

BIOMASS PRODUCTION OF FIVE *POPULUS* CLONES, SOIL CARBON AND
SOIL WATER CONTENT IN A CENTRAL MISSOURI FLOODPLAIN

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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

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

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS. ii

LIST OF FIGURES vi

LIST OF TABLES vii

INTRODUCTION 1

Utility of Short-Rotation Plantation Culture . . . 1

Leaf area characteristics and biomass production . 5

Soil C storage in plantation culture 7

Soil moisture and plant productivity 9

LITERATURE REVIEW 12

Poplar culture. 11

 Root:shoot ratio. 22

Light and plant productivity. 25

 Canopy structural components. 26

Soil Moisture and plant productivity. 30

 Flooding effects. 30

 Flooding and oxygen uptake. 31

 Chemical reductions in waterlogged soils. . . 32

 Flood induced morphological and chemical
 changes 32

Carbon sequestration capacity of *Populus* 34

 Long-term C storage. 35

 Biofuel 36

Soil C changes in short-rotation plantations.	36
Rotation length	37
Agricultural programs and soil C	38
MATERIALS AND METHODS	40
<u>Plant material.</u>	40
<u>Plantation design and establishment.</u>	43
<u>Biomass Accumulation Experiment</u>	51
Destructive harvesting of above ground	
biomass	51
Root excavation	52
Permanent plot tree measurements	54
Data analysis	54
<u>Light Conversion Efficiency Experiment</u>	56
Phenology recordings	56
Light Measurements	57
Data analysis	59
<u>Soil Moisture Case Study</u>	61
Clone and location	61
Data collection	62
<u>Soil C Experiment</u>	63
Data collection	64
Data analysis	65
RESULTS	67
<u>Biomass Accumulation Experiment</u>	67

Stepwise regression procedure	67
Plantation 1 five year trends in biomass . . .	73
Plantation 1 biomass statistical analysis . .	80
<u>Plantation 1 root:shoot ratio</u>	82
Mean root:shoot ratios calculations	82
Data analysis	83
<u>Light Use Efficiency</u>	90
Phenology	90
Leaf Area Duration vs. estimated biomass . .	90
LAD data analysis	98
<u>Plantation 1 Soil Carbon Analysis</u>	99
<u>Plantation 2 - Five Year Trends in Biomass</u> . . .	110
Biomass statistical analysis	111
<u>Plantation 2 - Root:Shoot ratio</u>	115
<u>Plantation 2 Soil Carbon Analysis</u>	123
<u>Soil Moisture Case Study</u>	124
DISCUSSION	137
<u>Productivity</u>	137
<u>Root:Shoot Ratio</u>	139
<u>Light Use Efficiency</u>	142
<u>Changes in Soil Carbon</u>	145
<u>Soil Moisture and Plant Productivity</u>	147
SUMMARY AND CONCLUSIONS	150
LITERATURE CITED	152

LIST OF FIGURES

	Page
Figure 1	46
Figure 2a and 2b	50
Figure 3	77
Figure 4a, 4b and 4c	79
Figure 5	88
Figure 6	92
Figure 7	96
Figure 8	102
Figure 9	107
Figure 10	109
Figure 11a, 11b, and 11c.	113
Figure 12	120
Figure 13	126
Figure 14	128
Figure 15	130
Figure 16	132
Figure 17	134
Figure 18	136

LIST OF TABLES

	Page
Table 142
Table 255
Table 368
Table 470
Table 571
Table 6a, 6b and 6c75
Table 7a, 7b and 7c85
Table 7d and 7e86
Table 8a, 8b and 8c89
Table 997
Table 10a, 10b, 10c	103
Table 10d and 10e	104
Table 11a, 11b and 11c105
Table 12a, 12b and 12c	116
Table 12d and 12e	117
Table 13a, 13b and 13c121

INTRODUCTION

Utility of Short-Rotation Plantation Culture

More than ever there is a growing need for alternative methods of cultivating natural products that are no longer available in adequate supply through traditional systems. Increasing human population, rural development, historic management and continuation of traditional non-sustainable agricultural practices are just a few of the factors that have led to shortages in wood production faced by the timber industry. At the same time, family farmers and small landowners in the 1980's found it increasingly difficult to compete with industrialized farming and to cope with chronically low commodity prices.

Solutions for these concurrent issues include development of short-rotation tree plantations to deal with increasing timber demands and a variety of government subsidy programs to aid small-acreage operations. In some ways these solutions have meshed, as awareness of the impact agricultural and timber management have on local ecosystems has greatly increased. These opportunities have given landowners the opportunity to participate in environmentally-oriented programs, while equipping them with the knowledge and incentives to fulfill their inherent role as land stewards.

Economic consolidation has resulted in the erosion of small operators' connection to their businesses and the land that supports it. Producers often do not own the commodities they produce, but serve more as curators and storage facilities to the products owned by corporations. Management practices that reduce the decision-making capacity of landowners run the risk of alienating business activities from the environment, perpetuating activities that may have negative ecological impacts while jeopardizing future yields.

Short-rotation plantation culture could be an alternative for small farmers and landowners who are looking for ways to diversify current operations, initiate new commodity production, or to better utilize marginal acreage and generate alternative sources of income. Short-rotation intensive culture involves the establishment of rapid growing trees at dense spacing, the application of intensive culture practices, harvesting within 10 years, and regeneration via coppice growth or sprouts (Debell et. al, 1993). Particularly intriguing for plantation culture is the floodplain acreage that includes many acres of highly fertile soils, capable of possessing large moisture holding capacities. Although highly susceptible to erosion and flooding damage when cultivated in row crop systems,

these areas have a high yield capacity, which has traditionally encouraged producers to maximize cultivation in these areas. The risk associated with flooding has kept some of these areas unplanted and left to the expansion of the riparian corridor. Many tree species that grow naturally within these floodplains, such as *Populus deltoides* Bartr. ex Marsh. (eastern cottonwood), *Platanus occidentalis* L. (sycamore) and *Salix nigra* Marsh. (black willow), have also produced well in plantation culture and are able to tolerate the characteristic high soil moisture levels and frequent incidents of flooding. Plantation culture also improves habitat for native wildlife when replacing row crop systems and is better able to filter contaminants from runoff, thereby improving water quality.

In order for landowners in a region to participate in short-rotation plantation culture, the need exists for testing of a variety of species, hybrids, and clones - such as with poplars - within the area, or at least in areas with similar environmental conditions. Characteristics particularly important to floodplain plantations include flood tolerance and the ability to adapt to site soil moisture conditions. Identification of locally-adapted, productive clones provides the best chance for the highest yields possible in the time allotted to the rotation.

Objective of the biomass comparison experiment

In the spring of 1999 a plantation of four clones of *Populus* were established at the Horticulture and Agroforestry Research Center near New Franklin in the Central Missouri River Floodplain (Lat. 39°01', Long. 92° 46') to test for biomass production in local clone plantation candidates. Although poplar culture and the study of poplar as a plantation species has been extensive in several regions of the U.S., there has been little research conducted in the lower Midwest to test for the physiological and morphological responses to the climate regime of the region (Pallardy et al., 2002). The objective of this experiment was to identify certain clones in *Populus* as possible candidates for wide-scale biomass production in plantation culture for the lower Midwest. Clones included three of *Populus deltoides* (2059, 1112, and 26C6R51) and a *P. deltoides* × *P. nigra* hybrid clone (I45/51).

In the spring of 2000 a replicate Plantation (Plantation 2) was established approximately 75 m northeast of Plantation 1 to determine if results reported in Plantation 1 remained consistent across sites. Clones tested included those planted in Plantation 1 and a second hybrid clone (*Populus deltoides* × *P. nigra* 'Eugenie'),

which had served as a buffer tree around Plantation 1 during the experiment.

Leaf Area Characteristics and Biomass Production

One of the most important determinants of biomass production in both herbaceous and woody plants is the leaf area produced and the length of time that leaf area is high active (Milne et al., 1992). The high growth rates exhibited by *Populus* have been linked to rapid and continuous leaf production, high leaf area and photosynthetic rates, which are among the highest of temperate deciduous tree species and rival many herbaceous species (Pallardy and Kozlowski, 1981; Rhodenbaugh and Pallardy, 1993). Leaf area is responsible for intercepting solar energy from the sun and converting it into usable energy that allows plants to capture CO₂ and convert assimilates into biomass components (Cannell, 1989). There has been extensive research on the relationship between leaf area characteristics and biomass production in a variety of *Populus* and *Salix* species (Cannell et al., 1988; Dickmann et al., 1992; Harrington et al., 1997).

Research has also focused on how converted biomass was distributed between above and below-ground components in pine, willow and poplar (Albaugh et al., 1997, Burkes et al., 2003; Cannell et al., 1988). This distribution is

referred to as the root:shoot ratio, which is an important measurement of how efficiently plants are partitioning assimilates to harvestable biomass. Participants in short-rotation plantations select for species or hybrids that produce the most above-ground biomass without outgrowing their support systems below ground. Rapid early growth, without adequate rooting, can be disadvantageous as a rotation progresses and plants are confronted with a variety of stresses, such as drought and competition for nutrients (Baker and Blackmon, 1977) and light (Green et al., 2001).

Although there are many factors of leaf production that influence how efficient plants are capable of capturing CO₂, this study primarily focused on Leaf Area Index (LAI) and Leaf Area Duration (LAD). Other related keys to efficient energy conversion include the phenological traits of early bud break in the spring and leaf retention in the fall. Collectively, these elements form LAD which integrates when, to what extent, and how long the canopy is constructed.

Objectives of Leaf Area Experiment

The objectives of the leaf area experiment were to compare leaf area characteristics with biomass production in order to compare light energy conversion efficiency

among all tested clones. These data, in conjunction with data from the biomass comparison experiment, could be important in selecting clones for the development of *Populus* plantation culture in the central Missouri River floodplain, as well as other locations in the region with similar climatic and environmental regimes.

Soil Carbon Storage in Plantation Culture

Another possible advantage of poplar in short-rotation plantation culture lies in its potential capacity to increase C in the soil, and in the biomass it produces, thereby preventing the C from residing in the atmosphere as CO₂. Build-up of C-based gases, such as CO₂ and CH₄, is thought to contribute to global warming and CO₂ has consequently been categorized as a greenhouse gas. Carbon sequestration is the long-term storage of C in oceans, soils, vegetation, and geologic formations thereby potentially ameliorating greenhouse gas accumulation. Forests are the earth's primary sink of vegetative terrestrial C, followed by semi-arid grasslands and shrublands (Hanan et al., 2000). Plantations of fast-growing trees would need to compare with these natural systems in soil C sequestration in order to justify their introduction into the landscape. Modeling studies have estimated higher soil C sequestration rates in plantation

culture than in natural systems due to the higher planting densities of faster growing trees putting greater quantities of C into the soil (Matthews and Grogan, 2001). The soil, along with geologic formations, is recognized as the most stable reservoirs for storing C (Markewich and Buell, 2005).

During the twentieth century, high levels of fossil fuel combustion and deforestation increased C levels in the atmosphere by 30% (Ecological Society of America, 2000). The first international attempt to address the potential dangers of global warming came in 1997 at the United Nations Framework Convention on Climate Change, which focused on the reduction of CO₂ emissions. Strategies proposed at the conference for reducing CO₂ emissions included increased use of non-fossil fuel energy sources and demonstrable sequestration of atmospheric C through changes in land/use management (Grogan and Matthews, 2002).

Much emphasis has been placed on plantation culture as a C sequestration method due to the C-storing capacities of growing trees in culture, the long-lived end products following tree harvest, and the possible use of the timber as a cleaner burning alternative fuel source. Increased soil C also has the supplemental environmental effects of improved soil and water quality, increased nutrient holding

capacity, reduced soil erosion, and increased water conservation. These effects stem from the increased organic material, consisting of roots, leaves, branches, and other woody material, introduced to the soil under plantation culture.

Objective of the Soil C Experiment

The objective of the soil C experiment was to determine if a change in soil C occurred over the course of a five-year period of short-rotation poplar on a site previously occupied by tall fescue (*Festuca arundinacea* Schreb.). Initial soil samples were taken before planting at both sites, in designated areas, and then were sampled again following the five-year rotation. The information gained from the research may aid in decisions concerning what site conditions are appropriate for establishing short-rotation plantations from an ecological perspective.

Soil Moisture and Plant Productivity

A final aspect of the HARC study examined the effects of varying soil moisture levels on *Populus* growth. Although floodplain forests are often found on fertile, well drained soils, a range of microtopographic sites in close proximity is common. These changes can result in substantial localized variation in soil moisture during periods of elevated precipitation.

Soil flooding can result in an inadequate supply of oxygen to the roots, which subsequently disrupts many physiological processes of the plant and can lead to the formation of phytotoxic compounds (Neuman et al., 1996). General symptoms associated with oxygen depletion include reduced growth, leaf chlorosis, leaf epinasty, formation of adventitious roots, and wilting (Kozlowski, 1985). Other negative effects of soil flooding on plant growth include slowed root and leaf expansion and a decrease in the uptake of nutrients (Neuman et al., 1996)

Typically, tree species growing along riparian corridors and floodplains are flood tolerant and able to survive extended periods of saturated soils. However, even the most tolerant of species show reductions in growth during long periods of root inundation and exposure to waterlogged soils. Conner et al. (1981) reported large reductions in basal area of ash trees (*Fraxinus* spp.) growing in permanently flooded soils when compared to the same species under periodic flooding regimes. Other flood-tolerant species (*Taxodium distichum* (L.) Rich. and *Nyssa aquatica* L.) also showed evidence of poor crown health, manifested in extensive branch senescence in highly waterlogged soils.

Objective of the Soil Moisture Case Study

The objective of the soil moisture case study was to determine if substantial differences in soil moisture existed between two plots of *Populus deltoides* x *P. nigra* 'Eugenie' with variable microtopography. Visible differences in biomass accumulation and drainage capacity were observed. It was hypothesized that a direct relationship existed between excessive soil water content and reduced production, indicating a flood tolerance threshold in varieties of plantation *Populus* spp.

LITERATURE REVIEW

Poplar Culture

There has been extensive research performed on *Populus* in the European community, Canada, Pacific Northwest, and southern United States as a plantation culture genus (Cannell et al., 1976; Heilman and Stettler, 1990; Weber et al., 1985). Farm production of woody biomass gained prominence in the late 1960's in the southeastern United States. Over the course of the subsequent decade, cultivation of *Populus* tree species in short rotations spread to other regions of the country (Debell et al., 1997). However, there is still a need for the study of the utility of *Populus* for the Midwest region of the United States, and more specifically central Missouri.

The reasons for identification of fast growing clones adapted to the Midwest are twofold. In the past fifteen years a trend emphasizing diversity of farming operations has been growing in the agricultural community in order to enhance the competitiveness of the traditional family farmer. Many landowners and producers are searching for new commodities, aside from row crop and livestock markets, as alternative products for reducing the risk attached to conventional operations. Short-rotation plantations are an option and particularly suited for marginal acreage that

may present challenges to traditional agricultural practices that are linked to frequent flooding. Constant pressures on forests due to growing populations and development are creating a need for faster growing timber and land on which to produce it (Ranney et al., 1987). This is a niche that smaller operators could fill while generating another income source. Environmentally, strategically placed short-rotation plantations could improve water quality, reduce soil erosion, decrease runoff of non-point source pollutants, and improve habitat for many species of wildlife (Brattne et al., 1999).

Members of the *Populus* genus are capable of quickly producing large amounts of valuable wood products (Zhang et al., 2003; Zsuffa et al., 1977). Uses for *Populus* wood include lumber, veneer, plywood, pulpwood, boxes, crates, food containers, interior furniture parts, agriculture implements, wooden ware, and cutting boards (Alden, 1995). Other uses that have been identified include oriented strand board and construction materials in agrarian communities (Heilman, 1999). Rates of growth in *Populus* species are among the fastest deciduous hardwood tree species and unequaled by most north-temperate woody plants (Dickmann et al., 1992). Considering its propensity for quickly generating superior amounts of harvestable biomass

and its many applications, poplar species are particularly attractive for short-rotation intensive plantation culture (Ceulemans et al., 1992). In many Canadian provinces these attributes have made hybrid poplar clones the preferred species for sawlog markets of the future (Zhang et al., 2003).

Rapidity and quality of biomass production are attributes that can provide both economic returns and environmental benefits. These are characteristics inherent to members of the *Populus* genus, which can be further enhanced through a variety of improvement measures, including interspecific hybridization, parental selection and clonal selection (Ceulemans et al., 1992; Stettler et al., 1988).

Another important attribute of *Populus* is its propensity for prolific coppice growth. Many studies have documented coppice biomass yields that were considerably larger than yields from initial plantation growth (Bowersox and Ward, 1976b; Heilman et al., 1972; Saucier et al., 1972). Cannell and Smith (1980) indicated that coppice yields of black cottonwood (*Populus trichocarpa* Torr. and Gray, clone 'Fritzi Pauley') were 10-30 percent greater than initial yields due to coppice growth's capacity to re-establish full cover canopy sooner than seedlings or

cuttings. A biomass yield study of short-rotation hardwoods near Manhattan, Kansas supported the findings of Cannell and Smith (1980), with 2-year coppice harvest yielding nearly 50% greater biomass than 2-year seedling harvest in a variety of fast-growing hardwoods (Geyer, 1989). The possibility of garnering multiple yields from one planting is an advantage unrivaled by traditional practices. Lacking large-scale research efforts to this point, there is a need for research on locally-adapted clones before Midwesterners can participate in the development of short rotation plantations of *Populus*.

Productivity of a short-rotation plantation is typically measured in tons per hectare on the basis of mean annual increment. It has been suggested that the working maximum of a short-rotation plantation is 10-12 tons ha⁻¹ yr⁻¹ (Cannell and Smith, 1980). It is estimated that the amount of wood biomass production necessary to fuel a biomass-to-gaseous fuels conversion facility would be 200,000 - 1 million tons annually. These amounts are comparable to those of an operating pulp mill (Ranney et al., 1987). Using these estimates, it would take from 20,000 to 100,000 ha of plantation to fulfill the demand of one of these operations. In 1997, there were approximately 33,000 ha of hybrid cottonwoods planted in the Northwest,

while in 1995 12,000 ha of poplar plantations were present in the Southeastern and North-central United States (Strauss et al., 1997). On an international scale, the 1992 report from the International Poplar Commission listed nineteen countries with at least 10,000 ha of planted poplars and seven with more than 100,000 ha (Heilman, 1999). Fortunately, *Populus* plantations have demonstrated growth rates well beyond the working maximum of Cannell and Smith (1980) (Scarascia-Mugnozza et al., 1997, Heilman et al., 1996). Nevertheless, a viable biomass-based energy industry will likely require faster rotations with greater yields and on more land (Ranney et al., 1987).

Numerous plant spacings, species and hybrids have been tested and compared for optimum matching of tree genotype with tree characteristics, adaptations, and site. The economic components of poplar plantations rely on the physiological and morphological responses of individual *Populus* clones under particular soil conditions, environmental regimes and rotation length (Debell et al., 1996). Bowersox et al. (1982) determined that in identical field trials of *Populus maximowiczii* × *P. trichocarpa*, energy values, defined as kilocalories/ha, increased by 28% on favorable sites (grown on silt loam soil) compared with those unfavorable for growth (grown on sandy loam soil).

Important economic implications were revealed in relative responses to treatments of irrigation, fertilization, and irrigation/fertilization, which were much reduced in the more fertile site, although absolute values of biomass and energy content were greater there. Blackmon et al. (1979) concluded that genotypes that show similar growth rates, while taking up significantly fewer nutrients, would be better adapted to nutrient-deficient sites. It follows that selection of trees able to reach their potential with fewer inputs would be an economic advantage on any site.

Equally important for culture are a clone's stockability and sustainability qualities. Stockability refers to a clone's tolerance to crowding and sustainability refers to a clone's ability to maintain adequate biomass production over time at a particular stocking (Debell et al., 1996). Therefore, the success of short rotation plantations requires a well planned and managed combination of site design and tree selection. Three of the biggest concerns associated with high productivity rates in short rotation intensive cultures include weed control, disease control, and site clone matching (Ranney et al., 1987).

Strategic fertilization and irrigation have also been recognized as important factors in determining stand

productivity (Brattne, 1999; Michael et al., 1988).

During the initial growing season of an eastern cottonwood (*Populus deltoides*) stand planted at 3 × 3 m spacing in western Mississippi, seventy-five percent of the above-ground biomass was added during August and September (Baker and Blackmon, 1977). It was concluded that fertilization in first year cottonwood plantations and nurseries, under similar environmental conditions, should be conducted in late summer to promote maximum nutrient uptake and minimize nutrient leaching from the soil (Baker and Blackmon, 1977). Such requirements can be adequately addressed with proper management.

It is necessary to test promising candidates for plantation culture in the area for which they are intended for use because of the local genetic adaptation in poplar, as well as many other genera that strongly influences tree performance (Weber et al., 1985). Species and hybrids that thrive under one set of environmental conditions and plantation design specifications may not produce well at an alternate site or at different spacings, even a short distance away. There are also evolutionary adaptations within provenances that have substantial implications in the success of genotypes in a plantation situation (Ledig and Korbobo, 1983).

Local source clones often perform better than non-native clones in biomass production. A *Populus deltoides* production study conducted at Urbana, Illinois identified a Wisconsin clone that produced superior height and diameter following the first year, but grew less in height and diameter than a native Illinois source as the rotation progressed. The Wisconsin clone had a superior potential for height growth due to the morphological structure of its leaves, giving it a greater capacity to photosynthesize than other clones under equivalent environmental conditions. The authors suggested that local selective pressures led to production advantages in the Illinois source plants, although both sources were only separated by three degrees in latitude. Moreover, there were notable decreases in production of the Wisconsin clone grown at Urbana compared to those when grown indigenously, although the study site was located only 5 degrees south of its native range (Drew and Bazzaz, 1978).

In a study conducted near Olympia, Washington of two local clones of *Populus trichocarpa* and two bred hybrid clones (11-11: *Populus deltoides* × *P. trichocarpa* and D-01: taxonomic identity unknown) the clones of the Washington-developed source (11-11) grew more rapidly at higher levels of competition than the other tested clones (Debell et al.,

1997). Interestingly, the hybrid developed from Idaho stock (D-01) produced much less at lower levels of stand density than all other clones, with the two local *Populus trichocarpa* clones producing nearer to the level of 11-11.

Similar results were observed in a productivity study in western Washington State, where locally collected clones of *Populus trichocarpa* far exceeded the volume and dry weight production of the *P. deltoides* × *nigra* hybrid 'Robusta' clone (Heilman and Stettler, 1985). Thus, there is substantial evidence in the literature to support the contention that in hybrid and species clones alike, the more distant the source of origin of a clone the less productive it likely will be when compared to more locally-adapted clones in plantation culture.

The proliferation of hybrid poplar cultivation, as opposed to pure poplar species, lies partly in an advantage of enhanced juvenile growth and propensity for vegetative reproduction (Pallardy and Kozlowski, 1981). Hybrids are an especially valuable option in areas where production is inherently poor, lending the possibility of genetic combinations overcoming natural limitations. These attributes are conferred by hybrid vigor and genetic selection for rapid early growth under favorable culture conditions (Braatne, 1996). Studies conducted comparing

clones of *Populus trichocarpa* and *Populus deltoides* and their interspecific hybrids have repeatedly confirmed yield superiority in the hybrids (Ceulemans et al., 1992; Heilman and Stettler, 1985).

