of other environmental variables in determining species distributions (Bell and del Moral, 1977; Robertson et al., 1978; Bendix, 1999). Similarly, where there are fluvial features such as river bends, islands, and backwater channels, hydrologic variability be greater and have more explanatory power vis-à-vis species distributions; where such features are absent, other environmental variables may be more important (Robertson et al., 1978; Yanosky, 1982; Scott et al., 1997; Piégay et al., 2000; Steiger et al., 2001; Steiger and Gurnell, 2002).

Species frequency and abundance

Garlic mustard occurs more frequently and at higher cover values where flow-return intervals are longer and where soil drainage is better. The tendency of garlic mustard to be more abundant on longer flow-return intervals is consistent with its association with mature, full canopied forests (Nelson, 2005; Struckhoff, 2013), which are also more abundant on sites with long flow-return intervals. Within the study area, most mature forests are limited to locations near the river and outside of protective levees (Struckhoff et al., 2011; Struckhoff, 2013) and which tend to have coarser soils as a result of their exposure to greater flow energy (Johnson, 1949; Steiger et al., 2001; Steiger and Gurnell, 2002; Heimann and Mettler-Cherry, 2004).

Johnson grass is significantly more likely to occur and become abundant on sites with longer flow-return intervals. Although the species thrives in disturbed habitats (Steyermark, 1963; Yatskievych, 1999), the data here suggest that flooding does not provide the disturbance type necessary for this species to spread. In fact, the implication of the data is that flooding may be one mechanism to control Johnson grass; however, flooding can be controlled on only a small fraction of the Missouri River floodplain. Programs to monitor and control the spread of Johnson grass may be more effective if efforts are focused on infrequently flooded locations. Johnson grass abundance is minimally related to variation in soil drainage, suggesting it is insensitive to soil drainage characteristics.

Japanese hops is significantly more likely to occur on excessively drained soils, but is more likely to become abundant on poorly drained soils (mean cover shows little variation between soil drainage types). Although hops are most likely to occur at moderate flow intervals, they are not more likely to become abundant at such sites. Because of their susceptibility to invasion by hops, poorly drained soils may be less desirable than other soil types when considering new land acquisitions. Monitoring and eradication efforts will likely be more effective if they focus on poorly drained soils.

Reed canary grass is more likely to occur and to become abundant on frequently flooded sites; it is also more likely to become abundant on poorly drained soils. This is consistent with the species' demonstrated ability to survive sedimentation by fine materials common on such sites (Mahaney et al., 2004). Thus, land acquisition and management concerns are similar to those of Japanese hops. Unfortunately, low lying sites with poorly drained soils are often high priority acquisition sites because of their ability to support wetland communities.

Sweet clover and velvet leaf occur more often on frequently flooded sites; the former species is also more likely to have high cover values on such sites. Both species are less likely to either occur or become abundant on excessively drained sites. Although identified as species of concern by resource managers in the study area, neither species appears to occur in such abundance as to create ecological or management problems at present.

Among native species groups, sedges and smartweeds occur more frequently and become abundant where flow-return intervals are shorter; smartweeds also become more abundant on poorly drained soils than on other soil types. These results are consistent with the fact that these species are often used in conjunction with hydrologic characteristics to identify and define wetland communities (Nelson, 2005; NatureServe, 2014). Among these are the sedge meadow and ephemeral pond communities encountered during this study.

Willows are most likely to occur across a broad range of flow-return intervals from 2 to 50 years; however, the likelihood that they will become abundant decreases significantly where flow-return intervals exceed 20 years. Willows are less likely to occur on poorly drained soils, but not less likely to become abundant. These results are consistent with research indicating the willows communities give way to other community types as soil texture becomes finer (Johnson, 1949; Shelford, 1954; Hosner and Minckler,

1960; Weaver, 1960; Hosner and Minckler, 1963; Viereck, 1970; Keammerer, 1972; Johnson et al., 1976; Teversham and Slaymaker, 1976; Friedman et al., 1996) and the broad tolerance for soil anoxic conditions among willows (Schaff et al., 2003; Shin and Nakamura, 2005). That tolerance may enable willows to become more abundant in the face of reduced competition from species that are unable to tolerate anoxic conditions associated with low-lying, poorly drained soils.

