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Autumnal Migration of Nitrogen and Carbohydrates in the Apple Tree

With Special Reference to Leaves

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A. E. Murneek and J. C. Logan*

Abstract.—Autumnal migration of nitrogen and carbohydrates from apple leaves to structural parts of the tree was studied for two years with three varieties. Analyses were made of green and yellowed (dropped) leaves, spurs, and 1- to 3-year-old twigs for water soluble, water insoluble and total nitrogen, total sugars, starch and hemicellulose. Chemical changes in concentration of these substances were correlated with end-season metabolic activities. Approximately 22 to 40% of N was reabsorbed from apple leaves before they abscissed. This nitrogen moved into the spurs and smaller twigs and thence to older wood. The nature and seasonal trend in autumnal migration of carbohydrates from the foliage to the permanent structure of the tree was not established. It is obscured by effects produced by temperature and probably other environmental factors. The possible bearing of these results on horticultural practice is briefly suggested.

In a study of the nutrition of fruit trees consideration must be given to the metabolism of leaves. Leaf tissues have a relatively high cell solute and protoplasmic content and hence, in aggregate, contain surprisingly large concentrations of soil nutrients. They are especially rich in nitrogen.

Considering this relative importance and significance of the foliage in plant nutrition, it is rather strange that, while various woody or structural parts of the apple tree have been the objects of chemical studies, the leaves have received comparatively little attention. The present investigation was undertaken with the purpose of adding to this particular part of our knowledge of the metabolism of the apple tree. It was the outgrowth of the senior author's previous interest in another phase of this subject[19]†. The work was confined to the end-season phenomena of removal and translocation of substances from the leaves preparatory to their abscission.

The autumnal migration of nitrogen and carbohydrates from the leaves to the woody structure has a direct bearing on some practical aspects of tree nutrition. If senescence or yellowing of the foliage proceeds normally then relatively large amounts of nitrogen and carbyhydrate compounds are removed from the leaves and there will be an ample supply of reserve food materials for growth in the following spring. But, on the other hand, if the leaves remain green until they are killed by heavy frosts and drop before there is a more or less complete transfer of these vital organic substances, then the reserves stored in the wood

*The 1927 data presented in this bulletin were embodied in a thesis by J. C. Logan in partial fulfilment of the requirements for the degree of Master of Arts at the University of Missouri, 1928.

†Numerical reference is made to the Bibliography, pages 23 and 24.

will be reduced and growth or fruit setting will be curtailed. Similarly, the premature destruction of the foliage by insects, diseases and other agencies will have a direct bearing on the subsequent behavior of fruit trees. Any method of overcoming such disturbances, of course, is subject to a more definite understanding of the normal autumnal metabolism of the leaves and adjoining structural organs.

Another interesting feature in this consideration is the amounts of nutrients, especially nitrogen, that are returned to the soil by way of the dropped leaves. This littering of the ground with organic debris of a relatively high nitrogen content is tantamount to a natural "fall fertilization". Upon decay a large proportion of the substances present in the leaves are transformed into inorganic compounds and are reabsorbed by the roots, thus contributing to the maintenance of an approximate equilibrium in the tree between the intake and outgo of soil nutrients. The fertilizer value of the dead foliage depends, of course, upon the composition of the leaves at the time of exfoliation, which in turn is subject to environmental factors, primarily the weather.

REVIEW OF LITERATURE

The most important biochemical studies on the autumnal changes in leaves of trees have been conducted by European investigators. Practically all of these investigations deal with forest trees. More recently, however, interesting contributions on the subject have been made in this country. We should feel indebted to Combes, whose excellent review[4-8] of the older literature is of great value and helps one to obtain a desirable perspective on this question. The present additional review perforce is limited primarily to nitrogen and carbohydrate changes and distribution in annually deciduous leaves toward the end of the growing season.

Nitrogen Changes in Leaves.—The nitrogen content of the leaves of most trees begins to decrease in mid-summer, but the greatest reduction undoubtedly occurs in the later part of autumn or about 2 to 3 weeks before the drop of the foliage is completed. The total quantity of nitrogen, and other soil ingredients, that may be reabsorbed from the leaves into the branches, depends very considerably upon environmental factors. Ramann[21] gives the following relative amounts of N, P_2O_5 and K_2O in percentages of the total quantity originally present, as having passed from the leaves into the stem of certain plants.