When looking at short-rotation culture of fast-growing genotypes (including hybrid poplars) from a broader perspective, a number of important issues emerge, each accompanied with its own set of cultural and environmental ramifications capable of having either positive or negative effects. The complexities of the components comprising each issue require comprehensive research efforts to determine the degree of benefit or risk attached to each.

A promising aspect of short-rotation culture includes a capacity for improving water quality by controlling agricultural nutrient and chemical runoff. Also a water-related benefit, somewhat shrouded in misconception, is poplar's ability to reduce ground water depletion. Studies have shown stomatal conductance to be relatively high in poplar, leading to the belief that transpirational water loss is much greater than other tree species and traditional agriculture crops. However, the dense canopy formed by poplar plantations prevents exposure to environmental conditions that exacerbate evapotranspiration in sparser canopies, including a reduction in solar

radiation that reaches the ground and increases soil evaporation (Braatne, 1996).

Another benefit poplar culture possesses is manifested from a production standpoint. As previously noted, hybrid poplars have exhibited increased growth of harvestable material (Ceulemans et al., 1992; Heilman and Stettler, 1985), providing greater economic returns to producers and an incentive for landowners to consider participation in short-rotation plantation culture.

Areas of concern associated with hybrid culture, per se, deal mainly with reproduction and the impact of hybrid stock on nearby native populations. As in all complex natural systems, there are possible unapprehended effects on native *Populus* stands (Braatne et al., 1996).

Unintended consequences from cross-pollinations between native species and introduced hybrids could impair regeneration in a variety of ways, including time of seed dispersal and seed viability. A reduction in defense from pests and pathogens, known as "hybrid breakdown", is also a primary concern (Stettler et al., 1996b). Hybrids also show great variation in growth traits and are sensitive to small changes in site conditions (Rogers et al., 1989).

Another important factor contributing to biomass productivity is the pattern of photosynthate partitioning

between the roots and shoot (Tschaplinski and Blake, 1989). Assimilate partitioning is a complex process that involves morphological, environmental, managerial, and physiological events (Gifford and Evans, 1981; Keyes and Grier, 1981). In order for optimum growth of harvestable material, a balance must exist between root growth and shoot development (Burkes et. al., 2003; Ledig and Perry, 1965), along with adequate resource availability (especially nutrients and water) and competition control (Albaugh et al., 1998). If aboveground growth is excessive then the roots are unable to adequately supply water and nutrients and the plant cannot reach its total growth potential. The reverse can also occur, where root systems become overly extensive and reduced leaf area is unable to supply both roots and shoots with sufficient photosynthate for vigorous growth (Kramer and Kozlowski, 1960). Thus, allocation of C below ground diverts C away from leaf area production, inherently reducing productivity on sites provided with adequate moisture. However, on sites where drought is likely, increased investment in root production can be beneficial, preventing chronic water-stress and tree mortality. These major tissues function in concert with others, collectively controlling growth while keeping the meristems active in producing new tissue (Dickmann, 1977).

Plantation culture seeks to exploit this natural equilibrium, and also to alter it as well, in order to maximize desired effects.

Stand density has also been shown to affect the ratio between roots and shoot. In a study conducted on two pine species (*Pinus taeda* L. (loblolly pine) and *Pinus elliottii* Engelm. (slash pine)) in the coastal plains of Georgia, there were similar relationships between assimilate partitioning and stand density. Higher stand densities resulted in higher partitioning to stem biomass relative to foliage or fine roots (Burkes et al., 2003). This trend was also present in three stands of *Populus deltoides* up to nine years of age (Puri et al., 1993). However, there is a limit on plant density that must be observed depending on site characteristics so that declines in total stem growth rates can be avoided, reducing the amount of harvestable material (Harms et al., 1994).

Root:shoot ratio has a direct relationship on C sequestered in the soil as well, where it is primarily stored as soil organic matter (Madeira et al., 2002). Higher root:shoot ratios result in increased fine root turnover, creating greater pools of C deeper in the soil (Grogan and Matthews, 2002). Carbon pools located deeper in the soil may be less susceptible to respiration and more

stable than those closer to the surface.

Light and Plant Productivity

A plant's capacity to intercept solar radiation and convert it into usable energy is critical to biomass accumulation. Biomass production has been linearly related to the radiant energy intercepted by the foliage in agricultural crops and forest stands (Cannell et al., 1988; Monteith, 1981). The leaves that comprise the canopy are the organs primarily responsible for carbon gain (Kikuzawa and Ackerly, 1999). The fraction of light intercepted by the canopy is largely controlled by the amount of foliage and canopy architecture (Cannell, 1989). The ratio with which an organism converts radiant energy into biomass is defined as Light-Use Efficiency (LUE) or conversion efficiency, often expressed as grams of biomass produced per megajoule of absorbed photosynthetically active radiation (PAR) (Heilman et al., 1996). Canopy structural components that determine light-use efficiency include LAI, leaf area duration, and leaf and branch morphology and their orientation (Isebrands et al., 1983). These attributes determine how quickly short-rotation plantations achieve canopy closure and how full those canopies are. Canopy closure and its subsequent leaf area display are essential to plantation establishment and growth (Heilman

and Xie, 1994). Harrington et al. (1997) found strong positive correlations between mean leaf area and total aboveground biomass in plantations of two-year old *Populus* clones.

Populus light-response attributes have been studied for a variety of reasons, with some common areas of focus being radiation interception, LUE, and optimization of canopy light environment. Optimization of canopy light environments refers to optimal leaf angles in the canopy and the subsequent penetration of light. Steeper leaf angles in the upper reaches of the canopy allow deeper penetration of light into the canopy, improving the overall canopy light environment and enhancing whole-plant photosynthesis (Green et al., 2001).

M.G.R. Cannell's research on woody biomass production at the Institute of Terrestrial Ecology in Scotland has been prominent, comparing *Populus* genotypes and other genera with similar phenotypic traits (Cannell and Willett, 1976; Milne et al., 1992). A main component of his *Populus* research has focused on the capacity of the trees to intercept PAR and how efficiently they convert light energy to dry matter. As already noted, a tree's capacity for capturing PAR and converting it to biomass is greatly influenced by the leaf area production and seasonal

duration of the canopy (Leaf Area Duration, LAD) associated with a particular species or hybrid.

LAD is defined as:

$$\sum_{days=1}^n LAI * days$$

(where LAI = Leaf Area Index).

The relationship between intercepted solar radiation and dry matter accumulation in *Populus trichocarpa* was linear up to the time of heavy leaf fall (Cannell et al., 1988). Also important in biomass production is the efficiency with which the leaves are able to convert solar radiation as the result of environmental and nutritional aspects, as well as genetic and morphological traits (Cannell, 1989). Together, LAI, LAD and LUE serve as the crucial determinants of biomass accumulation. In a field study of five poplar genotypes conducted near Arlington, Wisconsin, above-ground biomass and LUE were strongly correlated across genotypes ($r^2 = 0.99$) (Green et al., 2001).

A study conducted at the Institute of Terrestrial Ecology, Bush Estate, Penicuik, UK compared biomass production in relation to intercepted solar radiation of

three poplar clones ('Beaupre', 'Fritzi Pauley', and 'Robusta') (Milne et al., 1992). The 'Beaupre' clone performed best in short rotation culture for essentially two reasons: it developed a canopy more quickly and held its leaves longer than the other clones. 'Robusta', which produced the least dry matter of the three, actually had the greatest efficiency rate of converting solar radiation to dry matter (1.53 g MJ^{-1}) and the highest peak LAI (6.2). It was not enough, however, to make up the difference in seasonal interception, recognized as the canopy attributes responsible for producing biomass. 'Robusta's' propensity for late canopy development and early leaf drop resulted in a seasonal total of fractional interception about 30% less than the other two clones (Milne et al., 1992). It would benefit those invested in poplar clone production to have access to those varieties that achieve the optimum combination of conversion efficiency and leaf area display for their region.

Many studies performed in Europe have been done in conjunction with stands of clonal *Salix*, which show similar capacities to *Populus* concerning light use efficiency and biomass production. *Populus* has demonstrated the capacity to generate competitive biomass yields overseas in climates more conducive to *Salix* cultivation. In a study conducted

at the Bush Estate, Midlothian, Scotland, woody biomass production following one growing season from cuttings in containers was compared between clonal *Salix viminalis* L. and clonal *Populus trichocarpa* (Cannell et al., 1988). Several variables were considered for woody biomass production, including the proportion of dry matter partitioned to wood, the seasonal mean efficiency with which light was used to produce dry matter, the mean fraction of light intercepted by the canopies, and the amount of incoming solar radiation over the season. *Populus trichocarpa*, although ultimately out-produced by *Salix viminalis*, exhibited comparable light use efficiencies from the growing season of May 28 through October 14, 1986. Two major factors that led to the difference in biomass production were, again, greater LAD in *Salix*, and more partitioning of dry matter to stems versus roots (Cannell et al., 1988).

Results of a 1997 genetic selection trial conducted in the northern United States of forty willow and poplar clones simultaneously established in New York and Wisconsin, demonstrated that hybrid poplar clone NM6 (*Populus nigra* x *Populus maximowiczii*) was the top producer in leaf area and stem biomass production (Tharakan et al., 1998.) It should be noted, however, that these results

were for only one year of growth and that the comparative growth performance of poplars often changes over the course of a rotation (Zsuffa, 1975).

Soil Moisture and Plant Productivity

Excessive soil water content can deleteriously affect plant growth. Woody plants located in areas of frequent soil inundation experience a variety of reactions to prolonged flooding, depending on their adaptive capacities and flooding conditions (Kozlowski and Pallardy, 2002). Flooding can have either positive or negative effects on plant growth depending on timing, duration, and hydrologic energy (Megonigal et al., 1997; Robertson, 1992). Periodic flooding during dormancy may provide additional soil moisture during dry periods the following growing season, enabling trees to continue growth (Robertson, 1992). Mitsch and Rust (1984), finding no linear relationship in one to five year-sets of tree growth and flooding, suggested that any benefit conferred on trees from flooding might be offset by the ensuing stress of inundation. The Conner and Day (1976) conceptual model (later adapted by Odum (1979)), based on stands of baldcypress (*Taxodium distichum*) in Louisiana, identified stagnant flooding, when compared with slow-flowing floods of long duration and seasonal flooding, as causing the most physiological stress

and greatest reduction in growth. In most cases, flooding has a negative impact on height, leaf, cambial and reproductive growth of trees (Kozlowski, 1985).

Roots require oxygen to maintain aerobic respiration and function in mineral nutrient and water supply. Roots also provide hormonal growth regulators for various cell functions that promote root, shoot, and leaf growth (Kozlowski, 1985). Aeration in poorly drained-to water saturated-soils is greatly reduced, inhibiting oxygen diffusion to roots, much as it is in compacted soils, impermeable layers around roots, and roots newly covered with soil. Flooding, however, as opposed to the gradual onset of compaction, almost immediately leads to poor soil aeration.

Of all the agents of flood injury, oxygen deficiency is the most serious (Iremonger and Kelly, 1988; Kawase, 1981; Kozlowski, 1985). Optimal gas exchange and tree growth occurs when air space of about 20% is present in the soil (Bakker and Hidding, 1970). Oxygen diffuses in air-filled soil pores much more rapidly than pores filled with water (Regehr et al., 1975). Molecular diffusion of oxygen is normally unable to adequately supply microorganisms present in flooded soil, which quickly consume any that is available (Kozlowski, 1985).

Waterlogged soils have been defined as soils that are saturated with water for a sufficiently long time during the year to give the soil distinctive gley horizons resulting from oxidation-reduction processes (Ponnamperuma, 1972). Waterlogged soils can cause chemical reductions of certain elements (primarily iron, sulphur and manganese) that have adverse impacts on plant growth, oxygen depletion, CO₂ build-up, loss of volatile N through denitrification, and the release into solution of a number of potential plant toxins (Iremonger and Kelly, 1988; Kozlowski, 1985; Turner and Patrick, 1968). These same mineral elements are usually beneficial to plants in well-drained soils where they are more oxidized.

Several flood-induced morphological and physiological changes occur in trees that affect the way they acquire and transport assimilates and internally balance metabolites. One of the first physiological reactions to root inundation is stomatal closure, which in turn results in a reduction in photosynthesis through inhibition of CO₂ uptake by the leaves (Kozlowski, 1985). Regehr et al. (1975) reported 50% reductions in rates of photosynthesis and transpiration in *Populus deltoides* seedlings following 28 days of inundation. They suggested the reductions may be the result of potassium deficiency, which would result in an imbalance

in the turgor difference between guard cells and epidermal cells that control stomatal opening and closing.

Waterlogging also decreases the amount of gibberellin and cytokinin synthesized in the roots (Kozlowski, 1982).

These hormones aid in the regulation of a host of physiological processes, including leaf senescence, nutrient mobilization, and a variety of growth processes.

A study of forests in the Mississippi River Valley identified a definite vegetative gradient from wet to drier sites among 16 hardwood species, supporting the hypothesis that changes among species across soil drainage gradients depends on the relative tolerance of the species to soil saturation (Hosner and Boyce, 1962). In a pot study of four Irish wetland species, Iremonger and Kelly (1988) found that increasing the level of soil inundation decreased growth and killed plants. Thus, it may be that *Populus*, although typically found on moist bottomland soils, has variable growth potential on these soils, depending on genotype and flooding and soil waterlogging duration and degree.

Carbon Sequestration Capacity of *Populus* Plantations

Carbon sequestration is the process of removing C, in the form of CO₂, from the atmosphere and storing it in terrestrial, oceanic, or freshwater aquatic systems. There are environmental implications for the use of *Populus* and other short rotation intensive culture crops in sequestering atmospheric C by storing it in terrestrial pools, such as biomass and soil (Markewich and Buell, 2005). According to the Ecological Society of America, soils are the largest land pool of C at approximately 75% of all terrestrial carbon (Ecological Society of America, 2000). A combination of land clearing through traditional agriculture, deforestation, and most recently, increased development, have resulted in large increases of atmospheric C over the past century (Vitousek, 1991).

Atmospheric CO₂ and CH₄ (methane) are classified as greenhouse gases, and widely accepted as two of the main contributors to global warming. Biofuels, as an alternative to C source fossil fuels in power generation, also hold promise for the future (Vitousek, 1991). Geyer (1989) reported that 25% of the harvested roundwood in the United States was being used for fuel. In December of 1998 the US Department of Energy reported on their website that biomass was generating over 7,500 megawatts of electricity

in the U. S. annually, while supporting over 66,000 jobs (National Renewable Energy Laboratory, 1998).

The top two major contributors to CO₂ build-up in the atmosphere over the past 100 years have been deforestation early in the century, and the combustion of fossil fuels in the latter part (Vitousek, 1991). One possible solution to combating CO₂ build-up is the development of wide-scale short-rotation plantation culture for long-term storage of C that would otherwise be released to the atmosphere in a much shorter period of time. For short-term rotation plantations to result in long-term reductions in atmospheric C, harvested trees would need to be used in the development of long lasting organic products, such as lumber or engineered solid-wood products, or if being used for fuel, replace a substantial amount of fossil fuels. There is some consensus that a majority of plantation culture will focus on its utility as a replacement for fossil fuels (Grogan and Matthews, 2002). Some of the benefits of using biofuels include improved combustion and reduced pollutants due to a high biofuel oxygen content, low sulphur content and reductions in fossil-fuel based CO₂ and particulate matter (Zsuffa and Gamble, 1995). The important advantage of replacing fossil fuels with plantation stock is the C that the next growing crop would

take in and store, preventing it from accumulating in the atmosphere as CO₂ (Matthews and Grogan, 2001; Smith et al., 2000). However, considering a growing world population that needs land for food production, the economic diversity that exists around the world and the fundamental roles wood has in many societies, plantation culture can likely only ameliorate and not reverse increases in atmospheric C. Even so, these delays may prove to be invaluable while other programs and technologies are being developed to deal with atmospheric C (Vitousek, 1991).

Various patterns of change in soil C have been reported for newly-established short rotation plantations. Hansen et al. (1993) observed net losses in soil C during the initial years of tree crop establishment, but increases of 1.6 t ha⁻¹ yr⁻¹ over an 18 year study of hybrid poplars in the North Central United States. In a modeling experiment, Grogan and Matthews (2002) concluded that the rate of soil C sequestration in short rotation plantations would equal or surpass naturally regenerating woodlands. Makeschin (1994) found two times the amount of organic soil C under hybrid poplar compared to nearby arable fields in Germany following six to twelve year rotations. Tolbert et al. (1999) observed decreases in bulk density and increases in soil organic matter and soil C storage in the top 30 cm of

soil under plots of eastern cottonwood, sycamore, and sweetgum grown with a cover crop on three sites in the Tennessee Valley that historically had been in conventional tillage for corn, soybeans, and cotton (Tolbert et al. 1998). Following four years of growth in a short rotation plantation of *Salix dasyclados* Wimm., Ulzen et al. (2000) detected no significant differences of soil C concentration, mass, or carbon enrichment, which relates soil particle size fraction C to soil C, across sand, silt, and clay soils. A recurring theme in the literature is that implementation of short-rotation plantations, on a variety of sites, seems to have either a positive effect on soil C storage, or no significant impact.

One of the issues associated with plantation culture as it relates to soil C sequestration is rotation length. Russell et al. (2004) in a study of three native tree species in the tropics, noted strong effects of rotation length on soil C, with 4-year rotations of *Cedrela odorata* L. and *Cordia alliodora* (Ruiz & Pav.) often having higher soil C mass than uncut, long-term monocultures. Many studies have acknowledged the possibility of soil C accumulations in rotations for up to 30 years. As rotation length shortens, gain in soil C can decrease and cause a long-term decline in soil C if harvests result in extensive

soil disturbance (Harrison et al., 1995; Turner and Lambert, 2000).

There are a number of popular government agricultural programs that indirectly encompass C sequestration, essentially by default, as an inherent element of their structure. Many of the agricultural practices in the past have led to large releases of C into the atmosphere. Today, there is a concerted effort by the U.S.D.A. to correct, and even eliminate, many unsustainable land practices across the globe (www.fs.fed.us/global/globe/welcome.htm). Modern management techniques, such as the increased cultivation of forage crops, no-till seeding, reduced summer fallow, and reduced cultivation of marginal crop lands, all have a potential effect on the role of production land gaining momentum as a C sink as opposed to a C source.

Some local examples of government programs are the Conservation Reserve and Wetlands Reserve Programs, available to landowners through the U.S.D.A. These programs remove marginal land, susceptible to erosion and flooding, from cultivation and lock them into sustainable and stable situations. Other countries, such as Canada, have taken a more aggressive approach in combating C pollution with programs such as the Permanent Cover Program

(PCP). The PCP has taken over a half million ha of marginal land out of production and paid out \$74 million to Canadian landowners (Luciak et al., 2002). Keeping this in mind, there are potential roles for *Populus* in tying up C in terrestrial and sub-terrestrial media and in providing many other environmental benefits, while at the same time providing economic benefits (Tolbert et al., 1995).

Because of the success of *Populus* in plantation culture elsewhere, a study was conducted in the floodplain of the Horticulture and Agroforestry Research Center in New Franklin, MO in order to test for productivity in five clones as plantation candidates in Central Missouri. The specific objectives were:

1. comparing the biomass growth patterns of the selected clones in short-rotation culture;
2. comparing leaf canopy characteristics of the selected clones with biomass production;
3. determining if changes in soil C attend short-rotation poplar plantation culture; and
4. testing whether contrasting soil water regimes have effects on biomass production at different micro-topographic locations.

MATERIALS AND METHODS

Plantation Design and Establishment

Plant Material

Originally, three clones of the genus *Populus* were selected for use in C sequestration and biomass production experiments based on first year results of a test plot located at the Horticulture and Agroforestry Research Center: 26C6R51 (*Populus deltoides*), origin Pope County, Illinois: 2059 (*Populus deltoides*), origin Osage County, MO: and 1112 (*Populus deltoides*), origin New Madrid County, MO. A hybrid clone, I45/51 (*Populus deltoides* x *P. nigra* = *P. x euramericana*), was selected after recommendation from Dr. R.C. Schultz of Iowa State University on a hybrid that might be adapted to the central Missouri floodplain. All *P. deltoides* clones were acquired from the Missouri Department of Conservation Nursery (MDC). Clones 26C6R51 and 1112 were selected due to high and low first year growth, respectively, in the aforementioned test plot, and reached d^2h ($cm^2 \cdot m$) means of 987.7 and 2863.4, while 2059 was the clone closest to a local origin available (approximately 165 km distant) and therefore presumed to be well adapted to local conditions. Clone 2059 attained a d^2h mean of 1491.6 $cm^2 \cdot m$, resulting in clone selections below, near and above the MDC clones' mean first year d^2h

(1724.96 cm²·m). Eventually a fifth clone, *P. deltoides* × *P. nigra* 'Eugenei', was included in the study as a result of its success as a border tree (See Table 1 for details on clone information).

In order to provide for quick and easy identification, clones were color coded as follows: I45/51 - Blue, 26C6R51 - Red, 2059 - White, 1112 - Yellow, and Eugenei - Orange.

Table 1 - Origin and source information for five *Populus* clones grown in a short rotation plantation.

Clone	Parentage	Source	Origin	Latitude	Longitude
145/51	<i>Populus deltoides</i> x <i>P. nigra</i>	Iowa State Tree Nursery	-	-	-
Eugenei	<i>P. deltoides</i> x <i>P. nigra</i>		-	-	-
2059	<i>P. deltoides</i>	MDC Nursery	Osage County, MO	38° 27'N	91° 52'W
1112	<i>P. deltoides</i>	MDC Nursery	New Madrid County, MO	36° 35'N	89° 37'W
26C6R51	<i>P. deltoides</i>	MDC Nursery	Pope County, IL	37° 35'N	88° 34'W

Plantation Design and Establishment

The study area was located adjacent to Sulphur Creek in the Missouri River floodplain at the University of Missouri's Horticulture and Agroforestry Research Center (Latitude 39° 01'N, longitude 92° 46' W) near the town of New Franklin, Missouri. The initial plantation (hereafter Plantation 1) was installed in May of 1999, using 20 cm-long hardwood cuttings of four *Populus* clones obtained from the State Tree Nursery at Licking, MO (*P. deltoides* clones) and the Iowa State Tree Nursery (I45/51).

Prior to tree planting the site was a pasture dominated by tall fescue (*Festuca arundinacea* Schreb.), and was treated with a glyphosate herbicide (Roundup) to eliminate as much competition as possible. The process of eliminating herbaceous competition when dealing with plantation *Populus* cultivation has been found to be critical in former studies (Zsuffa et al., 1977). Proper weed control can lead to increased survival, tree height and diameter, and earlier crown closure in plantations. Some studies have also noted effects on the components of branch architecture (Marino and Gross, 1997). Without vegetation control in the first year, survival may be reduced by 25-50 percent and growth by at least 50 percent (Strauss et al., 1997).