Cottonwood is more likely to both occur and become abundant at moderate flow-return intervals (only the latter relationship is significant). The association of cottonwoods with slightly longer flow-return intervals than willows is consistent with the conceptual model in which these species are indicative of successional stages of floodplain community development, with cottonwoods representing the later stage (Johnson, 1949; Wistendahl, 1958; Johnson et al., 1976; Sigafos, 1976; Frye and Quinn, 1979). The greater abundance of cottonwood at moderate flow-return intervals is predicted by the cottonwood regeneration box model developed (Mahoney and Rood, 1998) and by previous research indicating that cottonwood forests are most abundant on the Missouri River where scouring floods are frequent enough to create new germinations sites, but infrequent enough to provide protection from flooding once seedlings become established, or about 9 years (Scott et al., 1997).

Cottonwood is also more likely to occur and to become abundant as soil drainage improves. This had been previously demonstrated in numerous studies on the Missouri River and elsewhere (Johnson, 1949; Shelford, 1954; Hosner, 1960; Weaver, 1960; Hosner and Minckler, 1963; Viereck, 1970; Keammerer, 1972; Johnson et al., 1976; Teversham and Slaymaker, 1976; Friedman et al., 1996). Greater cottonwood abundance on sandier soils has been attributed to their better ability to survive in soils with low available water capacity compared to other species (Hosner and Minckler, 1960, 1963; Friedman et al., 1996; Shafroth et al., 1998); better soil drainage often reflects coarser texture that is more likely to have lower available water capacity.

Late-successional species are more abundant where flow-return intervals are longer, consistent with previous research in a wide variety of settings (Johnson, 1949; Shelford, 1954; Wistendahl, 1958; Bell, 1974; Bell and del Moral, 1977; Tardif and Bergeron, 1999; Heimann and Mettler-Cherry, 2004; Turner et al., 2004; Dixon et al., 2010). Cottonwoods, willows, and sycamore have morphological and physiological adaptations that enable them to survive exposure to floods (Martens, 1993; Karrenberg et al.,

2002; Lytle and Poff, 2004); these traits tend to be lacking in late successional species. Although late-successional species are more likely to occur on excessively drained soils, this difference is not significant and they are not more likely to become abundant on better drained soils.

Community frequency and abundance

The trends in species' distributions are also evident in the distribution of community types based on vegetation maps for Big Muddy and on plots outside of the mapped area. Ephemeral ponds defined by the presence of smartweeds and sedges are more likely to occur where flow-return intervals are shortest and where soil drainage is poorer, consistent with the concept of that community type (NatureServe, 2014). Similarly sedge meadows and sandbar willow shrublands are more likely to occur where flow-return intervals are shorter, appropriately for communities defined by species adapted to frequent flooding (NatureServe, 2014). These results are internally consistent with earlier results relating to species occurrences and with the previously known habitat requirements for those species (Steyermark, 1963; Yatskievych, 2012).

The very abundant cottonwood and black willow forest reaches its maximum likelihood of occurrence in the 10 to 20 year flow-return interval, the same interval in which that species is most likely to occur, most likely to exceed 15 percent cover, and where it occupies the highest mean proportion of area. Cottonwood forests are also most likely to occur on soil with moderate drainage capacity, where they also occupy a slightly higher proportion of area. Cottonwood dominance diminishes as flow frequency increases, which accounts for the shift on shorter flow return intervals toward other community types where cottonwood is still abundant but is reduced in cover or shares dominance with other species (black willow forest, cottonwood-sycamore forest, cottonwood woodland) (Figure 86). This pattern supports observations made during 2012 mapping that frequent and prolonged flooding in low-lying areas was inducing mortality in cottonwoods more than other species, thereby reducing cottonwood dominance and causing shifts toward the other community types (Struckhoff, 2013). Results are consistent with other research that has suggested that intermediate flow-return intervals are favorable for cottonwood abundance (Rood and Mahoney, 1990; Scott et al., 1997; Mahoney and Rood, 1998; Shafroth et al., 1998).

Herbaceous old fields and woody old fields are broadly defined communities distinguished from one another by the presence of woody stems, particularly hackberry (*Celtis occidentalis*), sugarberry (*Celtis*

laevigata), and ash (*Fraxinus pennsylvanica*). These communities exhibit opposing trends with regard to flow-return interval, the former decreasing and the latter increasing as flow-return interval increases. Thus, on low elevation sites, it appears that exposure to frequent flooding limits the recruitment of woody stems and increases the likelihood of the herbaceous type occurring. Both communities are most likely to occur on poorly drained soils.