	N	P_2O_5	K_2O	
Beech	35.0%	26.5%	Marked increase	Fading leaves
Oak	25.6	31.9	No change	Fading leaves
Ironwood	25.6	33.9	31.5%	Fading leaves
Hazel	26.8	----	11.9	Fading leaves
Oak	50.6	20.2	44.3	Dead leaves
Birch	45.4	41.9	56.8	Dead leaves
Maple	71.1	18.4	26.6	Dead leaves
Locust	49.4	35. :	5.2	Dead leaves

From these figures it is apparent that there is a marked and definite removal of nitrogen from leaves. To be sure, phosphorus and potassium are also reabsorbed, but evidently this is subject to considerable fluctuation and uncertainty. (See also Schultze and Schutz[25].)

By far the largest quantity of nitrogen in this organ seems to be in the form of protein. Reissmüller[22] analyzed leaves of the beech during different times of the year and found that the protein content of 1000 leaves increased from 13.09 grams in May to 28.07 grams in July and then decreased to 8.76 grams in November. This is in agreement with Dulk's data[10] which show the protein content of the same number of leaves as follows: June—8.77 grams, August—9.8 grams, November—3.11 grams.

That nitrogen decreases rapidly during senescence of leaves is quite clear also from Molliard's data[18]. He collected and analyzed leaves of the chestnut during different phases of yellowing. The nitrogen percentages were: September 13, 2.26%; October 10, 2.22%; November 1 (greenish-yellow leaves), 1.21%; and November 2 (yellow leaves), 0.94%.

From his more recent studies of the transfer of nitrogen from leaves, Rippel[24] concludes that the coefficient of reabsorption for various plants is about 69%. He believes that the nitrogen compounds translocated from the leaves are mostly proteins, especially those forming the chloroplasts. Poplar leaves, collected on June 29, August 22, September 23, and November 11 contained the following percentages of nitrogen: 2.48, 2.19, 1.68 and 0.714. The highest nitrogen content was found in June and the lowest at the time of chlorophyll degeneration. The return of nitrogen to the tree seems to begin long before yellowing starts, possibly in early summer. With nitrogen deficiency, leaves begin to yellow early in the season and the oldest leaves first. The younger leaves may absorb nitrogen from the weaker, older ones.

Schultze and Schutz[25] have determined the nitrogen content of maple leaves. Using dry weight as a basis, they obtained 27% protein in May, but only 13% at the time of abscission. The concentration of various soluble nitrogen fractions throughout the period of investigation (May to September) was nearly the same and very fluctuating. These authors are decidedly skeptical concerning the migration of nitrogen from the leaves to the woody parts of the plant. They believe that in autumn no important evacuation of nitrogen (or any other substance) takes place, but instead there is a delay in their formation, the autumnal loss of N in leaves being due to respiration. This view has been held by several other investigators[20, 27]. Wehmer[30] has gone even a step farther in this negation by maintaining that nitrogen is not translocated into the woody tissues but is carried away by precipitation. This has not been demonstrated, however, in a way that is at all convincing. In this respect one must share the earlier opinions expressed by Bauer[1], Leclerc Du Sablon[14] and Combes[4-8] that the problem of what becomes of nitrogen compounds at the time of yellowing can only be solved by making an analysis of the branches and preferably the whole tree.

In general most workers seem to agree that there is less nitrogen in yellowed leaves than in green ones, but that the actual migration of N from senescent leaves to the branches has not been demonstrated. Those who have compared the nitrogen content of green and yellow leaves did not analyze twigs, stems and roots. On the other hand, studies of the nitrogen composition of the structural parts of the plant have not been associated with those of simultaneously collected leaves.