Clones established included the three clones of *Populus deltoides* and the hybrid of *Populus deltoides* and *Populus nigra* noted previously. The plantation design was a randomized complete block, with six blocks of four clones in plots of 10 trees x 7 trees planted at 1 x 1 m spacing, equivalent to 10,000 trees/ha after the design employed by Scarascia-Mugnozza et al. (1997). Surrounding the plantation was a double row of *Populus deltoides* x *P. nigra* 'Eugenei' plants serving as a buffer and border to the study trees. Border trees provided competition to the edge plot trees, preventing them from growing outward to free soil and light resources, biasing growth rates upward. During the first growing season cuttings emerged well in May, but there was significant mortality in some clones. In order to recover complete blocks for each clone, potted cuttings were first employed to replace dead trees, but were too few to provide complete 10 x 7 plots. Ultimately, transplanting from other blocks became necessary to establish complete plots. This left an incomplete block design with six complete plots for clone I45/51, five for 1112, three for 2059 and two for 26C6R51 (see Figure 1 for plantation progression photos).

Figure 1 - Photographs of Plantations 1 and 2 at various growth stages.



As the growing season of 1999 was dry (60.1 percent of normal precipitation), periodic watering, using water pumped from a nearby slough, was implemented in order to keep soil moisture high in the upper 30 cm of soil. This procedure was not continued in subsequent post-establishment years. Mean temperature ranged from -2.72° C in January to 25.95° C in July with an annual mean ranging from 6.61° C to 18.16° C. Mean precipitation ranged from 4.2 cm in January to 13.1 cm in May with an annual mean of 108.5 cm (Golden Gate Weather Services).

Initiation of a second study plantation (Plantation 2) began in the fall of 1999 with the application of glyphosate herbicide in preparation of spring planting. Plantation 2 was developed in order to provide replication for the study and for supplying data that could be used to obtain some idea of variation across sites. In addition, establishment of a second site allowed for a greater soil C sequestration sample size with greater variety in topographic positions. This second plantation's location was approximately 75 m NE of Plantation 1. A second application of glyphosate was made on March 27, 2000, followed by planting approximately two weeks later, with completion on April 17. Again, a randomized complete block design was employed with 10 x 7 plant plots as before.

However, on this site only four blocks were installed, as opposed to six, and five clones were included instead of four, with the fifth being *Populus deltoides* × *Populus nigra* 'Eugenei'. This clone was added to the second plantation in response to its success as a buffer tree in the original plantation. *Populus deltoides* × *P. nigra* 'Eugenei' was also used as a double-rowed buffer around the second plantation's edge. Following plantation establishment, the site was irrigated the week of April 20 using a gasoline-powered pump and the nearby water supply of a slough of Sulphur Creek. As precipitation in the second growing season of 2000 was adequate (52 cm, 102 percent of normal), no further irrigation was applied.

Survival rate within the second plantation was excellent, resulting in nearly full achievement of the number of plots designed, and was largely attributable to a more conducive planting time frame absent during the establishment of the first plantation (the former was planted late due to land purchase delays). However, because of a small shortage of planting material, block four's northern-most plot consisted of two rows of clone 26C6R51 and five rows of clone I45/51 (See Figure 2a and Figure 2b for experiment design).

Figure 2a and 2b - A map of Plantations 1 and 2 illustrating the plot designs.

FIG. 2A Poplar Plot #1 – May, 1999
Harvey Tract, HARC

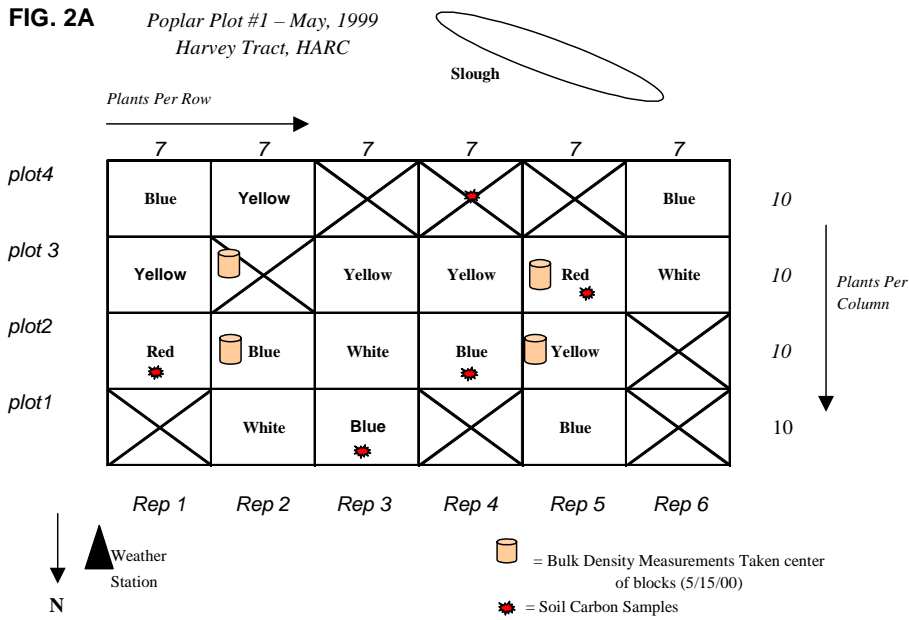
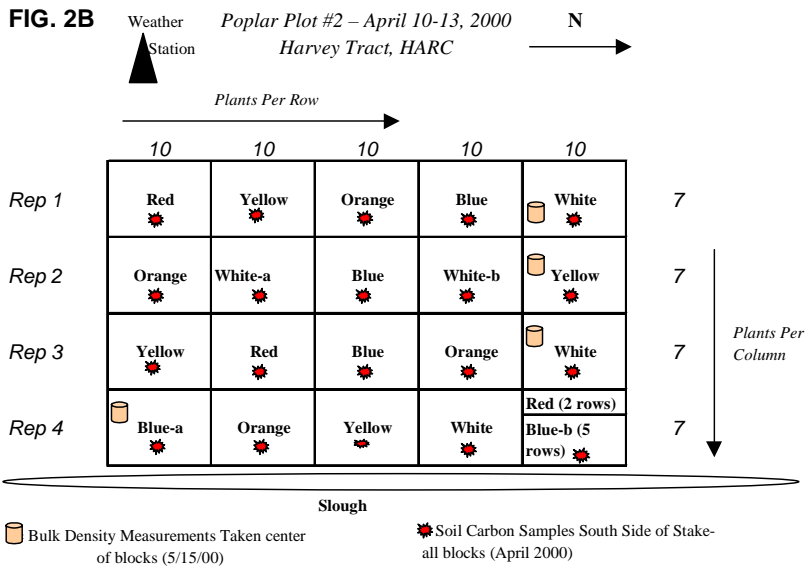


FIG. 2B Poplar Plot #2 – April 10-13, 2000
Harvey Tract, HARC



Biomass Accumulation Experiment

With a second plantation in place replicating Plantation 1, destructive harvesting was initiated in Plantation 1. Plantation 2 was reserved from disturbance for the whole of the Plantation 1 rotation. Biomass estimation equations were developed from harvested material in Plantation 1 and were applied to permanent plot trees in Plantation 1 during the five-year rotation as well as to measurements in Plantation 2 following the 2000-2004 growing seasons. During each of the five year's of Plantation 1 growth a number of trees were excavated for detailed study as follows: Year 1- 30 trees, Year 2- 10 trees, Year 3- 8 trees, Year 4- 8 trees, and Year 5- 8 trees. Each harvest began in early autumn (mid-late September) coinciding with the beginning of fall leaf abscission, assuring completion of the year's growth. Harvests were completed each year on the following dates: November 19, 1999, December 4, 2000, October 31, 2001, December 5, 2002 and December 8, 2003.

The following procedure was used to process above ground biomass. First, tree heights and diameters (approximately 4 inches from the ground) were measured prior to harvest. Next, stems were cut from the root systems at ground level. Branches were then removed from

the stem and accumulated. The stem and branches were then cut into small lengths using a 10" compound miter saw, a table saw and various hand loppers. Tree diameter dictated which method was used in each harvest year. Reduction in size of above ground biomass aided in transport and, more importantly, promoted thorough drying of material.

As much resulting saw dust as possible was recovered via a dust catcher located directly behind the blade of the saw. Air hoses and hand brooms were also employed in this task. Collected biomass was placed in paper bags identifying clone and plantation position, and then transported to the lab. At the lab, above-ground biomass was placed in convection ovens and dried at 70°C until reaching a constant weight. Weight was checked on a digital balance at approximately 24-hour intervals.

After above-ground harvest, root excavation was conducted. Prior to digging, a square meter block was laid out around the sample, with the tree on center. Soil and roots were removed to approximately 1 m depth, resulting in the excavation of one cubic meter of soil. This method allowed for a close estimate of tree root biomass, with roots of non-sample trees growing into the excavated volume compensating for roots of sample trees growing outside the cubic meter zone (Scarascia-Mugnozza et al., 1997). Roots

growing beyond one meter in depth were few and limited to three or four large single brace roots that terminated at depths of less than 25 cm beyond the 1 m excavation limit. As soil was removed from the root volume it was placed in plastic containers and separated from *Populus* roots by hand, within the container, to collect any *Populus* roots present. Soil was typically removed in three layers with each layer being approximately 33 cm deep. In the upper excavation layer it was especially important to distinguish *Populus* roots from the roots of herbaceous plants growing on the plantation floor. *Populus* roots consistently demonstrated an orange hue, making them relatively easy to differentiate from the dark brown appearance of herbaceous roots. Other distinguishing characteristics of *Populus* roots included a denser, less pliable and less succulent composition than herbaceous plants. *Populus* roots were also considerably less fibrous than herbaceous root systems and less uniform in size. Once identified and separated, *Populus* roots were then placed in paper bags and transported to the lab.

Once roots arrived at the lab they were washed free of soil using a 1 mm standard test sieve (Fisher Scientific Company), placed in an oven and dried at 70°C until reaching a constant weight.

After each tree harvest (occurring between mid-September and early December), heights and diameters were measured for a specified number of buffered permanent plot trees in plantation 1 (see Table 2). Trees were selected so adjacent trees on all sides buffered them. All trees were measured for height and diameter in Plantation 2 each year. These data were then entered into regression equations developed from destructive harvest data in order to obtain a yearly biomass estimation of permanent plot trees without harvesting them.

Data Analysis

Dry biomass data were assembled for root, shoot, and total plant for each sampled plant. Stepwise regression procedures were then employed with all possibly meaningful independent variables (clone, size, age at excavation) and their interactions, to develop predictive equations for root, shoot, and total dry weight as dependent variables. The equation, height and diameter measurements, clone identity and age were then employed to estimate biomass for each permanent plot tree.

Analysis of variance (PROC GLM, SAS Institute, Inc.,) was employed to assess clonal differences in biomass production. Least square means were calculated as mean

Table 2 -Plantation 1 permanent plot trees

Number of permanent plot trees - 2000

	I45/51	1112	2059	26C6R51
Block 1	4	4		9
2	4	4	7	
3	4	4	7	
4	4	4		
5	4	4		6
6	4		7	

Number of permanent plot trees - 2001

	I45/51	1112	2059	26C6R51
Block 1	4	3		8
2	4	4	7	
3	4	4	7	
4	4	4		
5	4	4		6
6	4		6	

Number of permanent plot trees - 2002

	I45/51	1112	2059	26C6R51
Block 1	4	3		8
2	4	4	5	
3	4	4	6	
4	3	3		
5	4	4		6
6	4		6	

Number of permanent plot trees - 2003

	I45/51	1112	2059	26C6R51
Block 1	3	3		8
2	4	4	4	
3	4	4	6	
4	3	3		
5	4	4		6
6	4		6	

comparisons performed at a significance level of five percent.

The final study design for both plantations was an incomplete block design using plot means for analysis. Mortality and the need for transplanting within Plantation 1 ultimately led to missing blocks, while one mixed block of I45/51 and 26C6R51 in plantation 2 resulted in the incomplete block structure.

Light Conversion Efficiency Experiment

In order to explore relationships between varying leaf characteristics (Leaf Area Index and Leaf Area Duration) of tested *Populus* clones and the biomass they produce, canopy measurements were conducted each year from the time of bud burst through leaf abscission in the fall.

Phenology recordings were conducted each year of the study to monitor the approximate day of bud burst in the spring and the approximate day of bud set at late summer. Recordings were made through weekly visual checks of the canopy at the appropriate time of year for each event. If the date recorded was 4-17, that tree broke bud during the previous week. The same held for bud set in the fall. A total of 20 plants were monitored for each clone in plantation 1, comprised of a complete row in each of two plots. Plantation 2 clone representation included four

rows of 1112, five rows of 2059, three rows of 26C6R51, five rows of I45/51, and four rows of 'eugeneii'.

Leaf area measurements were made using the LAI-2000 Plant Canopy Analyzer (LI-COR, Inc., Lincoln, NE), which measures the probability of seeing the sky looking up through a vegetative canopy in different directions, using five values of zenith angle. The LAI values provided by this method provided essential information for a clone's leaf development and leaf abscission throughout the growing season.

The LAI-2000 was employed in a systematic approach by which all plots were sampled. This was accomplished by following a standard pattern through the plantations each month during the growing season. In Plantation 1, measurements began at the most northeastward plot (block 1, plot 1) and progressed southward through all four plots of block 1 ending at plot 4. Subsequently, measurements continued in plot 4 of block 2 and progressed northward in each plot of block 2, ending at plot 1. This sequence was repeated for blocks 3 and 4 and blocks 5 and 6, resulting in measurements terminating for Plantation 1 at block 6, plot 6. In Plantation 2 measurements began at the outermost southwestward plot of block 1 (block 1, plot 1), and progressed in the same method used in Plantation 1

(although movement began south to north) terminating at block 4, plot 5. Within plots, measurements were taken randomly, with no designated point for initiation or termination. Leaf area measurements began in the second growing season, when height growth had become sufficient to allow placement of the sensor beneath the foliage, and continued through the fifth growing season (2000-2004).

LAI measurements with the LAI-2000 require overcast skies or clear skies with the sun at or below the local horizon. Measurements taken with the sun directly illuminating foliage underestimate LAI by as much as 50% (LAI-2000 Plant Canopy Analyzer Instruction Manual, LI-COR, Inc., Lincoln, NE). Accordingly, measurements were taken on cloudy days near mid-month when available. If no overcast days were available near the appropriate date, measurements were taken early in the morning prior to the sun rising over the riparian corridor canopy adjacent to Sulphur Creek, approximating overcast skies. An initial reference measurement outside of the canopy, devoid of interference from tree lines, vehicles, etc., began the cycle. Next, eight measurements were executed within the canopy, moving about the plot to a random spot for each sample. Here, the operator exited the canopy and recorded another calibration measurement, then reentered the same

plot and repeated the eight-measurement process for a total of 18 recordings per plot. This completed the cycle, which was repeated on each plot. Plantation 1 provided a total of 288 measurements recorded monthly. Plantation 2 provided 378 measurements also recorded monthly. An initial measurement was taken prior to the growing season to establish a leafless "LAI" measurement representing stem and branch interception of solar radiation that could be subtracted from gross measurements. All other measurements were obtained during the growing season.

Data Analysis

The objective of this analysis was comparison among clones of the patterns of leaf area display and the efficiency with which biomass was produced per unit of leaf area (i.e., LUE). Peak seasonal LAI and seasonal LAD were chosen as potentially useful canopy attributes to evaluate.

Mathematical calculations of LAD involved the following process. Date of bud break was used as a starting point for data collection with subsequent samples provided by LAI-2000. The initial phenology data represented the LAI value produced by the woody material, minus leaves (i.e., before leaf-out). The 2000 growing season began with a value of zero, with no significant stem material yet present at measurement height. Subsequent

growing season LAD values were subject to subtraction of a woody biomass estimate to account for the woody material accrued the previous year. This estimate was derived from either the last LAI measurement recorded near the time of bud set, from the earliest measurement available the ensuing year, or from estimations from like clone values. The estimation depended on which value best accounted for the woody material accrued the previous year. LAD was then calculated as area by summing LAI from one sample date to the next (LAI_1 , LAI_2), dividing by two, subtracting the woody contribution, and multiplying by the number of days between the two samples:

$$[((LAI_1 + LAI_2)/2) - \text{woody "LAI"}] * \# \text{ days in interval}$$

Finally, in order to calculate LAD for a growing season, sequential LAD results were summed for each sample plot. This process was repeated for each growing season.

To test for relationships between biomass and canopy attributes, the clone's estimated total tree biomass ($t \text{ ha}^{-1}$) for each plot was accumulated and subsequently plotted against corresponding cumulative LAD ($m^2 \text{ m}^{-2} \text{ days}$) values for each clone over the study. Because cumulative peak LAI and cumulative seasonal LAD were highly correlated

across clones ($r=0.99$, $p < 0.05$ for Plantation 1 data), seasonal LAD was chosen for analysis because of its better theoretical relationship with biomass production (i.e., it accounts for seasonal changes in LAI and light harvesting potential whereas peak LAI does not.) For this analysis, a steeper slope in the relationship between LAD and biomass production suggested a clone was able to convert light energy to biomass more efficiently. Regression lines were forced through the origin prior to comparison. Additionally, a year-by-year calculation of biomass divided by yearly LAD was also conducted, pooled across years and statistically analyzed for clonal difference. This procedure was necessary to provide independent data for years two through five, which were otherwise dependent on the previous years' growth.

Soil Moisture Case Study

To evaluate local soil drainage effects on the accumulation of biomass, two plots of the same clone showing substantial differences in growth were chosen. Due to micro-topographic changes within Plantation 2 it was hypothesized the growth variation might be the result of local variation in soil drainage. Eugenei, located in Plantation 2, was selected for this purpose. There were

obvious low and high areas within this plantation, with Eugenei located in both areas.

Once the clone and locations were decided, two CS616 Water Content Reflectometers (Campbell Scientific Inc., Logan, UT) were installed to measure water volumetric content to 30 cm depth on the plots. One CS616 unit was installed in Block 1; plot 3, which was located in a low-lying area of the plantation in poorly drained soil. The other unit was placed in Block 4; plot 2, which was located in a higher, better-drained area of the plantation. Factory calibrations were used in this study in order to establish whether soil moisture differences existed between the two plots. Results would have probably deviated from those reported here had the instruments been calibrated for the occupying soil type. However, factory calibration allowed differences in soil moisture to be established.

The CS616 instrument consists of two 30 cm long, stainless steel rods connected to a printed circuit board. The rods were inserted vertically into the soil. The probe uses frequency domain reflectometry to measure soil water content in the top 30 cm of soil (Topp et al., 1980). The travel time of a signal induced on the probe rod depends on the dielectric permittivity of the material surrounding the rods and the dielectric permittivity depends on the water

content. The probe output period ranges from about 14 microseconds with rods in the air, to about 42 microseconds with rods submerged completely in water (CS616 Instruction Manual). Information is transmitted between the instruments and a data-recording source (weather station) via coaxial cable. The cable was allowed to lie atop the soil within the plantation, where danger of being cut was limited. Outside the plantation cables were buried approximately 6 inches to protect them from severing. Data were recorded at the weather station centrally located between the two plantations.

Soil C Experiment

Tracking of variation in soil C content within each plantation was conducted at the beginning and end of the plantation's 5-year rotation. This was accomplished by taking soil samples from a number of randomly selected sample sites at Plantation 1's establishment, prior to the first growing season, and following each plantation's final growing season. All plots were sampled in Plantation 2. Soil type for the study site was Moniteau silt loam. The Moniteau series consists of very deep poorly drained, moderately slowly permeable soils formed in alluvium. Excavation of the root systems in the biomass accumulation experiment revealed soil containing very little clay and

homogenous up to 1 m in depth. Taxonomic description includes fine-silty, mixed, superactive, mesic Typic Endoaqualfs. Sample times for Plantation 1 were early May 1999, for pre-sample and early May 2004, following the rotation period. Plantation 2 pre- and post-rotation samples were taken in April of 2000 and April of 2005, respectively. The time of year for samples were kept consistent in an effort to avoid fall vs. spring C bias that can result from over winter C losses due to respiration. Plantation 1 had a total of five sample plots, while all twenty plots were sampled in Plantation 2 (see Figure 2a and 2b for sample locations). Sample sites were located at the center of their respective plot and marked with stakes of galvanized pipe for accurate identification of original sample positions. Four random samples were taken for bulk density measurements in both plantations. Locations for Plantation 1 were Block 2, plots 2 and 3 and Block 5, reps 2 and 3. Locations for Plantation 2 were Block 1, plot 1 and Block 5, plots 2, 3, and 4. All bulk density samples were taken center of the plot.

At each site soil was excavated to 50 cm in depth and the subsequent hole was divided into zones of 12.5 cm increments. Zone 1 ranged from 0 - 12.5 cm, Zone 2 from

12.5 - 25 cm, Zone 3 from 25 - 37.5 cm, and Zone 4 from 37.5 cm - 50 cm, resulting in 4 samples from each site. Soil samples were extracted approximately at mid-zone from the wall of the hole, preventing mixing of soil among zones. Zone 1 required the sample be taken deep enough to prevent contamination from herbaceous roots and other organic matter. Samples were placed in plastic bags identifying plantation, block, plot, clone, and zone.

Following excavation, samples were taken to the lab and transferred to paper bags with identical labeling and dried in ovens at 70° C to a constant weight. Once thoroughly dried, samples were finely ground using a mortar and pestle, and again placed in paper bags displaying identical labeling for lab analysis.

Data Analysis

Soil samples were taken to the University of Missouri Soil and Characterization Laboratory for analysis. Because there were different soil types present in the samples, bulk density of the different soil layers was used to convert percent C to mass-based C (g m^{-2}).

This transformation required the following formula for each sample layer noted previously:

$$\% \text{ Organic C} \times 125,000 \times \text{soil layer b.d. (g/cm}^3\text{)}$$

The four values were also summed to provide a total 50 cm soil depth sample.

RESULTS

Biomass Accumulation Experiment

Stepwise Regression Procedures

Independent variables used in developing predictive equations included clone, height, diameter, d^2h , age and their interactions. Each harvest tree's measured dry weight, used as dependent variables in developing predictive equations, is listed in Table 3, along with plot location, height, base diameter, and harvest date. Predictive equations from each year of Plantation 1's rotation are listed in Table 4. This table demonstrates how the equations changed over the rotation on an annual basis. Equation development included the current and previous year's harvest data. Also noteworthy in Table 4 is the successive increase in the R^2 values as the rotation progresses. This description of the stepwise process will focus on the final year's equations, which combine all data for the poplar plantation biomass over the five-year rotation. Abbreviations used in the biomass estimation equations are defined in Table 5.