The woody old field community species composition suggests that with additional time, it will develop into a mid-successional forest type dominated by ash, elm, and hackberry (Struckhoff, 2013). The latter community also tends to be more common on sites with longer flow intervals than on frequently flooded sites (Figure 86; Figure 90), consistent with descriptions for that type (Nelson, 2005; NatureServe, 2014). The greater abundance of ash-dominated forests on sites with long flow-return intervals supports these results and is consistent with vegetation types that require stable locations on which to develop (Johnson, 1949; Shelford, 1954; Wistendahl, 1958; Bell, 1974; Bell and del Moral, 1977; Tardif and Bergeron, 1999; Heimann and Mettler-Cherry, 2004; Turner et al., 2004; Dixon et al., 2010).

The uniform distribution of box-elder forests across all but the most frequently flooded sites is consistent with that species' well documented tolerance of a broad range of ecological conditions (Steyermark, 1963; Yatskievych, 2006). Additionally, this community type is considered a degraded, post-agriculture type (NatureServe, 2014), suggesting that past land use may be a more important factor in determining its distribution than flow frequency.

Although LCPI flow-return intervals and soil drainage classes provide dependable indications of where species and communities are likely to occur or become abundant, there are a few caveats applicable to its use. Variations in species and community distribution between ecological provinces illustrate the limitations of the LCPI as a tool for predicting species and community occurrence at broad scales. Variability becomes even more pronounced when site-level differences in land-use history and successional progression are considered. Additionally, at smaller scales, small sample sizes in some flow-return intervals or soil drainage classes make it difficult to detect relationships between species' distributions and environmental variables. Nevertheless, the "big data" approach employed here—incorporating data from numerous studies across a broad geographic range to examine the occurrence of individual species and

species groups—shows clear tendencies among some species and communities to be more or less abundant according to LCPI flow-return and soil drainage classes.

The analyses here show that flow-return interval and soil drainage can be used to identify where species and communities are most likely to occur and become abundant with little or no management effort. The information pertaining to exotic species distributions are valuable for acquisition planning in that they provide important information for discerning sites susceptible to invasion by exotic species from those that are unlikely to provide suitable habitat for their expansion. Within the context of resource management, LCPI classes can be used to identify where specific actions are required to reduce the likelihood that exotic species become established. Management actions that may benefit from application of the LCPI information include development of early detection/rapid response programs to control invasive species and habitat manipulation to facilitate community development into stages that are less susceptible to invasion by exotics.

The information included here can also be used to manage for target communities. Herbaceous wetlands such as the Midwest ephemeral pond are clearly associated with low lying positions possessing poorly drained soils. Cottonwoods forests are most likely to occur at moderate flow-return intervals with well drained soils. Late-successional species are more likely to occur on sites with longer flow-return intervals. The LCPI model can be used to identify where these communities are most likely to occur, thereby providing a tool to aid in resource planning at multiple scales. At the regional level, the model can be used to ensure that the conservation portfolio includes the suite of LCPI classes necessary to provide habitat suitable for all of the target communities (even if individual sites are not suitable for all communities). At the site level, the LCPI model can be used to determine the likely spatial arrangement of communities and whether that arrangement will facilitate broad habitat management objectives.

It has yet to be determined if the LCPI classes can be used to guide specific habitat manipulation. Additional research is required that examines the efficacy of management actions in the context of LCPI classes. Numerous bottomland hardwood restoration efforts have been implemented on the Missouri River floodplain. Comparison of survival, growth, and seed production of species planted during these efforts using the LCPI model as a framework for analysis is one potential application of the model to understanding variation in management success. For example, poor soil drainage is often cited as a reason

for failure of bottomland hardwood restoration plantings (Kabrick et al., 2005). One option to address this issue is to physically alter the soil to improve drainage, as in Kabrick et al. (2005); but another option is to focus restoration efforts intended to promote bottomland hardwoods on sites with better drainage.

Adaptive management in conjunction with future restoration projects may benefit from explicit incorporation of the LCPI model to stratify treatments and analyze results.

Advancement to science and management

The value of the results presented here lies in the demonstrated utility of the LCPI in anticipating where species and communities are likely to occur and become abundant, and the potential to inform management for or against particular species. The LCPI provides a spatially explicit model of abiotic factors known to influence plant species and community distributions, and the results indicate that the specific classes are relevant to a broad array of taxa at multiple thematic scales (from species to communities). The LCPI model can be used at broad spatial scales to develop a conservation portfolio that incorporates a variety of lands likely to support desired taxa, and at local scales to direct specific management actions to detect and control exotic species and to promote desired communities. The utility of the LCPI also suggests that similar hydrogeomorphic models could be easily developed for other river systems, and that they would likely be valuable tools to inform habitat management.