Probably the most exhaustive studies of this question have been undertaken by Combes[4-8], who, to begin with, determined nitrogen in leaves, stems and roots of young trees at set intervals during yellowing of leaves. The nitrogen content of beech, chestnut and horse chestnut leaves, yellowing normally on the trees, was compared with behavior of leaves on short branches (5-10 cm.), detached when the leaves were still green and kept in water. Leaves undergoing senescence on the trees lost much of their nitrogen; those yellowing off the trees lost very little, even though attached to a piece of the branch toward which nitrogen would normally move. Horse chestnut leaves contained before yellowing 67.23 mgm. of nitrogen per leaf, after yellowing on the tree, 23.36 mgm., and after yellowing off the tree, 53.03 mgm. Under identical conditions the N content of chestnut leaves was 11.86 mgm., 5.74 mgm., and 12.18 mgm. respectively.

If the nitrogen is calculated as percentage of dry weight, then beech leaves lost 40% of their N content during yellowing on the tree, horse chestnut leaves 65%, and chestnut leaves 50%.

Combes states that a part of the nitrogen which passes out of the leaves accumulates in the branches near the point where the leaves are attached. But since the N content of the leaves and branches eventually show a decrease, it is evident that the greater part of the nitrogen migrates into the stem and roots. Atmospheric precipitation may remove a certain fraction of N from the dying leaves.

In another experiment Combes determined the nitrogen content of leaves, stems and roots of two- and three-year-old oak and beech trees during normal autumnal yellowing. The two-year-old oak trees showed the following changes in nitrogen distribution: green leaves, 2.30%, stems, 0.78%, roots, .82%, brown leaves, 1.09%, stems, 1.04%, roots, 1.02%. The N content of the entire plant exhibited little variation during these three periods, being of the order of 1.10, 1.06 and 1.04%.

The author concludes that these investigations confirm completely the fact of migration of nitrogen from the leaves to the stems and thence to the roots. This autumnal transfer of N usually occurs during a period of some two months. The suggestion is ventured that under certain conditions the roots may excrete N substances into the soil.

Preliminary work on some autumnal changes in nitrogen content of leaves of fruit trees, which is the subject of our attention, has been done by several investigators. Richter[23] analyzed samples of 100 leaves of the apple, pear, cherry and plum. The greatest decrease in N content occurred in September, indicating a rapid depletion in the leaves preparatory to their abscission. A decided relation between weather and translocation seems to exist. If warm weather continues well into the fall, much of the mineral matter together with N, will be removed, but if an early drop in temperature occurs, the leaves are likely to drop before normal translocation has taken place. Thomas[18] thinks that the nitrogen content of leaves of the apple begins to decline as soon as active growth ceases. The most rapid decrease occurs during yellowing and continues until defoliation is complete. His chemical data show a decided increase in the percentage of N of one- and two-year-old wood from September to November, followed by a decline after defoliation. The belief is expressed that there can be no question as to the phenomenon of autumnal migration of nitrogen from the leaves to the branches in the apple: Storage appears to be mainly in the one- and two-year-old wood. Thomas did not analyze the older wood of his trees.

The results secured by Lincoln[15] and Lincoln and Bennett[16] indicate that the loss of nitrogen from mature pear leaves is actual and is not due to leaching. The amount lost from basal leaves was 38%, 37% and 33% when related to area, dry weight and fresh weight respectively. The terminal leaves lost but slightly less. This close agreement between the results calculated to area and to dry weight show that the losses concerned were actual and not due to variations in other solids. The water soluble fraction of nitrogen increased toward the end of the exfoliation period. Since in one year approximately 35 to 38% of N left the leaves and in another almost 50.%, the suggestion is advanced by the authors that the amount of N which returns to the tree from the leaves is governed by the nitrogen content of the tree. The higher the N content of the plant as a whole the less of this constituent will be absorbed from the leaves prior to their defoliation.

Carbohydrate Changes in Leaves.—In the leaves, of course, we have the source of practically the total supply of carbohydrates for woody plants. Their manufacture and translocation is extremely rapid and subject to wide diurnal and periodic fluctuations. Hence the study of carbohydrate changes in leaves is beset with considerable difficulty and there is very little exact knowledge on the typical autumnal alteration of these substances. Much of our information on this particular phase of the subject has come indirectly from studies of the carbohydrate concentration in spurs, twigs, and other structural parts of the apple tree.