For the final analysis, sixty four trees were entered into the stepwise selection procedure (PROC REG, SAS Institute, Inc., SAS Manual) including fifteen trees of clone 2059, sixteen of 26C6R51, sixteen of 1112, and

Table 3 - Plantation 1 harvest dry weights 1999 - 2003

Color	Rep, Row, Plant	Ht. (cm)	Stem base diameter (cm)	Harvest date	Shoot wt. (g)	Root wt. (g)	Total wt. (g)
WHITE	6, 6, 1	56	.791	7/29/1999	33.2	2.5	35.7
WHITE	6, 7, 1	24	.551	7/29/1999	8	1.6	9.6
WHITE	2, 4, 2	117	1.58	8/13/1999	192.4	29.6	222
WHITE	3, 1, 5	44	.61	8/13/1999	18.4	3	21.4
RED	1, 3, 1	35	.632	7/29/1999	17.8	5.2	23
RED	5, 6, 5	133	1.974	8/17/1999	395.6	109	504.6
RED	1, 1, 9	27	.6	8/3/1999	11.9	3.5	15.4
RED	1, 2, 4	68.5	1.097	8/11/1999	74	19.2	93.2
BLUE	2, 2, 6	49	.716	8/11/1999	21	7.6	28.6
BLUE	2, 6, 9	142	1.688	8/19/1999	292	80.5	372.5
BLUE	1, 1,10	95	1.397	8/5/1999	188.3	50.3	238.6
BLUE	5, 3, 1	167	2.202	7/29/1999	557.4	90.9	648.3
BLUE	6, 6, 9	99	1.304	8/20/1999	106.4	56.7	163.1
YELLOW	5, 6, 4	167	2.409	8/10/1999	618	162.6	780.6
YELLOW	4, 4,10	29	.5	8/3/1999	9.3	5.8	15.1
YELLOW	2, 7, 1	29	.499	8/3/1999	5.7	3	8.7
YELLOW	2, 7, 3	155	2.18	8/24/1999	505	207.6	712.6
YELLOW	3, 1, 3	37	.709	8/3/1999	19.1	5.5	24.6
WHITE	2, 6, 4	191	2.228	9/20/1999	73.88	26.59	100.47
WHITE	3, 2, 6	144	1.506	11/9/1999	39.4	38.11	77.51
WHITE	6, 6, 5	146	1.802	10/11/1999	49.88	41.64	91.52
RED	1, 3, 2	141	2.31	11/19/1999	90.25	138.15	228.4
RED	5, 5, 9	154	1.591	10/28/1999	105.56	184.4	289.96
RED	1, 2, 2	163	2.465	9/21/1999	90.03	61.53	151.56
YELLOW	1, 5, 2	2.2	2.146	11/15/1999	115.59	40.46	156.05
YELLOW	3, 2, 3	210	2.749	10/15/1999	129.96	48.62	178.58
YELLOW	5, 2, 9	239	3.131	10/1/1999	149.94	38.13	188.07
BLUE	3, 6, 9	119	1.575	10/29/1999	46.04	90.99	137.03
BLUE	4, 2, 9	148	1.989	10/25/1999	83.93	79.42	163.35
BLUE	5, 2, 9	235	3.144	10/6/1999	261.63	135.54	397.17
BLUE	5, 6, 8	602	7.72	9/5/2000	3781.28	680.03	4461.31
BLUE	6, 7, 2	396	5.653	10/4/2000	1514.1	570.54	2084.64
BLUE	2, 2, 3	333	2.885	12/4/2000	332.53	246.61	579.14
RED	5, 6, 2	537	7.332	9/27/2000	2999.77	707.66	3707.43
RED	5, 3, 2	495	4.735	10/20/2000	1343.4	415.91	1759.31
RED	5, 4, 4	406	3.573	11/27/2000	524	219.8	743.8
YELLOW	5, 2, 5	590	6.75	9/19/2000	2796.03	405.07	3201.1
YELLOW	4, 6, 2	460	3.357	10/26/2000	584.36	191	775.36
WHITE	2, 2, 9	529	4.72	9/29/2000	1095.6	249.99	1345.59
WHITE	6, 3, 8	512	3.66	11/1/2000	794.18	245.24	1039.42
BLUE	5, 2, 7	848	7.3	10/9/2001	5139.5	747	5886.5
BLUE	1, 3, 8	806	6.9	9/25/2001	4508	912.3	5420.3
RED	5, 6, 7	790	7.75	10/17/2001	4657.3	1326.1	5983.4
RED	1, 3, 9	693	6.4	10/31/2001	3161.6	664.11	3825.71
YELLOW	5, 3, 3	820	6.75	10/11/2001	3808.7	807.9	4616.6
YELLOW	4,1, 7	692	5.5	10/31/2001	2487.5	496.2	2983.7
WHITE	6, 6, 3	799	7.2	10/31/2001	4268.2	1216.9	5485.1
WHITE	2, 3, 7	774	5.45	10/8/2001	2064.8	553	2617.8
YELLOW	5,6,6	911	7	10/7/2002	4267.1	966.4	5233.5
YELLOW	4, 3, 9	842	5.8	10/15/2002	3064.6	735.8	3800.4
BLUE	1, 4, 3	872	8.6	10/31/2002	5764.5	1513.1	7277.6

BLUE	1, 4, 5	785	6.5	11/21/2002	3242.4	910.6	4153
RED	5, 6, 6	953	8.1	12/2/2002	6470.5	709.5	7180
RED	1, 6, 4	872	6.2	12/5/2002	3565.5	537.2	4102.7
WHITE	3, 4, 6	896	8.3	10/17/2002	5208.1	1177	6385.1
WHITE	2, 2, 2	744	5.3	11/5/2002	2381.6	723.1	3104.7
YELLOW	1, 4, 5	1100	10.25	9/22/2003	11376.3	2281.1	13657.4
YELLOW	5, 6, 9	1095	11.4	11/6/2003	14491.7	2821.8	17313.5
BLUE	5, 6, 2	1075	9.8	10/28/2003	10689.2	1279.5	11968.7
BLUE	3, 2, 8	963	8.5	10/21/2003	7460.3	1099.7	8560
RED	1, 5, 7	1004	9.7	9/29/2003	7873	1661.7	9534.7
RED	5, 5, 5	1054	10.7	12/2/2003	10694.2	2084.6	12778.8
WHITE	2, 5, 6	1144	11.7	10/14/2003	14431.9	2684.8	17116.7
WHITE	6, 4, 5	1009	8.3	12/8/2003	6727.2	1318.8	8046

Table 4 - Biomass Estimation Equations

YEAR	COMPONENT	EQUATION	R ²
1999	ROOT	$-135.4345 + (1.5866*AGE) + (100.2815*C1) + (103.9233*C2) + (41.2166*C3) - (1.1440*C1*AGE) - (1.144*C2*AGE) - (0.6144*C3*AGE) + (0.00036*C3*D2H)$.93
1999	SHOOT	$27.8313 - (19.2556*C1) + (0.000008*AGE*D2H) - (0.0004*C2*D2H)$.88
1999	TOTAL	$-92.9383 + (0.0014*D2H) + (1.4589*D2H) + (1.4589*AGE) - (38.9125*C3) - (0.5574*C1*AGE) - (0.0010*C2*D2H)$.89
2000	ROOT	$-36.088 + (0.2063*D2H) + (0.3377*AGE) - (0.1059*D2HXC2) - (0.0514*D2HXC3)$.96
2000	SHOOT	$5.2093 + (1.1018*D2H) + (0.2212*AGE)$.99
2000	TOTAL	$-36.0173 + (1.2800*D2H) + (0.6112*AGE) - (0.1107*D2HXC2)$.99
2001	ROOT	$-19.243 + (0.2341*D2H) + (0.1922*AGE) - (0.07527*D2HXC2) - (0.07086*D2HXC3)$.97
2001	SHOOT	$19.7136 + (0.97712*D2H) + (0.27667*AGE) + (0.11467*D2HXC3)$.99
2001	TOTAL	$0.5216 + (1.19231*D2H) + (0.46008*AGE) + (0.06438*D2HXC3)$.99
2002	ROOT	$-25.452 + (0.206*D2H) + (0.233*AGE) + (0.163*D2HXC1) - (0.05113*D2HXC2) - (0.0001683*D2H*AGEXC1) - (0.00007193*D2H*AGEXC3)$.97
2002	SHOOT	$39.552 + (1.213*D2H) + (0.520*AGE) - (0.050*D2HXC1) - (0.00032329*D2H*AGE) + (0.00010563*D2H*AGEXC3)$.99
2002	TOTAL	$-23.218 - (0.983*HEIGHT) + (1.573*D2H) + (1.329*AGE) - (0.00045218*D2H*AGE) - (0.00004993*D2H*AGEXC1) + (0.00005987*D2H*AGEXC3)$	
2003	ROOT	$-26.943 + (.27960*D2H) + (.2443*AGE) - (.15973*D2HXC2) - (0.05612*D2HXC3) - (0.00008253*D2H*AGE) + (0.00011305*D2H*AGEXC2)$.99
2003	SHOOT	$-125.20441 + (11.56886*DIAM) + (0.77584*D2H) + (0.16238*D2HXC3) + (0.00003566*D2H*AGEXC1) + (0.00008544*D2H*AGEXC2)$.99
2003	TOTAL	$-214.85987 + (18.29153*DIAM) + (0.90478*D2H) + (0.11405*D2HXC3) + (0.00003512*D2H*AGEXC1) + (0.00009637*D2H*AGEXC2)$.99

Table 5 - Independent Variable Abbreviations

Abbreviation	Definition
D2H	Proxy volume calculated as height (m) × diameter squared (cm ²)
C1	Clone identifier dummy variable (0,1)
C2	Clone identifier dummy variable (0,1)
C3	Clone identifier dummy variable (0,1)
AGE	Tree age (days)
DIAM	Diameter of clone stem at the base (cm)
D2H×AGE	Interaction variable of D2H multiplied by AGE
D2H×C1	Interaction variable of D2H multiplied by C1
D2H×C2	Interaction variable of D2H multiplied by C2
D2H×C3	Interaction variable of D2H multiplied by C3
D2H×AGE×C1	Interaction variable of D2H multiplied by AGE multiplied by C1
D2H×AGE×C2	Interaction variable of D2H multiplied by AGE multiplied by C2
D2H×AGE×C3	Interaction variable of D2H multiplied by AGE multiplied by C3

seventeen of I45/51. The significance level for a variable's entry into the equation was 0.15, while the significance level to remain in the equation was 0.05. The final equation's variables and their R^2 values are listed in Table 6. In all three cases (root, shoot, and total) of biomass estimation, the volume proxy variable (d^2h) accounted for nearly all of the predicting power of the equations. For root biomass estimation d^2h accounted for 0.948 of a final model R^2 of 0.989. D^2h accounted for 0.99 of a 0.998 R^2 for the shoot biomass model, and 0.991 of the 0.997 R^2 for the total biomass model. Figure 3 provides a graphical illustration of estimated biomass compared to harvest dry weights. The 1:1 line running across the graph delineates a perfect relationship between variables. In 2004 five harvest trees from Plantation 2 were analyzed with the predictive equations developed from Plantation 1. This analysis included one tree sample of each clone present in Plantation 2. Although scatter of Plantation 2 data points expanded from the 1:1 line, it was minimal and did not diminish confidence in the predictive ability of the equations.

Following the development of the predictive equations, they, along with the variables height, diameter, clone identity, and age were used in estimating biomass for each

permanent plot tree using the PROC MEANS procedures (SAS Institute, Inc., Cary, NC, USA). This procedure provided means for height, diameter, root, shoot, and total biomass on a plot basis. Those means were then used as experimental units and assessed for clonal differences in root, shoot and total biomass estimates. Least squares means were calculated at the 0.05 significance level (PROC GLM, SAS Institute, Inc., Cary, NC, USA).

Plantation 1 - Five Year Trends in Biomass: Overview

Over the course of the rotation the clonal trend in root biomass essentially reversed (see Figure 4a, Table 7). Following the 1999 growing season I45/51 produced the greatest amount (1.66 t ha^{-1}), followed by 26C6R51 producing 1.25 t ha^{-1} , then 2059 at 0.78 t ha^{-1} , and 1112 producing the least at 0.54 t ha^{-1} . The 2003 growing season estimates showed 2059 and I45/51 first and last on the cumulative production scale at 15.02 t ha^{-1} and 7.57 t ha^{-1} , respectively. Clones 1112 cumulatively produced 13.15 t ha^{-1} and 26C6R51 produced 10.47 t ha^{-1} , also reversing their positions in root biomass production over the rotation.

Shoot biomass production data in 1999 indicated that clone I45/51 produced the greatest amount of shoot biomass (2.84 t ha^{-1}). The remaining order of production was 2059

(2.45 t ha⁻¹), 1112 (1.95 t ha⁻¹), and 26C6R51 (1.17 t ha⁻¹). The trend of I45/51 producing the most shoot biomass held until the third growing season, at which time *P. deltoides* clone 2059 had outgrown I45/51. Following the fourth growing season the order of cumulative shoot production, from greatest to least, was 2059 (44.54 t ha⁻¹), followed by I45/51 (38.79 t ha⁻¹), and 1112 and 26C6R51 (35.39 and 34.30 t ha⁻¹, respectively). By the end of the rotation, the hybrid clone had been surpassed by all *P. deltoides* clones in shoot production, except for 26C6R51 (see Figure 4b). The yield of shoot biomass over the rotation included 2059 producing the most at 76.0 t ha⁻¹, 1112 producing 56.42 t ha⁻¹, 26C6R51 at 39.47 t ha⁻¹, and I45/51 at 47.69 t ha⁻¹.

Total cumulative biomass production displayed trends similar to those exhibited by shoot biomass, with the hybrid clone (I45/51) at first producing the greatest amount of biomass, but being surpassed by local *P. deltoides* clones by rotation's end (see Figure 4c). Estimated root, shoot and total biomass dry weights are summarized in Table 7 for each year of the rotation.

Table 6a - Final equation variables and R² values for root biomass

Variable Entered	Variable Removed	Partial R ²	Model R ²
D2H		0.948	0.948
D×A×C3		0.017	0.965
HEIGHT		0.013	0.978
D×A×C2		0.002	0.979
D2H×C2		0.004	0.983
D2H×AGE		0.003	0.986
AGE		0.003	0.989
	HEIGHT	0.0006	0.989
D2H×C3		0.0023	0.988
	DXAXC3	0.0004	0.99
HEIGHT		0.0004	0.991
	HEIGHT	0.0004	0.989

Table 6b - Final equation variables and R² values for shoot biomass

Variable Entered	Variable Removed	Partial R ²	Model R ²
D2H		0.99	0.99
D2H × C3		0.003	0.993
D2H × C2		0.003	0.996
DIAM		0.001	0.997
D×A×C1		0.001	0.997
D×A×C2		0.0002	0.998
	D2HXC2	0	0.997
D2HXC1		0.0001	0.997
	D2HXC1	0.0001	0.998

Table 6c - Final equation variables and R² values for total biomass

Variable Entered	Variable Removed	Partial R ²	Model R ²
D2H		0.991	0.991
DIAM		0.002	0.993
D×A×C2		0.002	0.995
D2H × C3		0.001	0.997
D×A×C1		0.0004	0.997
D2H×AGE		0.0002	0.997
	D2HXAGE	0.0002	0.997

Figure 3 - Plantation 1 and Plantation 2 harvest dry weights vs. predicted dry weights derived from the equations. Pl. 1 represents weights from Plantation 1 and Pl. 2 represents weights from Plantation 2. The line indicates a 1:1 relationship of harvested dry weights.

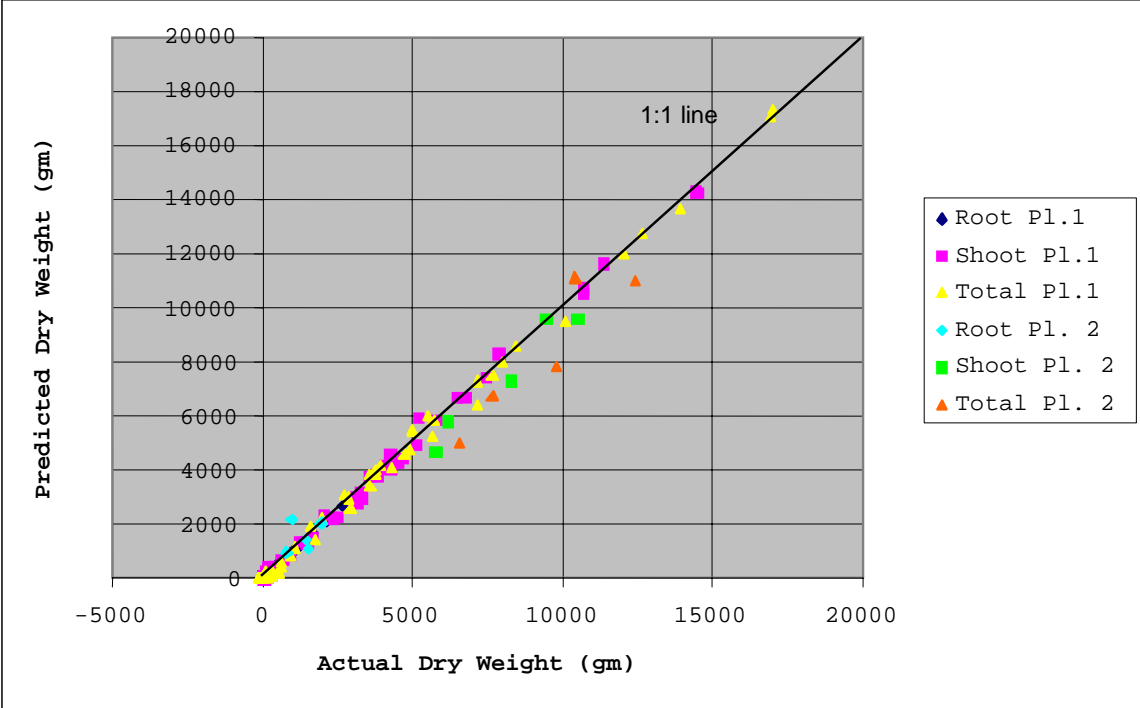


Figure 4a, 4b and 4c - Five-year trends in root (a), shoot (b) and total(c) biomass, respectively, for Plantation 1.

Fig. 4a

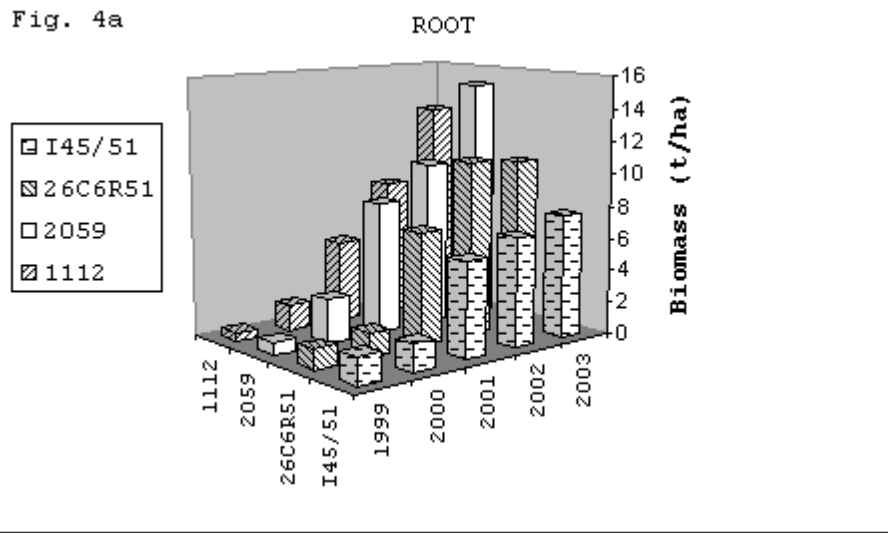


Fig. 4b

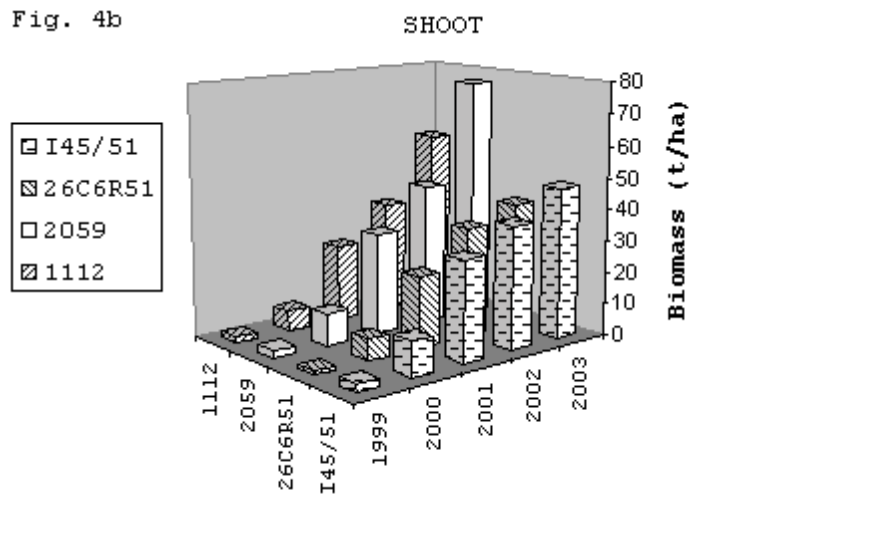
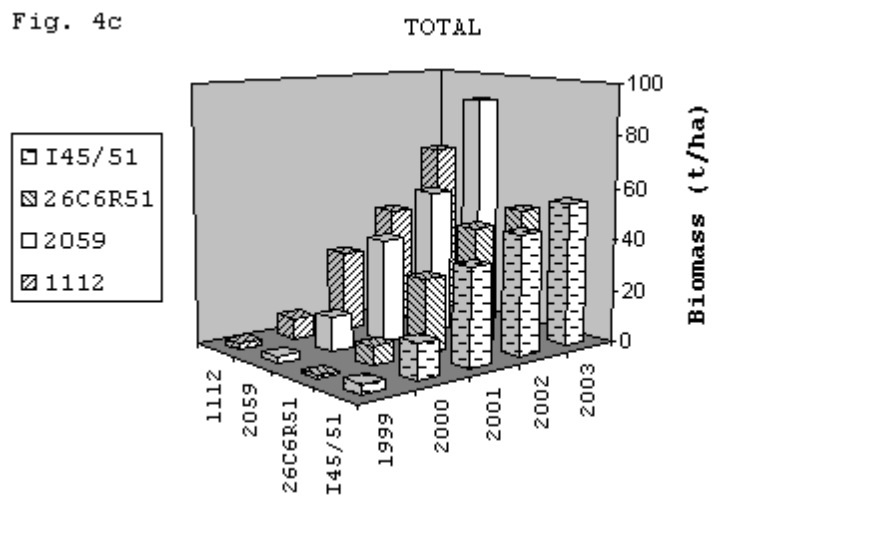


Fig. 4c



Plantation 1 - Biomass Statistical Analysis

1999 - In root biomass production, I45/51 was significantly greater than all other clones at the 0.05 significance level (see Table 7a). Clone 26C6R51 was significantly greater than 1112 and 2059. In shoot biomass 26C6R51 produced significantly less than all other clones. No other significant differences were present among the three remaining clones regarding shoot biomass. Clone I45/51 produced significantly more total biomass than clones 26C6R51 and 1112. No other significant differences occurred in 1999.

2000 - Clone 2059 was significantly greater than all other clones in cumulative root production (see Table 7b). Clones I45/51 and 1112 were significantly different at the high and low ends of shoot production, respectively. Clones I45/51 and 26C6R51 were not significantly different in shoot production at the 0.05 level, but the difference neared significance ($p=0.06$). Similarly, the difference in shoot biomass between clones 2059 and 1112 neared significance ($p=0.08$). These significant and nearly significant differences in p-values defined two groups in shoot biomass production. Clones 2059 and I45/51 tended to produce greater shoot and total biomass than clones 26C6R51 and 1112.

2001 - Clone 2059 produced significantly greater than I45/51 and 1112 in root cumulative biomass production (see Table 7c). 26C6R51 produced significantly greater root biomass than 1112. In shoot biomass production clone I45/51 produced significantly greater than 1112. There were no other significant differences to report. P-values that fell between 0.05 and 0.10 include I45/51 and 26C6R51 at 0.0694, I45/51 and 1112 at 0.0422, and 2059 and 1112 at .0892. There were no significant differences in total biomass. The comparison of clones I45/51 and 1112 produced a p-value of 0.0858 between them.