The LCPI model can be most effective as a decision support tool within an adaptive management framework. The specific relationships presented here between LCPI classes and species, species groups, and communities are consistent with much that is already known about those taxa, and with previous research identifies a set of initial assumptions that can be made about plant species distributions in relation to the LCPI model. However, site-level variation and limitations imposed by biogeography suggest that those relationships are neither definitive nor immutable; additional information from other research and knowledge of the local hydrology and soils are likely to be useful in understanding relationships between the LCPI and particular species. Additionally, there is a much larger array of species and communities that have not been studied as part of the research presented here, but for which there is a sufficient body of research to inform our initial assumptions about if and how species distributions will relate to LCPI classes. Use of the LCPI as a framework for acquiring lands, implementing management action, and monitoring

management results will help to refine our understanding of those relationships, which can improve future management planning.

The documented relationships between ecological setting and LCPI classes can be used by resource managers to identify factors affecting the relative abundance of LCPI classes, thereby informing the development of a conservation portfolio at multiple scales. Clear differences in the abundance of LCPI classes between ecological provinces define regional limitations on management for many taxa. Geomorphological features and tributaries have local effects on the abundance of LCPI classes that may provide opportunities to manage for species and communities for which appropriate LCPI classes are otherwise locally scarce. Climate change is anticipated to reduce flow-return intervals throughout the study area. This will place additional limitations on management for species and communities that thrive on sites with longer flow-return intervals, but the severity of the effects will vary ecological setting.

The relationships between groundwater response to flow pulses and LCPI classes suggest one mechanism by which plant distributions on the floodplain are affected by soil drainage. Results suggest that better drained soils have larger groundwater response, shorter lag times, and longer durations of elevated groundwater following flow pulses. If these results can be confirmed by additional research, it would improve our understanding of how LCPI classes relate to species distributions mechanistically. Such information would be particularly germane in locations that are protected from flooding by levees and other flow-impeding structures, and at which, groundwater will likely play a more important role in determining the soil moisture regime that affects the distribution of species.

Chapter V:

Conclusions

The LCPI was intended as a coarse-scale decision support tool for the management of floodplain resources, particularly terrestrial habitat as defined by plant species and communities. Because the model incorporates abiotic variable known to affect species distributions, it was assumed that it could be applied at smaller scales to anticipate species distributions and to inform habitat management on the Missouri River floodplain. These assumptions were tested by addressing a number of hypotheses concerning the

relationships between LCPI classes and the distribution of naturally occurring vegetation in a post-agricultural setting:

1. The likelihood of occurrence for species does not vary between LCPI flow-return intervals or soil drainage classes.
2. Mean percent foliar cover for species does not vary between LCPI flow-return intervals or soil drainage classes.
3. The likelihood of a species becoming abundant does not vary between LCPI flow-return intervals or soil drainage classes
4. The likelihood of occurrence for communities does not vary between LCPI flow-return intervals or soil drainage classes.
5. Mean area occupied by communities does not vary between LCPI flow-return intervals or soil drainage classes.

Although not all species and community distributions were significantly related to LCPI classes, the null hypotheses above can be rejected for most of the examined taxa. Thus, the research presented here validates the assumption that the LCPI is relevant to the distribution of naturally occurring species.

The results presented here identify relationships between LCPI classes and a small subset of species and communities. At minimum, the results can be used to identify sites on which non-native species are more or less likely to occur and become abundant and locations that are more or less likely to support desired communities with little or no intervention. They can be used along with other research, local knowledge, and past management experience to anticipate where other species are likely to occur naturally. Additionally, it can be used to identify sites that are susceptible to invasion by exotic species, providing a framework for early detection/rapid response program for controlling the spread of non-native species.

Although this research does not explore the value of the LCPI as a framework for management actions to promote particular species, if the probabilities of species occurring and becoming abundant are indicative of the relative suitability of LCPI classes for those species, it is reasonable to assume that the LCPI can provide such a tool. An adaptive management system using the LCPI as a framework for implementation and assessment of management actions would provide benefits at multiple time scales. In the near term, it would allow management of floodplain habitat based on the best current information; in the long-term, it would provide a framework for assessing the efficacy of management actions in achieving habitat objectives and for improving management efficiency. Such an application of the LCPI should not be

based solely on the specific results of this study. Many of the relationships documented in this research were anticipated by the results of previous studies, and a vast body of information exists to enable informed assumptions about how the distributions of species not examined here will relate to LCPI classes and how species establishment, growth, and survival following management actions will vary across LCPI classes.

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