2002 - Clone 26C6R51 produced significantly greater cumulative root biomass than clones 1112 and I45/51 (see Table 7d). Clones 2059 and 1112 produced significantly greater root biomass than I45/51. The root biomass difference between clones 1112 and 2059 approached significance ($p=0.08$). There were no significant differences among clones in shoot or total biomass.

2003 - Clones 2059 and 1112 were significantly greater than I45/51 in cumulative root biomass production (see Table 7e). Clone 2059 was nearly significantly greater than 26C6R51 in root biomass production ($p=0.051$). In shoot and total biomass production 2059 was significantly greater than all other clones. Cumulative shoot and total

biomass production of clone 1112 was nearly significantly greater than that of 26C6R51 (shoot, $p=0.053$) and I45/51 (total, $p=0.058$).

In 2003, there were two major groupings among clones. Clones 2059 and 1112 produced biomass significantly greater, or nearly significantly greater, than 26C6R51 and I45/51. It is worth noting that clone 2059 had the nearest geographic origin in this study (Osage County) and 1112 was of Missouri origin as well (New Madrid, County), while clone 26C6R51 was from Pope County, Illinois.

Plantation 1 - Root:Shoot Ratio

Mean root:shoot ratio values for Plantation 1 are presented in Figure 5. Root:shoot ratios were calculated using cumulative biomass weights. Ratios were not calculated following the initial growing season (1999) due to the distortion of the values that would have been created by the influence of cutting weight. A slight overall downward trend in partitioning of assimilates to roots occurred over the course of the rotation (see Figure 5). The hybrid clone, I45/51, partitioned the least to roots, followed by clone 1112, then clone 2059, and lastly clone 26C6R51.

Statistical analysis for clonal differences in Plantation 1 indicated an increasing gap in root:shoot

ratio between the hybrid clone (I45/51) and the three *P. deltoides* clones with the progression of time (see Table 8a). In 2000, clones 2059 and 26C6R51 partitioned significantly more assimilates to root production than did I45/51. Clone 2059 was significantly different from 1112 in relative root production, as well. By 2001, clones 2059 and 26C6R51 had partitioned significantly more assimilates to root production than had 1112 and I45/51. Root:shoot ratio of clone 1112 was significantly greater than that of I45/51, as well. By 2002 all three *P. deltoides* clones and the hybrid clone had separated statistically from I45/51, which partitioned proportionately fewer assimilates to roots for the remainder of the rotation. With the hybrid clone distributing less assimilate to roots than *P. deltoides* clones one might expect it to be more productive aboveground, but it was not. An explanation of this apparent contradiction will be explored in the next section.

Single degree of freedom statistical analysis of the hybrid clone vs. *P. deltoides* clones resulted in significant p-values of <.0001 for the clone effect and <.0001 for the year effect on root:shoot ratio (see Table 8b). The interaction effect between clone and year was not statistically significant. Table 8c illustrates how the

relationship of root:shoot ratio between the hybrid and *P. deltoides* groups changed on an annual basis.

Table 7a - LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$) and total biomass($t\ ha^{-1}$) for 1999

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	1.66a	2.84a	3.86a
26C6R51	1.25b	1.17b	1.05bc
2059	0.78c	2.45a	2.65ac
1112	0.54c	1.95a	2.38bc

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 7b - LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$) and total biomass($t\ ha^{-1}$) for 2000

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	1.67b	11.04a	13.87a
26C6R51	1.49b	6.85ac	7.35bc
2059	2.70a	10.07ab	13.42ac
1112	1.63b	6.51bc	8.24b

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 7c - LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$) and total biomass($t\ ha^{-1}$) for 2001

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	5.85bc	31.54a	37.36a
26C6R51	6.94ab	22.42ab	28.53a
2059	8.12a	32.05ab	39.77a
1112	5.09c	24.41b	30.71a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 7d - LS Means for clone effect on root(t ha⁻¹), shoot(t ha⁻¹) and total biomass(t ha⁻¹) for 2002

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	6.70c	38.79a	46.28a
26C6R51	10.77a	34.30a	45.06a
2059	10.20ab	44.54a	55.66a
1112	8.51b	35.39a	45.14a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 7e - LS Means for clone effect on root(t ha⁻¹), shoot(t ha⁻¹) and total biomass(t ha⁻¹) for 2003

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	7.57bc	47.69b	54.87b
26C6R51	10.47ac	39.47b	49.18b
2059	15.02a	76.0a	90.65a
1112	13.15a	56.42b	68.22b

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Figure 5 - Plantation 1 root:shoot ratio trends for each clone on an annual basis. A slight overall downward trend is present as each clone ages, representing a reduction in relative root partitioning with time.

PLANTATION 1
Root:Shoot Ratio

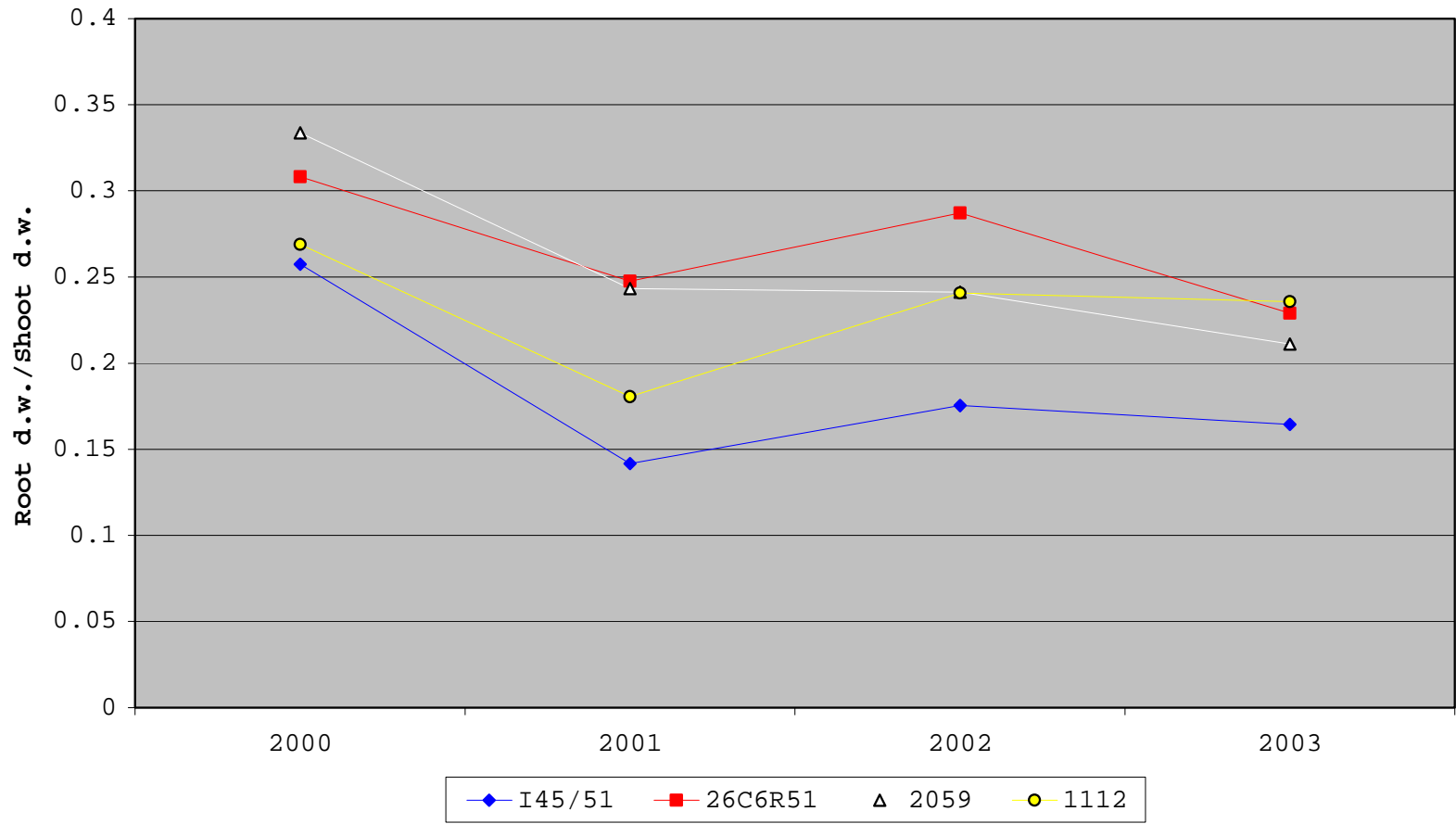


Table 8a - Least Squares Means for the effect of clone and year on root:shoot ratio in the second through fifth years of growth.

CLONE	2000	2001	2002	2003
I45/51	0.26c	0.14c	0.18b	0.16b
26C6R51	0.31ab	0.25a	0.29a	0.23a
2059	0.33a	0.24a	0.24a	0.21a
1112	0.27bc	0.18b	0.24a	0.24a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 8b - Least Squares Means for the single degree of freedom comparison between hybrids (clone = 1) and *P. deltoides* (clone = 0) and for pooled clone values across years for root:shoot ratio

CLONE TYPE	R:S LSMEAN
0 Hybrid	0.18b
1 <i>P. deltoides</i>	0.25a

YEAR	R:S LSMEAN
2000	0.28a
2001	0.18c
2002	0.21b
2003	0.20bc

LSMEANS within a column with at least one letter in common are not significantly different at the five percent level

Table 8c - Least Squares Means for the interactive effects between *P. deltoides* clones and year and between hybrids and year in the second through fifth years of growth for root:shoot ratio

CLONE	2000	2001	2002	2003
<i>P. deltoides</i> parentage	0.30a	0.21a	0.25a	0.23a
<i>P. deltoides</i> × <i>P. nigra</i> parentage (hybrid)	0.26b	0.14b	0.18b	0.16b

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Light Use Efficiency

Phenology

Average dates of bud break (Figure 6) indicated relatively stable patterns of bud break for both plantations over the rotation. In contrast, date of bud set appeared to occur earlier as the rotation progressed.

Leaf Area Duration vs. Estimated Clone Biomass

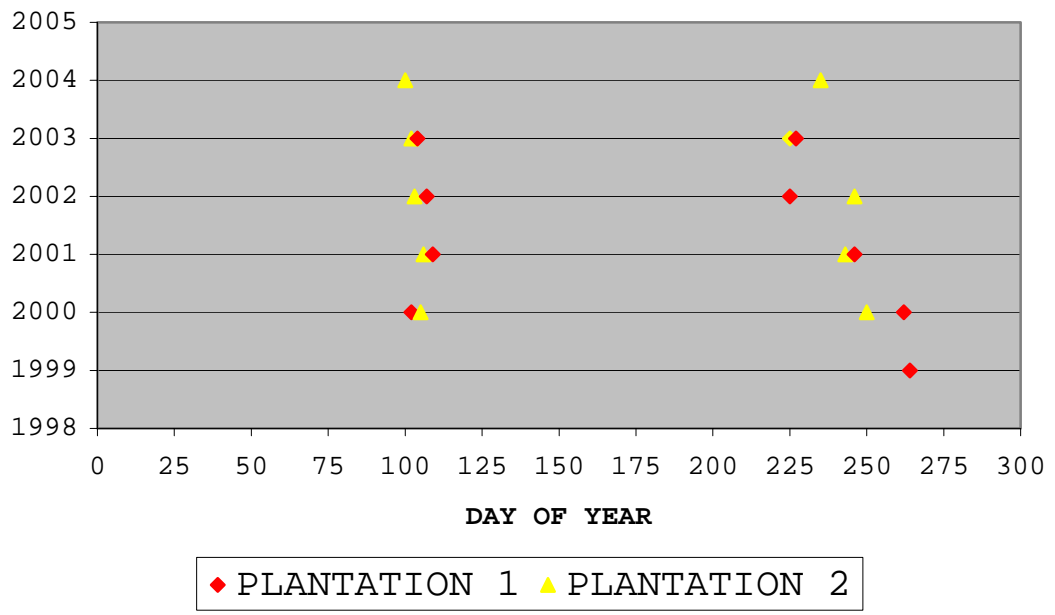
Slopes of the relationship between cumulative Leaf Area Duration LAD, ($\text{m}^2 \text{ LA m}^{-2} \times \text{days}$) values for each clone plotted against corresponding estimated total tree biomass suggested that clone 2059 was most efficient at producing biomass per unit of LAD in Plantation 1 (see Figure 7).

A statistical analysis of the annual biomass divided by the annual LAD indicated that clone 2059 had the highest efficiency in converting light energy to biomass and was significantly higher than all other clones at the 0.05 significance level except for clone 1112 which had the second highest efficiency (see Table 9a). Also notable in the analysis was the previously observed grouping of clones 2059 and 1112 (both of Missouri origin) apparently converting absorbed light to biomass more efficiently than other clones.

Results in Table 9b compare the accumulated biomass divided by accumulated LAD on the basis of a single degree

Figure 6 - Average annual dates of bud burst (left) and bud set (right) for Plantation 1 and 2 beginning in the fall of 1999 and ending in the fall of 2004.

PHENOLOGY DATES



of freedom comparison of the hybrid clone vs. all three *P. deltoides* clones. A significant difference was present, identifying the *P. deltoides* clones as more efficient than the hybrid in converting light energy to biomass. For this reason, the *P. deltoides* clones selected for this study were able to out-produce the hybrid clones, although the hybrid clone partitioned fewer assimilates to roots.

In order to determine if the relationship between clone cumulative LAD and clone biomass exhibited in Plantation 1 would remain consistent on an alternate site, the slopes were plotted in Plantation 2 for the corresponding data (see Figure 8). The order of the efficiency slopes found in Plantation 1 was repeated, with less scatter within the two major groups (2059 and 1112 more efficient, 26C6R51 and I45/51 less efficient). The less efficient group's slopes practically fell one on top of one another, although compared to Plantation 1 the two clones did switch places in efficiency. The fifth clone included in Plantation 2, the hybrid *Populus deltoides* x *P. nigra* 'Eugenei', grouped with the other hybrid and was fourth among five clones in efficiency.

A statistical analysis of yearly change in biomass/yearly LAD data from Plantation 2 again found 2059 to be significantly more efficient in conversion of light

energy to biomass than all other clones except 1112 at the 0.05 significance level (see Table 9c). Clone 1112 had significantly greater LUE than did the two hybrid clones. Notable again was the higher efficiency of clones 2059 and 1112 in conversion compared to hybrid material, reinforcing their similarity in performance and as superior-performing clones.

A single degree of freedom comparative analysis of hybrid clones vs. *P. deltoides* clones for Plantation 2 was statistically significant at the 0.05 level. Hybrids had lower values of LUE than did *P. deltoides* clones (0.0464 vs. 0.0926 t ha⁻¹/m² m⁻² x days, respectively), indicating there were biologically meaningful differences in LUE between hybrid and *P. deltoides* clones in Plantation 2.

Figure 7 - Plantation 1 plot cumulative Leaf Area Duration vs. corresponding estimated cumulative total biomass demonstrating light-use efficiency among clones. Each data point represents a time progression of accumulated LAD and accumulated biomass for an individual plot. Steeper slopes of fitted lines indicate more efficient utilization of light energy.

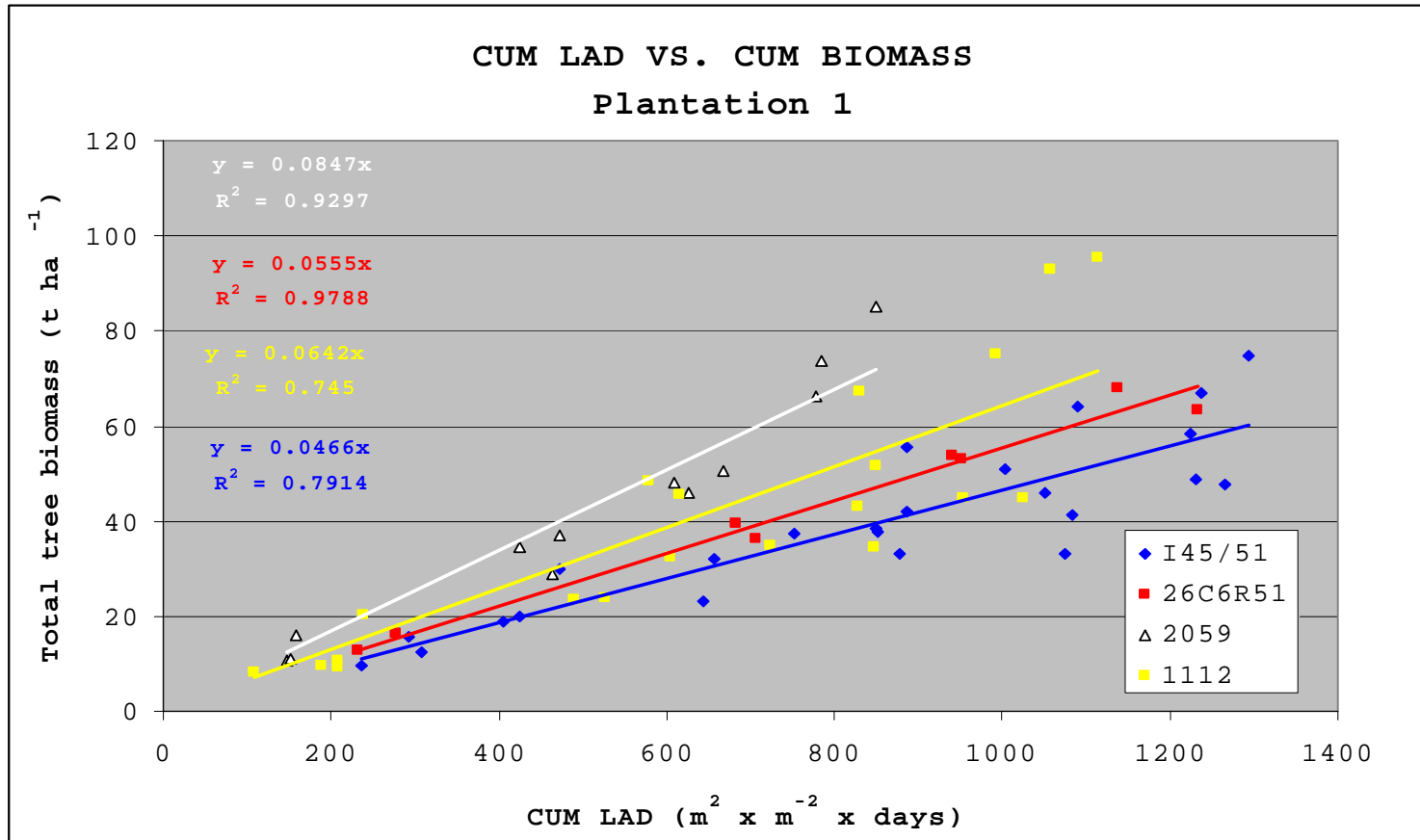


Table 9a - Plantation 1 least squares means for the effect of clone on BIO/LAD (yearly biomass increase/corresponding year's LAD), indicating efficiency in converting light energy to biomass

Least Squares Means	
BIO/LAD [Σ (yearly biomass increase/corresponding year's LAD)]	
CLONE	LS MEAN (t ha ⁻¹ /m ²) LA m ⁻² × days)
I45/51	0.0445b
26C6R51	0.0568b
2059	0.1021a
1112	0.0757ab

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 9b - Plantation 1 least squares means for the effect of hybrid vs. clone on LAD indicating efficiency in converting light energy to biomass

Least Squares Means	
BIO/LAD (yearly biomass increase/corresponding year's LAD)	
CLONE	LS MEAN (t ha ⁻¹ /m ²) LA m ⁻² × days)
Hybrid	0.0445a
<i>deltoides</i>	0.0798b

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 9c - Plantation 2 least squares means for the effect of clone on LAD, indicating efficiency in converting light energy to biomass

Least Squares Means	
BIO/LAD (yearly biomass increase/corresponding year's LAD)	
CLONE	LS MEAN (t ha ⁻¹ /m ²) LA m ⁻² × days)
I45/51	0.0455c
Eugenei	0.0475bc
26C6R51	0.0597b
2059	0.1107a
1112	0.0909ab

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

In order to thoroughly understand potential mechanisms responsible for differences in growth a statistical analysis of annual LAD also was conducted. All analyses were conducted at the 0.05 significance level. Table 10a shows that this approach again resulted in clones 2059 and 1112 forming a group, although a significant difference existed between them, while no statistical difference occurred in the group containing clones I45/51 and 26C6R51. Table 10b reveals statistically significant differences also existed between years 2000, 2001, and 2003. 2002 was also different than 2001. Notable in the interactive effect of clone and year on LAD (see Table 10c) is the trend of clone 2059 consistently displaying the lowest LAD, The hybrid clone I45/51 produced a statistically higher LAD than 2059 through 2001, at which point the gap closed to a non-significant level. These results reflect those drawn in the analysis of the annual biomass divided by annual LAD, in which clone 2059 was shown to convert light to biomass more efficiently than other clones per unit of LAD. However, they also suggest that the progressive late decline of biomass growth (e.g., Fig. 4c) in the hybrid clone may be at least partially attributable to its subsequent decline in LAD in the latter half of the rotation.

A single degree of freedom analysis comparing clones on the basis of hybrids versus non-hybrid (Table 10d) showed the hybrid clone to have significantly higher LAD. Results of the interactive effect in Table 10e, when added through all growing seasons, confirm those found in 10d.

An analogous analysis of LAD in Plantation 2 lent support to that found in Plantation 1 for the effect of clone on LAD (see Table 11a). Clone 2059 again attained the lowest LAD while producing the greatest biomass, although it was statistically different only from clone 26C6R51. Hybrid clones I45/51 and Eugenei placed third and fourth respectively in LAD, providing further evidence for clone 2059's superior production efficiency per unit of LAD. Clone 26C6R51 produced the highest and only statistically different LAD. The only other statistically significant results were the effect of year on LAD displayed in Tables 11b and 11c. In both cases 2001 and 2002 are the only years when there were not statistical differences.

Soil Carbon

T-tests on soil total organic C indicated a significant loss in percent C in the soil in the first layer only (0-12.5 cm) over the rotation in Plantation 1 (see Figure 9). In the second layers (12.5-25 cm) there was a slight

decrease in percent soil C. In the third and fourth layers (26-50 cm) there was a slight increase.

T-tests on soil C on a mass basis resulted in a non-significant loss of C from the soil over the rotation (see Figure 10). Again, there were slight decreases in soil C in the first 25 cm of soil depth and slight increases in the second 25 cm. In total, there was approximately 500 g m⁻¹ or 5 t ha⁻¹ of soil C lost between 1999 and 2004. Carbon content of above-ground biomass is calculated using an average of 50 percent C (Madeira, et al., 2002). Thus, using the biomass produced by clone 2059 (approx. 75 t ha⁻¹), the C-content conversion factor and subtracting the lost soil C, one can estimate from Plantation 1 that it is possible to tie up a net of 32.5 t ha⁻¹ of C in a short-rotation poplar plantation.

Bulk density average measurements for Plantation 1 were 1.415 g cm⁻³ ± 0.017, 1.47 g cm⁻³ ± 0.032, 1.532 g cm⁻³ ± 0.038 and 1.531 g cm⁻³ ± 0.076 for depth 0-12.5, 12.5-25, 25-37.5 and 37.5-50 cm respectively.

Figure 8 - Plantation 2 plot cumulative Leaf Area Duration vs. corresponding estimated total biomass indicating light-use efficiency among clones

CUM LAD VS. CUM BIOMASS
PLANTATION 2

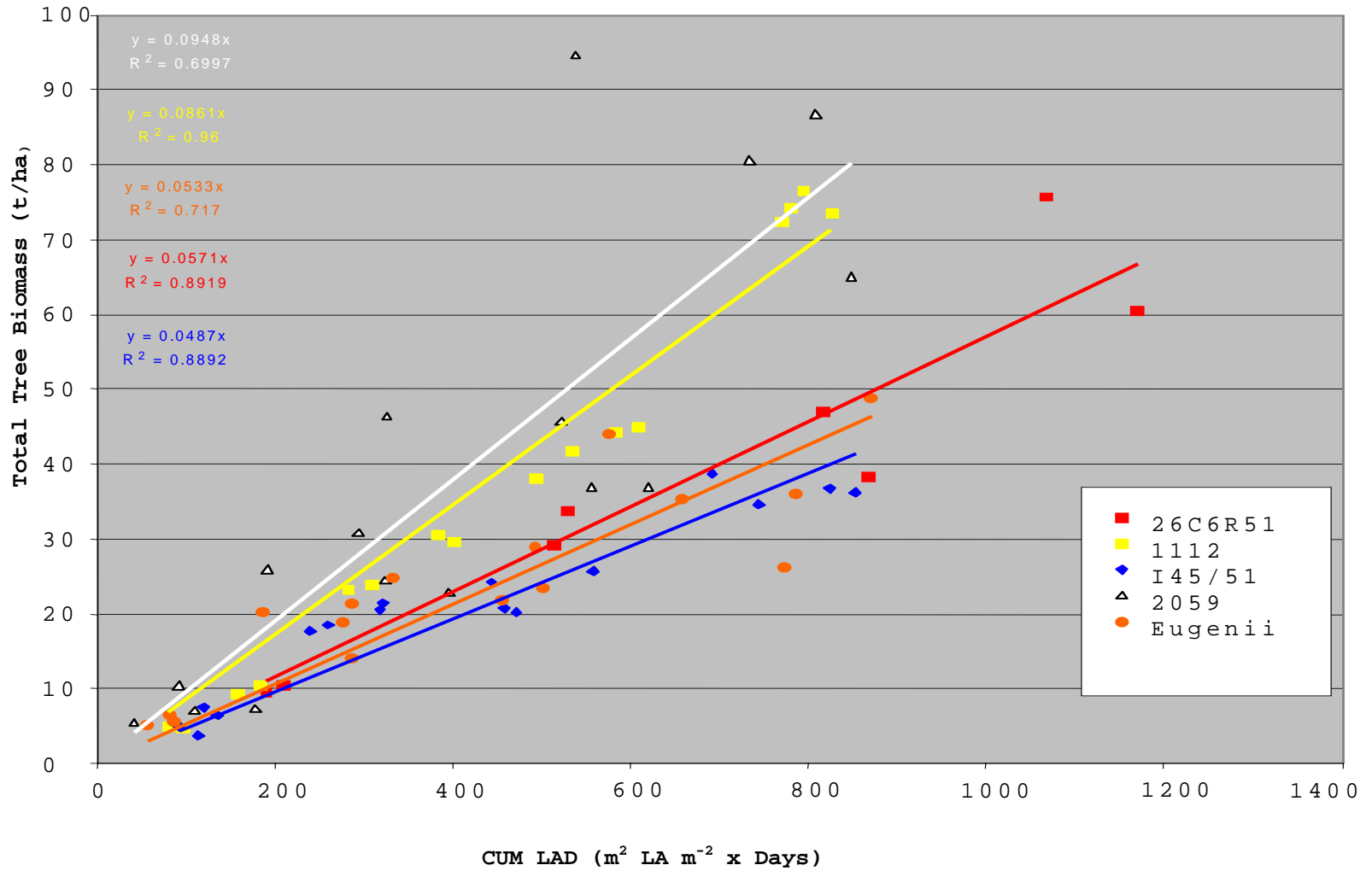


Table 10a - Plantation 1 least squares means for the effect of clone on LAD

CLONE	LSMEAN LAD ($m^2 m^{-2} \times days$)
I45/51	295.75a
26C6R51	296.44a
2059	200.90c
1112	257.08b

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 10b - Plantation 1 least squares means for the effect of year on LAD

CLONE	LSMEAN LAD ($m^2 m^{-2} \times days$)
2000	238.31a
2001	382.80c
2002	226.35ab
2003	202.71b

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 10c - Plantation 1 least squares means for the effect Clone and year on LAD ($m^2 m^{-2} \times days$) in the second through fifth years of growth.

CLONE	2000	2001	2002	2003
I45/51	356.08a	417.48a	220.17ab	189.26a
26C6R51	254.66b	440.06a	251.05a	239.91a
2059	152.02c	301.29b	181.02b	169.29a
1112	190.5bc	372.38a	253.05a	212.39a

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 10d - Plantation 1 least squares means for the single degree of freedom comparison between hybrids (clone = 1) and *P.deltoides* (clone = 0) and for pooled clone values across years

CLONE TYPE	LAD ($m^2 m^{-2} \times \text{days}$)
0 Hybrids	295.75a
1 <i>P.deltoides</i>	248.10b

YEAR	LAD ($m^2 m^{-2} \times \text{days}$)
2000	273.93b
2001	391.03a
2002	225.62c
2003	197.11cd

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 10e - Plantation 1 least squares means for the interactive effects between *P. deltoides* clones and year and between hybrids and year in the second through fifth years of growth for LAD ($m^2 m^{-2} \times \text{days}$)

CLONE	2000	2001	2002	2003
<i>P.deltoides</i> x <i>P. nigra</i> parentage (hybrids)	356.08a	417.48a	220.17b	189.26a
<i>P.deltoides</i> parentage	191.79b	364.59a	231.06a	204.96a

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 11a - Plantation 2 least squares means for the effect of clone on LAD

CLONE	LSMEAN LAD ($\text{m}^2 \text{m}^{-2} \times \text{days}$)
I45/51	197.89b
Eugenei	187.56b
26C6R51	279.43a
2059	177.94b
1112	198.19b

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 11b - Plantation 2 least squares means for the effect of year on LAD

CLONE	LSMEAN LAD ($\text{m}^2 \text{m}^{-2} \times \text{days}$)
2000	137.75c
2001	214.14b
2002	219.35b
2003	261.56a

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Table 11c - Plantation 2 least squares means for the effect of year on LAD of pooled clone values across years when analyzing clones as hybrids and P.deltoides.

YEAR	LAD ($\text{m}^2 \text{m}^{-2} \times \text{days}$)
2000	129.24c
2001	197.65b
2002	204.45b
2003	261.62a

LS Means within a column with at least one letter in common are not significantly different at the five percent level.

Figure 9 - Percent C in the soil according to soil depth over the course of a rotation. Samples include initial (1999) and final (2004) dates. Soil depth is divided into four 12.5 cm descending layers

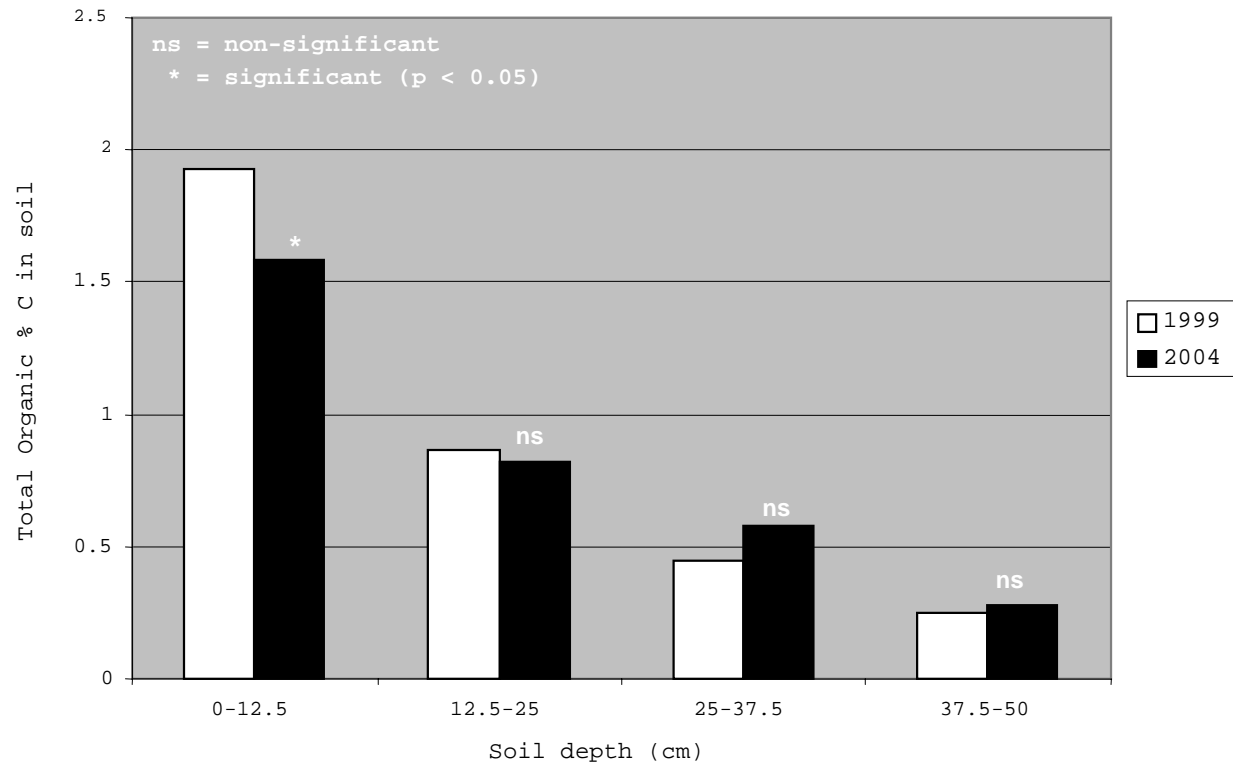
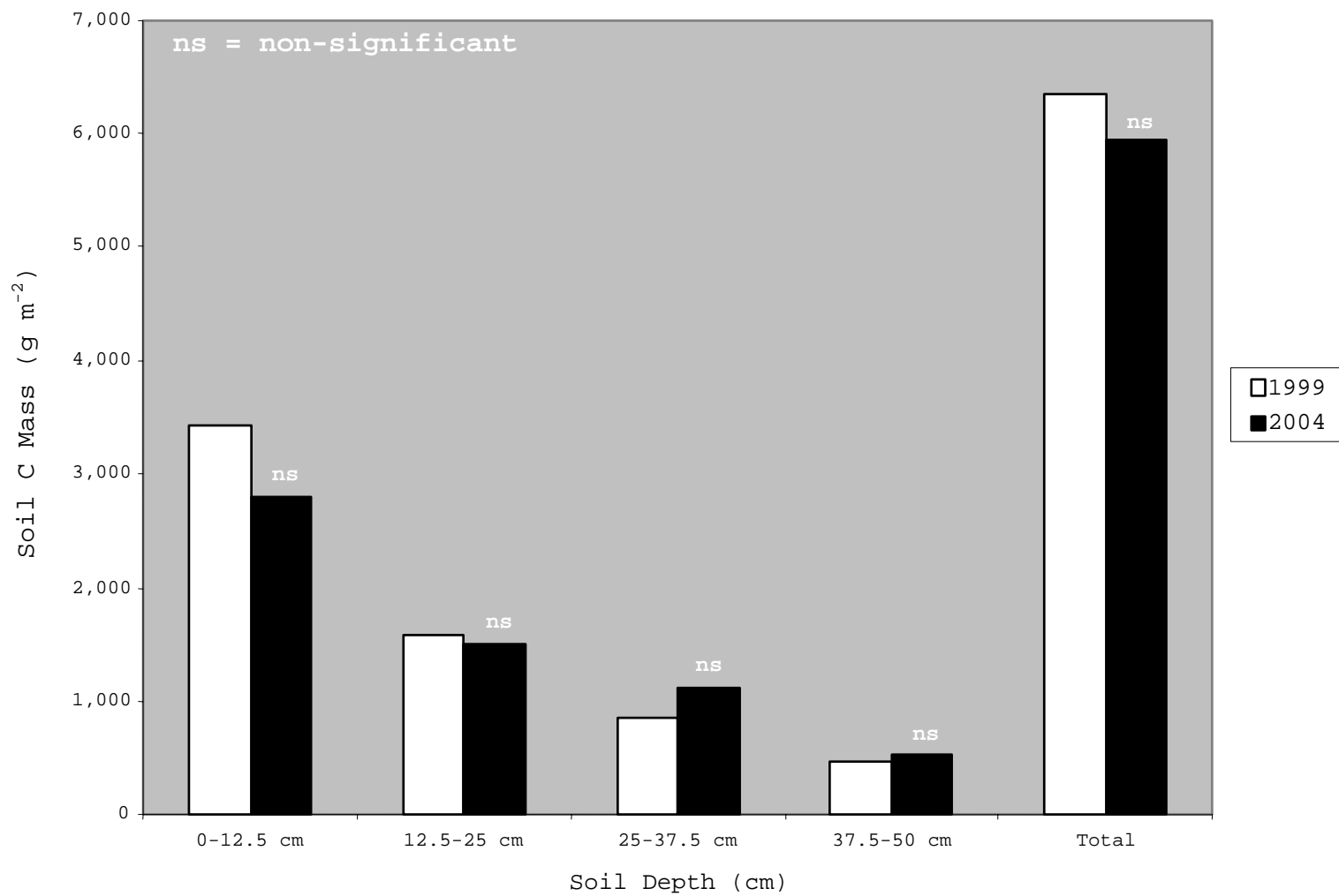


Figure 10 - Soil C on a mass basis corresponding to soil depth over the course of a rotation. Samples include initial (1999) and final (2004) dates. Soil depth is divided into four 12.5 cm descending layers.



Plantation 2 - Five Year Trends in Biomass: Overview

There was little similarity in root biomass production among *P. deltoides* clones in 2000. There was, however, similarity between the hybrid clones. Eugenei and I45/51 produced much greater amounts of root biomass than did clones 2059 and 1112 (see Figure 11a and Table 12a for values). The *P. deltoides* clone, 26C6R51, out-produced all other clones in root biomass. By the final year of the rotation the *P. deltoides* clones had clustered into a group, greatly out-producing the hybrids in cumulative root biomass, the latter of which had formed a group as well. This result was the same trend observed in Plantation 1; however, the reversal of group root biomass production occurred much earlier in the rotation. By year two all *P. deltoides* clones were producing greater root biomass than their hybrid counterparts.

In the second year there were no significant differences among clones in shoot production. However, as in Plantation 1, a hybrid clone produced the greatest amount of shoot biomass (see Figure 11b for values) although this time it was the added clone Eugenei. By 2002 all *P. deltoides* clones were out-producing both hybrid clones in cumulative shoot biomass. This trend held for the remainder of the rotation with the final order of shoot

biomass being clone 2059 producing 61.67 t ha⁻¹, 1112 (55.66 t ha⁻¹), 26C6R51 (51.98 t ha⁻¹), Eugenei (30.25 t ha⁻¹) and I45/51 producing 28.54 t ha⁻¹. This was the same order of shoot production (except for *Populus deltoides* x *P. nigra* 'Eugenei') observed in Plantation 1.

Eugenei began the rotation by producing the second greatest total biomass in the first year. Especially noteworthy is the performance of the other hybrid I45/51, which produced fourth in total biomass from the beginning (1.64 t ha⁻¹). Therefore, the trend of a hybrid clone beginning the rotation near the top in producing total biomass was consistent across sites. However, the hybrid clone was Eugenei, as the hybrid employed in Plantation 1 produced near the bottom in the first year in Plantation 2. Following the second growing season, both hybrid clones were out-produced by all *P. deltoides* clones, with the final season cumulative total production trends essentially mirroring that of Plantation 1 (see Figure 11c).

Plantation 2 - Biomass Statistical Analysis

2000 - In yearly root biomass production there were two statistically significant divisions between hybrid and *P. deltoides* clones (see Table 12a). Clone 26C6R51 was

Figure 11a, 11b and 11c - Five year trends in root, shoot
and total biomass for Plantation 2

Fig. 11a

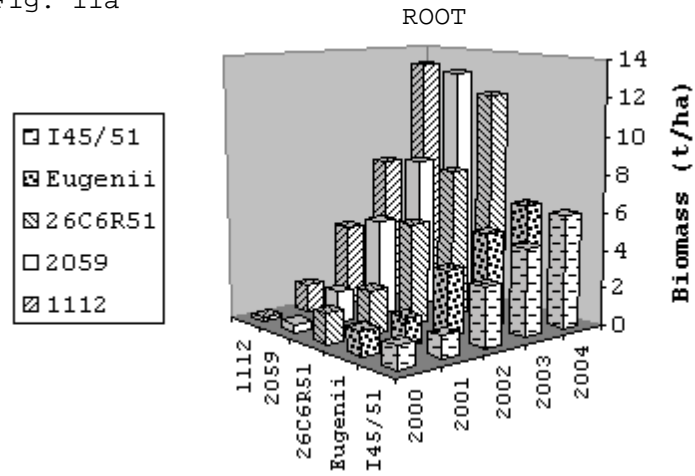


Fig. 11b

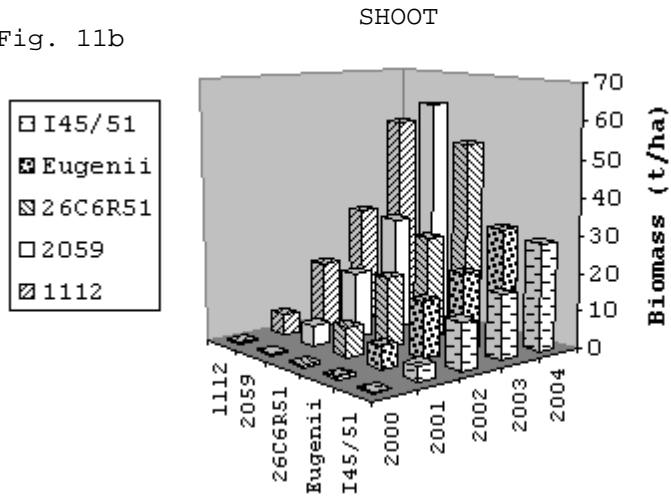
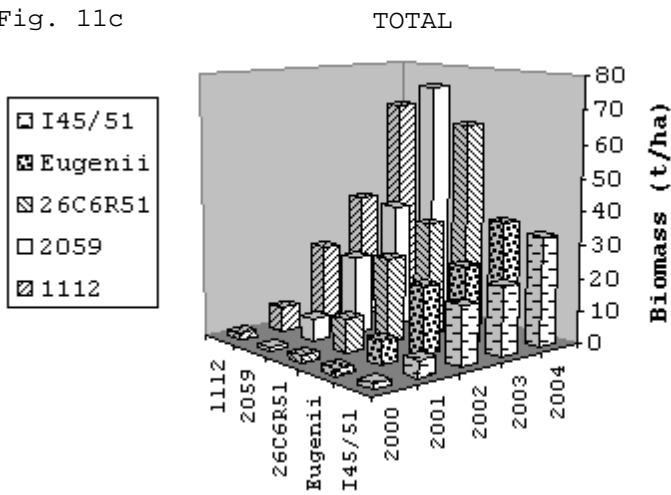


Fig. 11c



significantly greater than both hybrid clones, between which there was no significant difference, and also greater than *P. deltoides* clones 2059 and 1112. Both hybrid clones were significantly greater in root biomass than clones 2059 and 1112. There was also a difference between 2059 and 1112, with 2059 producing significantly greater root biomass than 1112. There were no significant differences among clones in shoot biomass. In total biomass clone 2059 produced significantly less than all other clones.

2001 - Clone 26C6R51 again had significantly greater cumulative root biomass than did hybrid clones and *P. deltoides* clone 1112 (see Table 12b). However, it did not have more biomass than clone 2059 as in the previous year. No other significance differences in root biomass occurred, although the difference between clone I45/51 and 2059 was nearly significant ($p = 0.057$). No significant differences were present in cumulative shoot biomass, but the difference between 26C6R51 and I45/51 approached significance ($p = 0.057$). Clone 26C6R51 produced significantly greater cumulative total biomass than did hybrid clone I45/51. There were no other significant differences in total biomass.

2002 - All *P. deltoides* clones had significantly greater cumulative root biomass than hybrid clone I45/51

(see Table 12c). Clones 2059 and 26C6R51 also had significantly greater root biomass than the hybrid Eugenei. Clones 26C6R51 and 1112 produced significantly greater cumulative shoot biomass than I45/51. In total biomass production all *P. deltoides* clones significantly out-produced I45/51. There were no other significant differences in 2002.

2003 - A clear statistical division was present between *P. deltoides* clones and hybrids in all categories (see table 12d). The only similarity between the two groups existed between 26C6R51 and Eugenei for shoot biomass with a nearly significant p-value of 0.052.

2004 - The groupings from the previous year of hybrids vs. *P. deltoides* clones were nearly identical for cumulative root, shoot, and total biomass (see Table 13e). There were no significant differences within these two major groups and no similarities between groups. A complete statistical division had occurred.

Plantation 2 - Root Shoot Ratio

Although root:shoot ratio patterns varied somewhat across sites, there were some similarities. As in Plantation 1, an overall downward trend in relative biomass partitioning to roots occurred over the rotation (Fig. 12). The hybrid clone Eugenei generally partitioned the fewest

Table 12a - Plantation 2 LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$), and total biomass($t\ ha^{-1}$) for 2000.

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	1.2b	0.33a	1.64a
Eugenei	1.3b	0.78a	2.04a
26C6R51	1.6a	0.57a	2.24a
2059	0.43c	0.45a	1.04b
1112	0.20d	0.51a	1.98a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 12b - Plantation 2 LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$), and total biomass($t\ ha^{-1}$) for 2001

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	1.17b	3.99a	5.12bc
Eugenei	1.44b	5.78a	7.18ac
26C6R51	2.27a	7.92a	10.05a
2059	1.69ab	5.28a	6.85ac
1112	1.51b	5.79a	7.48ab

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 12c - Plantation 2 LS Means for clone effect on cumulative root($t\ ha^{-1}$), shoot($t\ ha^{-1}$), and total biomass($t\ ha^{-1}$) for 2002

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	3.1b	12.32c	17.7b
Eugenei	3.45bc	14.99ac	20.33ab
26C6R51	5.36a	18.84a	25.84a
2059	5.12a	17.56ac	23.60a
1112	4.38ac	18.01a	24.37a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 12d - Plantation 2 LS Means for clone effect on cumulative root (t ha⁻¹), shoot(t ha⁻¹), and total biomass (t ha⁻¹) for 2003

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	4.65b	17.34c	20.63b
Eugenei	4.96b	20.27bc	23.95b
26C6R51	7.85a	27.64ab	34.39a
2059	8.13a	30.64a	37.63a
1112	7.75a	31.2a	38.32a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 12e - Plantation 2 LS Means for clone effect on cumulative root(t ha⁻¹), shoot(t ha⁻¹), and total biomass(t ha⁻¹) for 2004

CLONE	LS MEAN ROOT	LS MEAN SHOOT	LS MEAN TOTAL
I45/51	5.99b	28.54b	33.25b
Eugenei	6.13b	30.25b	35.18b
26C6R51	11.76a	51.98a	63.36a
2059	12.79a	61.67a	74.14a
1112	13.10a	55.66a	67.26a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

proportion of assimilates to roots, followed by *P.*

deltoides clone 1112, then the second hybrid I45/51. Clone 2059 and then 26C6R51 had the highest root:shoot ratios.

A single degree of freedom comparison between hybrid and *P. deltoides* groups in Plantation 2 indicated differences in root:shoot ratio between groups ($p = 0.0348$) and by year ($p = <.0001$). Further, analysis of root:shoot ratio across all clones indicated decreasing differences among all clones with time, and a significant difference between hybrid and *P. deltoides* clones as groups only in 2002 (see Tables 13a and 13c). Analysis also showed *Populus deltoides* clones trended toward higher root:shoot ratio than hybrids in three of four years.

The trend of diminishing differences with time between *P. deltoides* and hybrid clones is contrary to the pattern observed in Plantation 1, where the hybrid clone tended to exhibit an increased reduction in root:shoot ratio as the rotation proceeded. By 2003 there were no significant differences in root:shoot ratio among clones in Plantation 2. In 2002 there was an unusual situation where significant differences existed among all *P. deltoides* clones. Hybrid clones exhibited no significant differences throughout the rotation.

Figure 12 - Plantation 2 annual root:shoot ratio trends for each clone. An overall downward trend is present as each clone ages, representing a reduction in relative root partitioning with time.

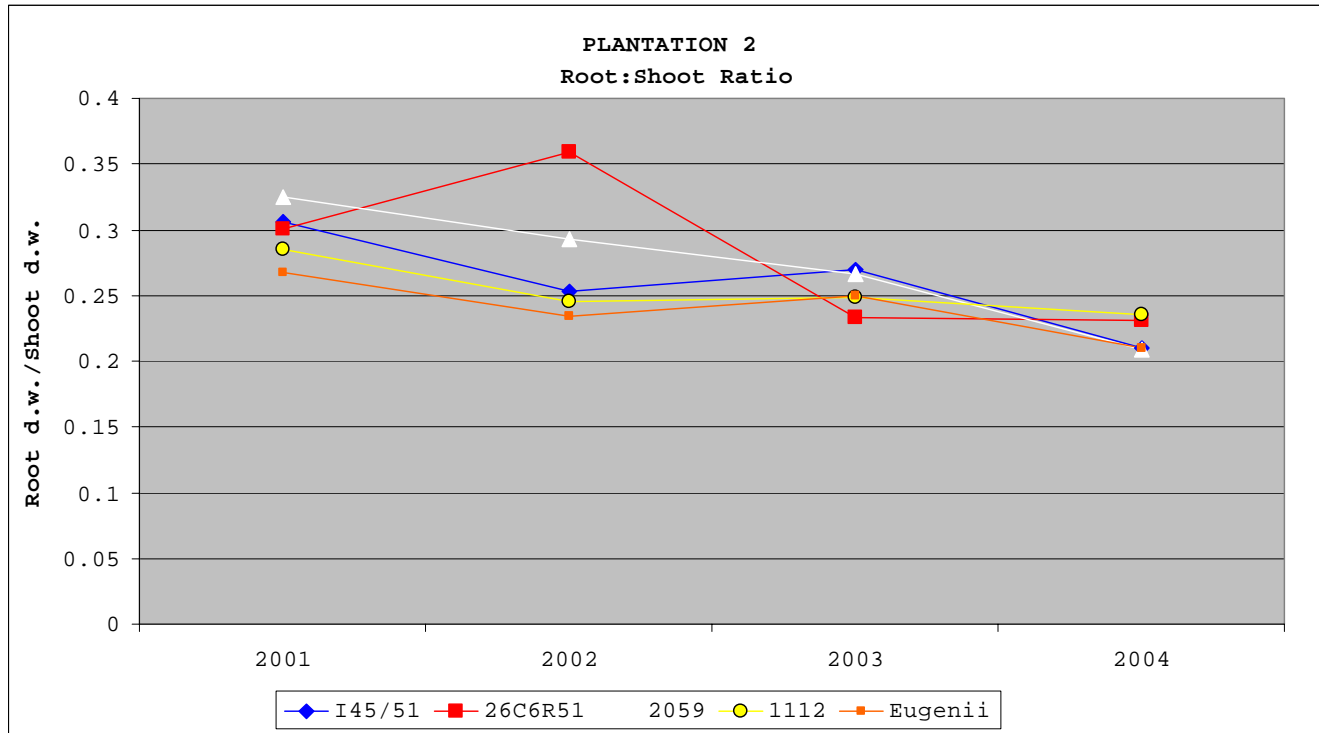


Table 13a - Least Squares Means for the effect of clone on root:shoot ratio in the second through fifth years of growth.

CLONE	2001	2002	2003	2004
I45/51	0.31ab	0.25c	0.27a	0.21a
Eugenei	0.27bc	0.23c	0.25a	0.21a
26C6R51	0.30a	0.36a	0.24a	0.23a
2059	0.32a	0.29b	0.27a	0.21a
1112	0.29a	0.24c	0.25a	0.24a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 13b - Least Squares Means for the single degree of freedom comparison between hybrids (clone = 1) and *P. deltoides* (clone = 0) and for pooled clone values across years for root:shoot ratio

CLONE	R:S LSMEAN
0 Hybrids	0.27a
1 <i>P. deltoides</i>	0.25b

YEAR	R:S LSMEAN
2001	0.30a
2002	0.27b
2003	0.26b
2004	0.22c

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Table 13c - Least Squares Means for the interactive effects between *P. deltoides* clones and year and between hybrids and year in the second through fifth years of growth for root:shoot ratio

CLONE	2001	2002	2003	2004
<i>P. deltoides</i> parentage	0.30a	0.29a	0.25a	0.22a
<i>P. deltoides</i> × <i>P. nigra</i> parentage (hybrids)	0.29a	0.24b	0.26a	0.21a

LSMeans within a column with at least one letter in common are not significantly different at the five percent level.

Plantation 2 - Soil Carbon

T-tests on percent soil C indicated a statistically significant loss (~ 1 percent) in the top layer (12.5 cm) of the soil over the rotation in Plantation 2 (see Figure 13). Layers two through four exhibited only slight, non-significant losses in soil C.

T-tests on soil C on a mass basis resulted in a statistically significant loss in total C over the rotation (see Figure 14). The loss was approximately 2222 g m^{-2} , or 22 t ha^{-1} . There were statistically significant losses in soil C in layers 1, 3, and 4 and a nearly significant loss in layer 2 ($p = .06$) at the 0.05 significance level. Using the biomass produced by clone 2059 in Plantation 2 (approx. 74 t ha^{-1}) and the previously mentioned conversion factor (mass of C = 50 % of plant dry mass), a net 15 t ha^{-1} of C was sequestered by this clone/plantation.

An analysis of variance of soil C differences on a mass basis by depth, using clone as the treatment variable (Figure 15), revealed no significant differences among clones, however *P. deltoides* clones more often lost less soil C than hybrid clones in each sample layer. A single degree of freedom statistical analysis of total soil C changes between hybrids and *Populus deltoides* clones as groups found *Populus deltoides* clones to retain more soil C

at the 0.05 significance level (see Figure 16). The hybrid clone I45/51 was the only clone exhibiting a significant loss ($p \leq 0.05$) in total soil C.

Bulk density average measurements for Plantation 2 were $1.324 \text{ g cm}^{-3} \pm 0.215$, $1.434 \text{ g cm}^{-3} \pm 0.033$, $1.416 \text{ g cm}^{-3} \pm 0.034$ and $1.497 \text{ g cm}^{-3} \pm 0.089$ for depth 0-12.5, 12.5-25, 25-37.5 and 37.5-50 cm respectively.

Soil Moisture Case Study

The first soil water content data were obtained on September 7, 2002. Therefore, it should be noted that soil moisture data from 2002 were collected at the approximate time of bud set. The final measurement was recorded on October 12, 2004. This measurement period provided two full years of soil moisture data and biomass growth. Figure 17 illustrates the complete record of daily mean soil water content data for the entirety of the period.

Mean growing season (April - late September or early October) soil moisture was similar from year to year, as was the tendency for "wet" plots to maintain substantially greater soil water content. There was a large difference in biomass productivity between the wet and dry plots (see Figure 18). In 2002 estimated cumulative total biomass was 18.48 t ha^{-1} in the wet plot and 26.17 t ha^{-1} in the dry plot. In 2003 the estimates were 22.54 and 32.02 t ha^{-1} ,

respectively, with the same soil water content values. This was a difference of nearly 9.5 t ha⁻¹. The 2004 data indicated 39.97 t ha⁻¹ in the wet plot and 44.25 t ha⁻¹ in the dry plot, varying 4.3 t ha⁻¹.

Flooding of the plantations occurred in the spring and fall each year. Flooding typically lasted one to two days. Following the descent of the floodwater the lower lying areas in Plantation 2 remained wet many days after higher areas had dried.

Figure 13 - Percent C in the soil according to soil depth over the course of a rotation. Samples include initial (2000) and final (2005) dates. Soil depth is divided into four 12.5 cm descending layers.

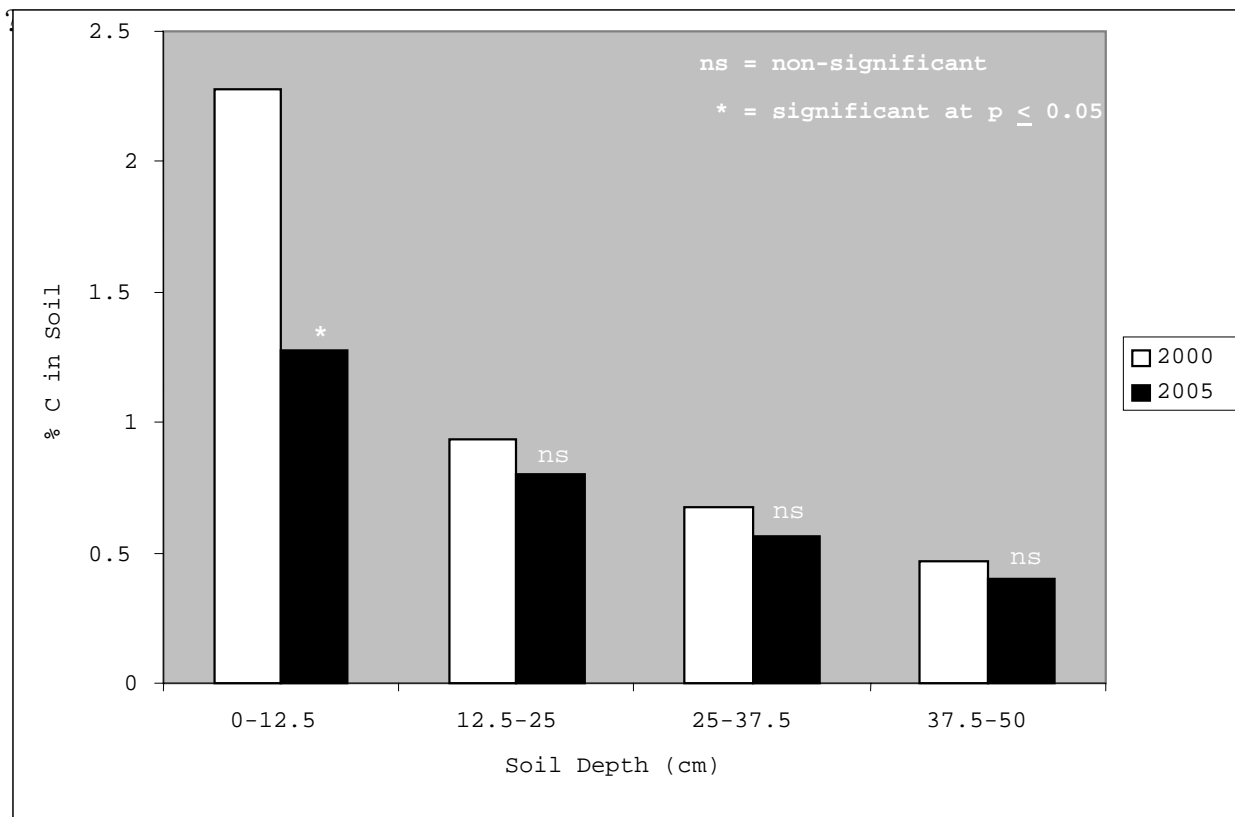


Figure 14 - Soil C on a mass basis corresponding to soil depth over the course of a rotation. Samples include initial (2000) and final (2005) dates. Soil depth is divided into four 12.5 cm descending layers.

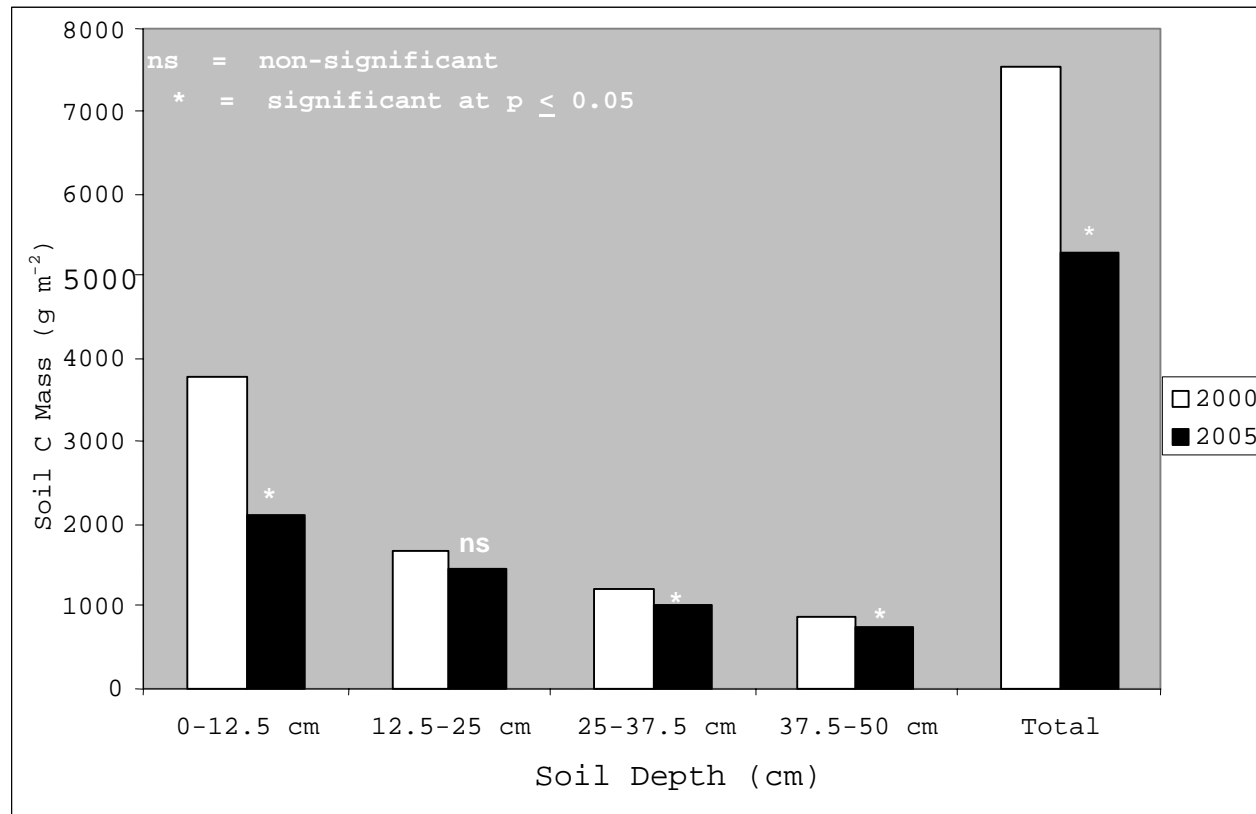


Figure 15 - Changes in soil C among clones on a mass basis between 2000 and 2005 in Plantation 2. Data are organized in four 12.5 cm depths.

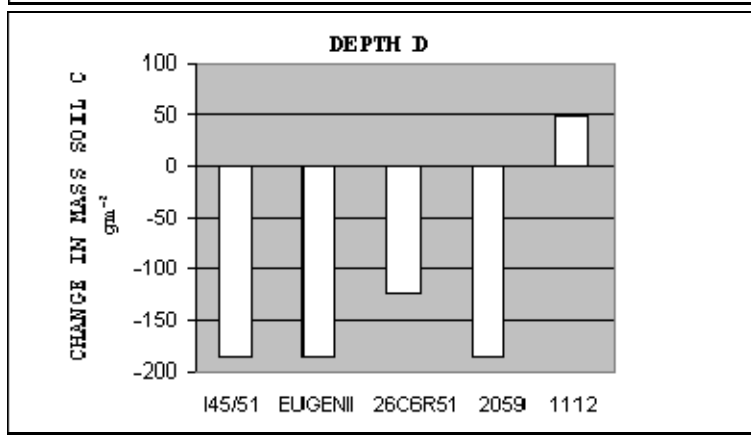
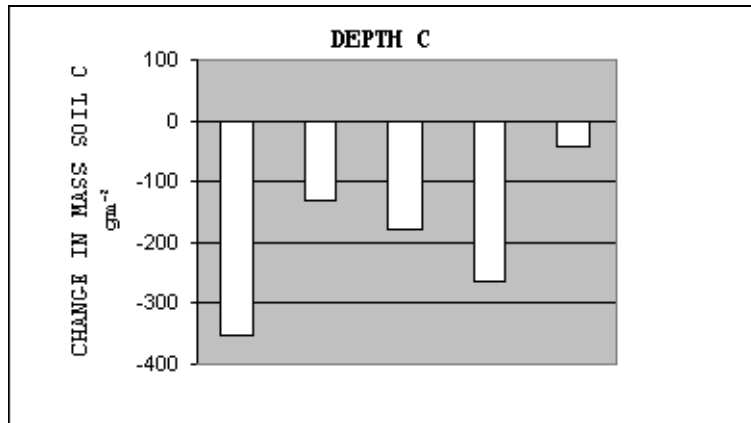
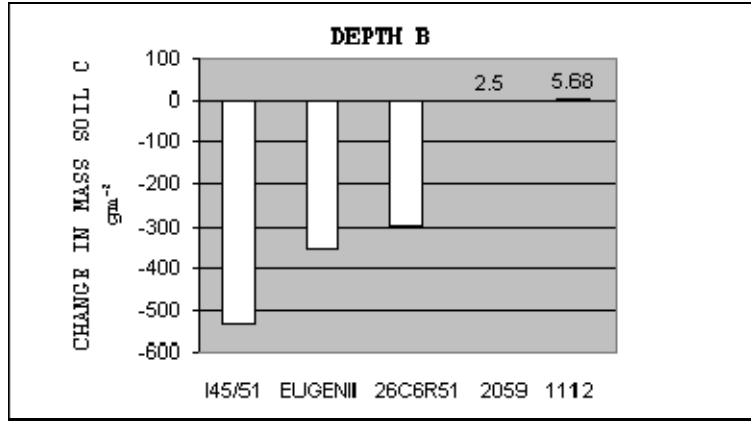
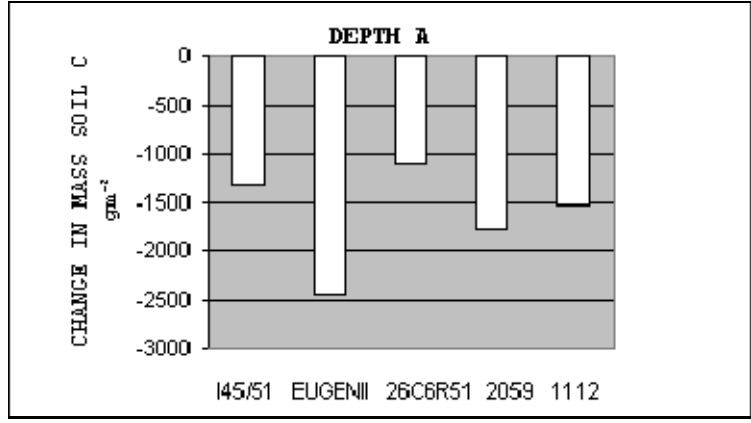


Figure 16 - Total change in soil C on a mass basis between 2000 and 2005 in Plantation 2 for plots containing *Populus deltoides* clones vs. hybrid clones.

TOTAL CHANGE C

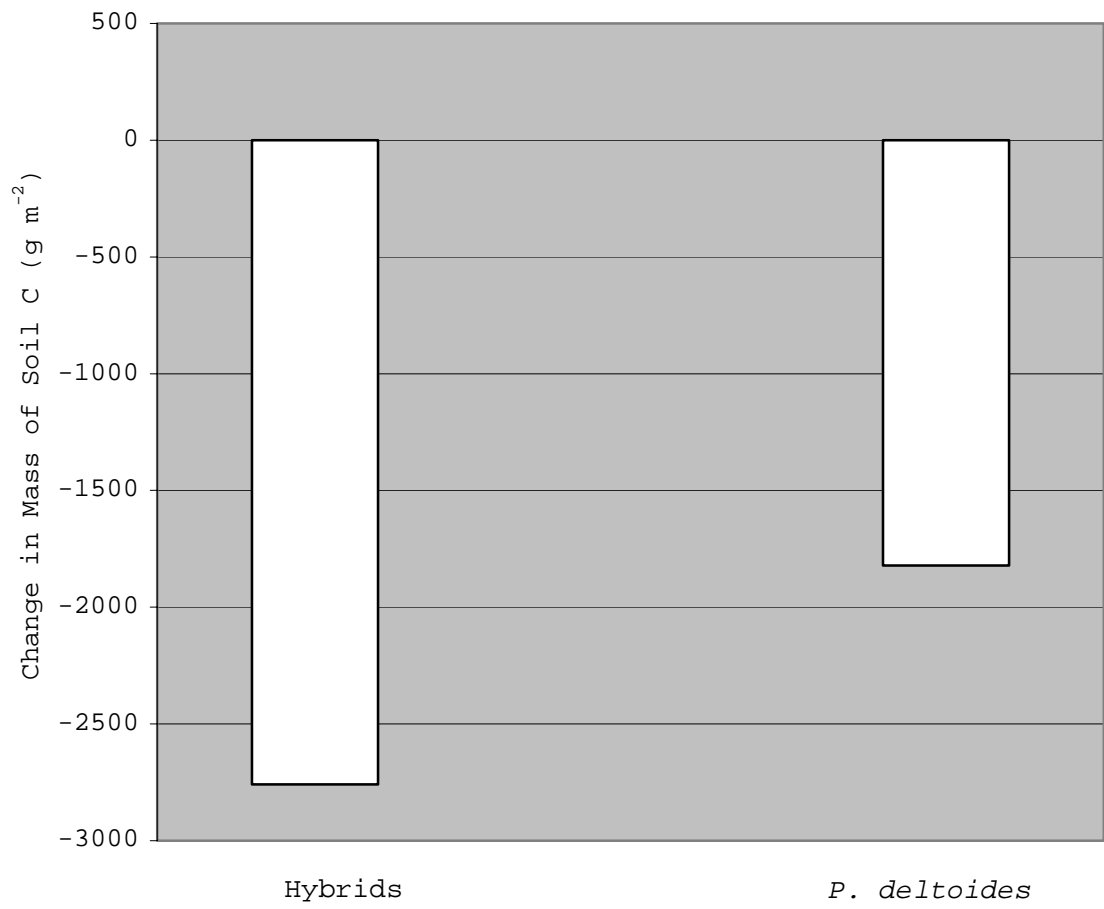


Figure 17 - Soil water content of wet and dry plots of *Populus deltoides* x *P. nigra* clone 'Eugenei' located in Plantation 2. Data collection began on September 7, 2002.

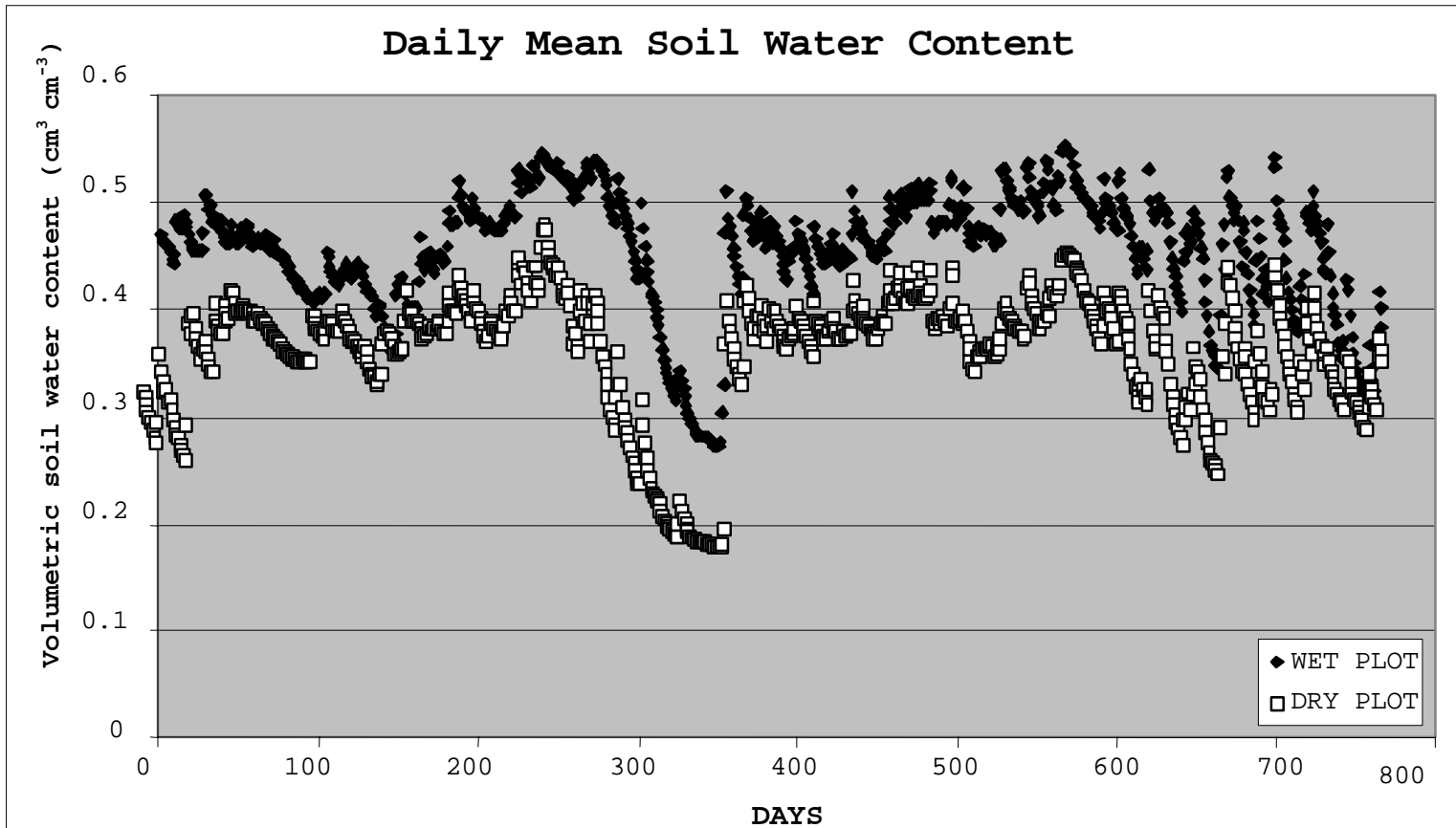
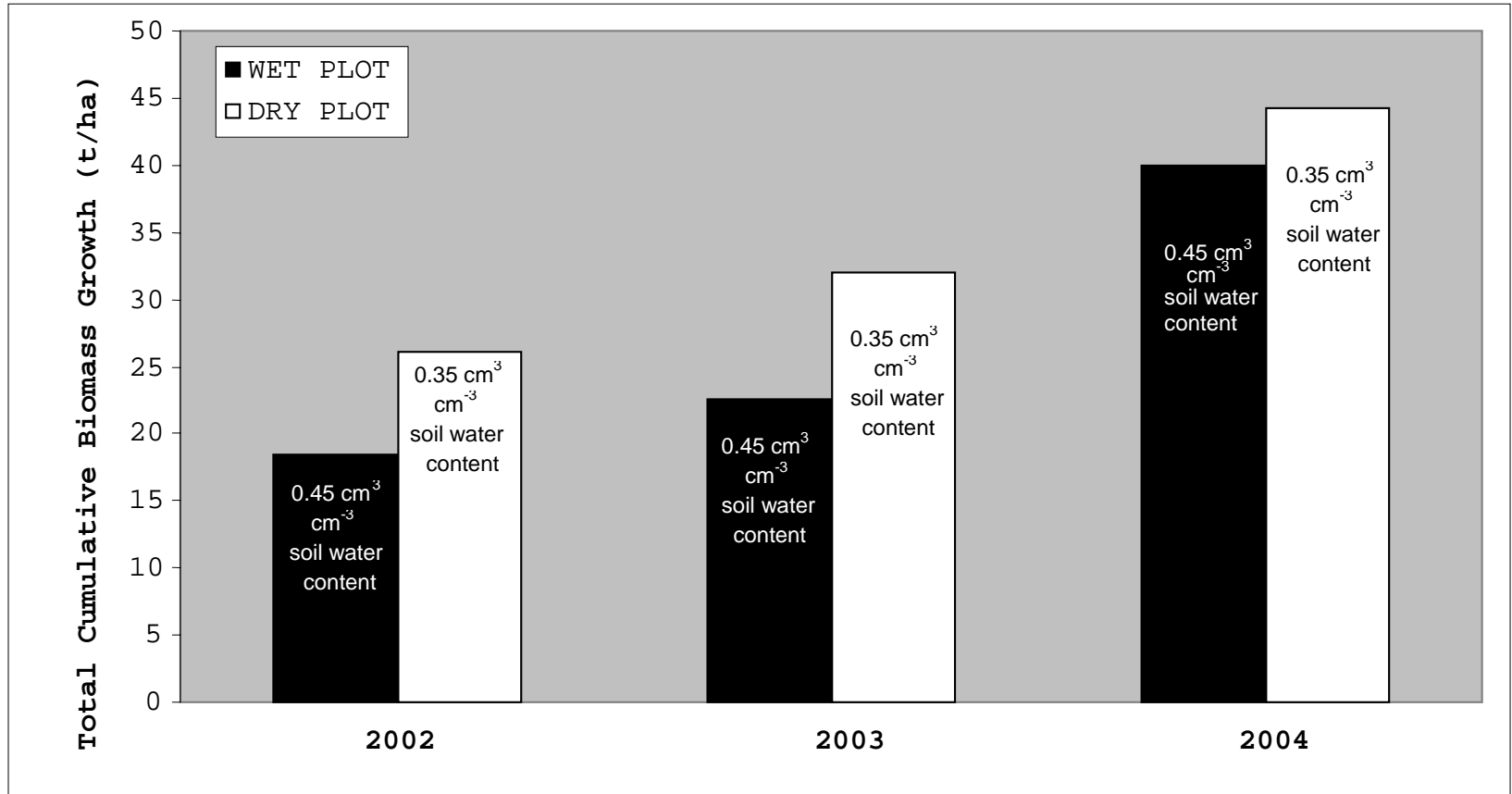


Figure 18 - Biomass accumulation and mean growing season soil moisture for wet and dry plots of *Populus deltoides* x *P. nigra* clone 'Eugenei' located in Plantation 2.



DISCUSSION

Productivity

Early in the rotation of Plantation 1, hybrid clone I45/51 produced the greatest in root, shoot, and total biomass. However, as the rotation progressed, it ultimately produced the least in root production and third in shoot and total biomass. The two local *P. deltoides* clones (1112 and 2059) produced the least root biomass during the first growing season, but produced the most cumulative root biomass by the end of the rotation (2059 followed by 1112). The *P. deltoides* clone 26C6R51 finished behind the two local clones in cumulative root production.

The pattern of shoot production was very similar, with the only change occurring between I45/51 and 26C6R51, where clone 26C6R51 produced the least cumulative shoot biomass. Total cumulative biomass revealed the two Missouri clones as the greatest cumulative biomass producers, with the final order being 2059 (90.65 t ha⁻¹), 1112 (68.22 t ha⁻¹), the hybrid I45/51 (54.87 t ha⁻¹) and finally 26C6R51 (49.18 t ha⁻¹). A similar study conducted by Scarascia-Mugnozza et al., (1997) in Western Washington, USA reported two hybrid clones, 11-11 and 44-136, to produce the greatest cumulative aboveground biomass at 35.2 t ha⁻¹ y⁻¹ and 23.1 t ha⁻¹ y⁻¹ following four growing seasons. The native

phenotype 1-12 finished third at $16.3 \text{ t ha}^{-1} \text{ y}^{-1}$, with the Illinois sourced phenotype Ill-005 producing the least at $14.1 \text{ t}^{-1} \text{ y}^{-1}$. These hybrid vs. species findings contrast with those reported here. However, an important distinction between these studies was the presence of regular irrigation throughout the Scarascia-Mugnozza rotation; no irrigation treatments were applied in the present study after plants were established during the first year of growth. It is possible regular irrigation neutralized any local phenotypic adaptations that otherwise may have been manifested. One similarity between the two studies was the poor biomass production of a phenotype far-removed from its native range.

Another study conducted by Heilman et al. (1985) in western Washington, USA reported clones of black cottonwood exceeding the volume and dry weight of the hybrid 'Robusta' and nearing dry weight production of hybrid 8 (*P. trichocarpa* × *P. deltoides*), which had been previously tested for biomass production along with hybrids 5 and 11 of the same crosses. The final growing season produced means of $12.5 \text{ t ha}^{-1} \text{ y}^{-1}$ for *P. trichocarpa*, $10.9 \text{ t ha}^{-1} \text{ y}^{-1}$ for 'Robusta', and $15.6 \text{ t ha}^{-1} \text{ y}^{-1}$, $27.8 \text{ t ha}^{-1} \text{ y}^{-1}$, and $27.5 \text{ t ha}^{-1} \text{ y}^{-1}$ for the hybrids 8, 5, and 11 respectively. These totals represent above-ground biomass estimates developed

under treatments of irrigation and N fertilization. Again, these findings contrast with those from the present study. Wide genetic variation in natural populations of *Populus* and a lack of tested clones may be partly responsible for these disparities (Heilman et, al., 1985). Ultimately, clone 2059 produced up to 18 t ha⁻¹ y⁻¹ in Plantation 1 without the benefit of regular fertilization or irrigation treatments.

Root:Shoot Ratio

Generally, production between above and below-ground allometry (the functional balance between roots and shoots) were similar among *P. deltoides* clones. Hybrid clones I45/51 and Eugenei generally partitioned the fewest assimilates to roots in Plantation 1 and 2 respectively, while producing the least amount of cumulative biomass in all categories, most notably above-ground harvestable biomass. A balance between root and shoot production has been shown to be beneficial to plants in biomass production and in stress reduction occurring from environmental extremes (Ledig and Perry, 1965; Tschaplinski and Blake, 1989). Cannell and Willet (1976) found four different clones of *Populus trichocarpa* Torr. and Gray to distribute dry matter above and below-ground similarly up to the time of height growth cessation. Imbalances in root and shoot

masses that developed in late summer or autumn were corrected the following spring or early summer. It is possible that the adaptations responsible for correcting seasonal imbalances between roots and shoots are either underdeveloped or lacking in the hybrid clones cultivated in the HARC study.

Statistical analysis of the root:shoot ratios revealed the hybrid I45/51 to progressively partition fewer assimilates to roots throughout the rotation. The trend of the hybrid being overtaken in above-ground biomass production by the *P. deltooides* clones could be the result of an inadequate root system, incapable of maintaining water and nutrient demands to growing stems and foliage, ultimately slowing the clone's growth and reducing its annual yield of harvestable material. The differential pattern in root:shoot ratio between hybrids and *P. deltooides* clones reported in Plantation 1 was observed to a lesser extent in Plantation 2. However, the hybrid clone Eugenei did produce the least root biomass in Plantation 2, while producing just above I45/51 in all dry matter sinks.

Keyes and Grier (1981) reported stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to allocate between roots and shoots according to the level of site productivity. They concluded that on sites designated as

low-productivity or harsh (droughty and nutrient poor), shifts from above-ground to belowground biomass are necessary to avoid or lessen the impacts of stress. Hybrid clones monitored in the HARC study may have lacked adequate capacity to shift dry matter to roots during periods of drought, compared to *P. deltoides* clones, possibly contributing to reduced shoot and total growth as the rotation progressed. Michael et al. (1988) reported more extensive root systems in clones of Tristis poplar (*Populus tristis* Fisch. × *P. balsamifera* L.) than in Eugenei. They concluded that favorable weather and Eugenei's predisposition to rapid and prolonged shoot growth enabled it to outgrow Tristis, but would also leave it susceptible to drought and windthrow. Moreover, the study emphasized the benefit of a clone exhibiting a low root:shoot ratio when grown under conditions conducive to it reaching its growth potential.

The key to root:shoot ratio, when selecting for short rotation plantation culture, is to select clones that direct the smallest possible portion of assimilates to below-ground biomass, without creating inadequate supplies of water and nutrients and diminishing above-ground production. In order to make effective clone selections that fully utilize the growing season, environmental

conditions, site characteristics and clonal nutrient and moisture requirements should be considered.

Light Use Efficiency

Clonal patterns of LAD, per se, could not fully account for variability in biomass production. In fact, low LAD patterns in certain clones (especially 2059) were associated with high productivity (a result that is opposite that which would be expected given the theoretical dependence of biomass production on light harvesting). However, it is worth noting that the decline in LAD in hybrid clone I45/51 in Plantation 1 in the last two years was associated with reduced biomass growth (Table 11c). In a Scottish study concentrating on biomass production of three poplar clones, early canopy development, LUE, and continuation of stem growth into November were paramount in poplar clone production (Milne et al. 1992). Additionally, in the Lake States region of the U.S.A., Nelson et al. (1982) reported longer periods of green leaf retention in exotic *Populus* hybrids over a native aspen hybrid (*P. tremuloides* Michx. × *P. grandidentata* Michx.), allowing the former to maintain relatively high levels of carbon assimilation for an additional 2-6 weeks compared to the aspen hybrid. Any additional autumn leaf photosynthate could be used either for current biomass production or

formation of reserves (Nelson and Isebrands, 1983).

The most important overall factor associated with high biomass production in this study was the apparent efficiency with which a clone could convert incident light into useable energy. This attribute was manifested in greater biomass growth per unit of LAD. Mechanistically, greater efficiency most likely accrued from greater photosynthetic production per unit of leaf area. In support of this assertion, photosynthetic studies of the clones employed here have indicated that *P. deltoides* clones exhibit greater rates of light saturated photosynthesis and higher maximum rates of carboxylation and electron transport than do hybrid clones (unpublished observations). Variation in conversion efficiency in the present study was clearly associated with clone. Clonal origin appeared to outweigh the importance of hybrid vigor, placing importance on the local adaptations of Missouri native clones as more local *Populus deltoides* out-produced exotic hybrids in biomass production at all levels of LAD. These findings differ from the previously mentioned results reported by Nelson et al. (1982) and those of (Ceulemans et al., 1992). In the latter study, a growth comparison study of native *P. trichocarpa*, *P. deltoides* and their hybrids, hybrids were superior to parental species.

The present study provides strong evidence that enhanced productivity can accrue from modest LAD if LUE is high (as in clone 2059). In contrast, reduced LAD and low LUE (as was observed late in the rotation for I45/51) diminishes biomass production potential.

Although hybrids consistently partitioned fewer assimilates to roots across both plantations and had the high peak LAI and LAD, they were the least efficient at converting light energy and in producing biomass. Apart from LUE, local adaptation can help plants avoid stress and injury caused by water and nutrient deficiencies, temperature, and day length (Dickmann, 1977). Furthermore, locally-adapted genotypes may have defense mechanisms in place that protect against pest and diseases that can contribute to stresses imposed on exotic plants. (Drew and Bazazz (1978) concluded that local selective pressures were responsible for variation in height growth following one year of growth, where clones of a Wisconsin ecotype displayed adaptive responses for enhanced stem growth and an Illinois clone did not, although growing indigenously only a short distance from the study site. However, following five years of growth the more local Illinois clone attained the greatest height growth. These results are similar to those reported in the present study, where

within the top two producing clones, both of Missouri origin, the most local clone (2059) produced at the highest level. Here, clone 2059 and 1112 were separated by only 2° in both longitude and latitude.

Changes in Soil Carbon

Plantation 1 had a slight decrease in total soil C as the trees matured over the five-year rotation. Soil C decreased slightly in the first two 12.5 cm sample layers and increased slightly in the deepest two sample layers. In both cases, the presence of an extended, deep penetrating, and intertwining tree root system could be the cause of the estimated changes. Reduced input of C by *Populus* into the soil compared to grass may have impacted soil C levels in the first 25 cm. Greater C release through decomposition during dry periods may have also played a role in the reduction. In the lower 25 cm of sampling depth fine root turnover of *Populus* may be partially responsible for increases of soil C.

Plantation 2 exhibited a statistically significant decrease in total soil C in all sample layers except at 12.5-25 cm depth. One reason for the greater losses in soil C in this plantation may be the generally poorer biomass production of hybrids in Plantation 2, leading to less organic matter input to the soil from leaf and branch

litter and reductions in root production, compromising fine root turnover. Root:shoot ratio trends exhibited in Plantation 2 reflect losses in soil C, where the ratio decreased much more gradual than in Plantation 1 and was based on less amounts of biomass above and below-ground. Also, Plantation 2 was at a slightly lower slope position and the data suggested it had higher initial soil organic matter content, especially in the surface soil (cf. Figs. 10 and 14). The greater availability of C substrate in this plantation, combined with the increased aeration of the soil pore space by intense transpiration of the poplar stand may have promoted greater soil C loss.

The losses of soil C observed here must also be considered in the context of plant cover before plantation establishment. In this study, the pre-existing vegetation was forage grass, which because of its large annual turnover of plant dry matter and lack of cultivation, might have elevated soil C above that which would be encountered in plantations established after row-cropping. Soil beneath row-cropped sites often has already been "purged" of much of the surface soil C because of cropping practices (Parton et al., 2005). Hence, any losses in soil C found in the present study might be greater than those expected in growing poplars on formerly row-cropped land and it has

been hypothesized that the greatest potential for net soil C storage in short-rotation culture will be on sites previously under traditional row crop management (Grogan and Matthews, 2002). Considering the historical fence line to streamside row cropping practices of many Missouri producers, short rotation poplar culture may offer the potential for increased soil C storage. Further, despite the soil C losses reported in Plantation 2, it was estimated clone 2059 was capable of producing a net gain in total stored C (above and below ground) of at least 15 t ha⁻¹ over the rotation. Results from Plantation 1 suggest a stored C net gain capacity of at least 32.5 t ha⁻¹ for clone 2059.

Soil Moisture and Plant Productivity

Following the second growing season of Plantation 2 it became apparent that plots containing the same clone were producing at different levels according to their location within the plantation. Elevation of the plots located in the northern section of the plantation was lower than that of southern sections causing water ponding in the latter following high water or heavy precipitation. As a result, these plots became and remained wetter during the growing season. Trees growing in the wetter northerly plots produced at lower levels than those of the same clone

growing in the dryer southern section. Therefore, *Populus* plantation production could be susceptible to soil moisture thresholds which could be imposed via micro-topographic variation within a plantation.

Anderson and Pezeshki (2000) reported decreases in leaf area and height growth in baldcypress (*Taxodium distichum*), Nuttall oak (*Quercus nuttallii* Palmer) and swamp chestnut oak (*Quercus michauxii* Nutt) in response to soil flooding, reducing total biomass production. Flooding treatments lead to significant reductions in root:shoot ratio as well, which can have negative effects on water and nutrient uptake capacity. Interestingly, the *Populus deltoides* x *P. nigra* 'Eugenei' clone evaluated in the HARC study also displayed a low root:shoot ratio and clear differentiation between dry and wet plots in height growth. Hosner and Boyce (1962) determined *Populus deltoides* seedlings subjected to 60 days of completely saturated soils developed extensive adventitious root systems initially, but both primary and secondary roots eventually died. This result could partially explain the Eugenei clone's lower root:shoot ratio and low overall production in Plantation 2.

Throughout the three-year case study the seasonal mean soil water content remained consistent in the dry and wet

plots at 35 and 45 percent, respectively. A disparity in biomass production also existed throughout the rotation. However, this difference had been reduced by over half by the final year of observation. Possible explanations for these reductions include adaptation of tree roots to high soil moisture, such as the development of supplementary adventitious roots, and the pattern in which the average moisture occurred over the growing season. Temporary flooding with moving water has been shown to increase growth of certain flood tolerant species, such as *Nyssa aquatica* (Kozlowski, 1985). Iremonger and Kelly reported seedlings of *Alnus glutinosa* appeared to undergo changes in the first year of waterlogging that facilitated growth in subsequent years of hypoxic conditions.

SUMMARY AND CONCLUSIONS

1. *Populus deltoides* clones 2059 and 1112, both of Missouri origin, showed the greatest capacity for biomass production of all clones tested. Hybrid clones had a tendency to produce at greater levels early in the rotation but were unable to sustain biomass production rates compared to *P. deltoides* clones. Comparisons of biomass production between hybrid and local clones in the present study with other studies identified greater advantage of local clones than generally reported.
2. Hybrid clones I45/51 and Eugenei exhibited the lowest root:shoot ratio in Plantations 1 and 2, respectively.
3. Light Use Efficiency was greatest in 2059 and 1112. *Populus deltoides* clones converted solar energy to biomass more efficiently than hybrid clones. The order of light use efficiency corresponded with biomass production.
4. Neither plantation gained large amounts of soil C during the rotation. Total soil C losses were statistically significant, however, in Plantation 2. These losses may have been partially attributable to successively poor biomass production with time among hybrid clones. The true benefit of C storage came in the production of biomass, resulting in substantial total C gains at both sites.

5. A soil moisture threshold that reduced growth seemed probable in plots of Eugenei in Plantation 2. Micro-topographic changes characterized by poor soil drainage were thought to be primarily responsible for poorer growth in lower-lying areas. A reduction in the disparity between plot biomass production as the rotation progressed may have indicated increasing acclimation to flood stress in exposed trees.

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