Regarding carbohydrate metabolism, Durant[11] distinguishes two stages in the life of the leaf: first, "a period of carbohydrate synthesis and polymerization extending from the time the leaves begin to function until the end of summer, during which period carbohydrate assimilation is active and carbohydrates of all types increase in amount; second, a period of hydrolysis and simplification, beginning about the time when the leaves turn yellow. This is marked by a decrease in the amount of compound carbohydrates and a further accumulation of simple sugars. The development of the abscission layer at the base of the leaves of deciduous plants is correlated with this accumulation of simple sugars in the leaf blade, so that their removal to the branches is soon stopped. The sugars increase until they are respired, fermented or washed out by rain." A maximum of reducing sugars was found just before yellowing after which they rapidly disappeared. Change to soluble forms of carbohydrates is favored by cold weather. The greater portion, but not all, of the carbohydrates that disappear at the close of the vegetative period go to the trunk.

That considerable quantities of starch may remain in the leaves at the time of abscission has been demonstrated by Harter[12], who found 6 to 14% of starch in dropped leaves of *Liquidambar*, *Ginkgo* and other trees. He has expressed the opinion that leaves of lignified plants frequently are unable to remove all of the starch from their tissues due to inactivation of diastase caused by a rapid lowering of temperature or for some other reason. These results are more or less in agreement with those presented a year earlier by Combes[3]. More recently Combes and Kohler[9] have shown that, in the case of the beech tree (*Fagus silvatica*), of the total soluble and readily hydrolyzable carbohydrates in the leaves before yellowing, approximately 46% were still present at the time the leaves were yellow, 34% had been lost, probably by respiration and leaching, and 20% evidently had been evacuated and moved into the branches.

Investigations dealing with seasonal changes in carbohydrate concentration in the woody parts of the apple furnish further evidence on the movement of carbohydrates during senescence of leaves. The chemical data by Butler, Smith and Curry[2] on distribution of storage reserves in various parts of 7-year-old apple trees indicate that between the period when active growth ceased and leaf fall there was a noticeable increase in concentration of reducing sugars and starch in 2-, 3- and 4-year-old branches. An end-season increase in concentration of starch in apple branches of various ages has been observed microchemically also by Swarbrick[26] and a rapid increase in total carbohydrates in 2- to 3-year-old apple twigs was found to occur in October by Traub[29]. Determinations of the seasonal changes in chemical composition of apple spurs by Hooker[13] likewise show that the greatest accumulation of starch and other polysaccharides occurs in September and of sugars in November and thereafter. Evidently in the beginning of winter there is a hydrolysis and movement of carbohydrates into the older regions of the tree. That temperature may play an important part in the translocation of carbohydrates is suggested by Mitra[17]. He likewise found that starch and the total amount of carbohydrates in apple spurs increased markedly during August and reached a maximum in September. As the seasonal temperature decreased, there was a parallel decrease in the starch content of spurs. Glucose and maltose* seem to be the principal sugars of translocation in apple wood. In general, then, there appears to be some circumstancial evidence that carbohydrates are removed from leaves of the apple preparatory to their normal dropping but there is lack of information on the extent of and quantitative relationships in this phenomenon.

MATERIAL AND METHODS

Collection of Material.—Material for this investigation was secured in 1927 and 1928 from trees growing in one of the Missouri Experiment Station orchards. Five trees of uniform size of each of the varieties, Grimes, Delicious and Stayman, were selected for this purpose. The last variety, however, had to be substituted by an equal number o Jonathan trees in the second year because of somewhat abnorma behavior in growth and fruiting of the Staymans. All of these trees received an application of 4 pounds of ammonium sulphate per tree each spring. They were 17 and 18 years old in the respective years, healthy and productive. The soil moisture conditions were quite uniform. All of the Stayman and Delicious trees were in a more vigorous state than the Grimes at the time the material was collected. The leaves of the first two varieties were larger and remained green later and the current year's growth was longer. All the trees had a light crop of fruit in 1927 and therefore made fairly vigorous shoot growth in that year. The fruit crop in 1928 was heavy and vegetative development correspondingly less. In this year the orchard was infested to some extent by the white fly (*Empoasca mali*). Although all injured leaves were scrupulously avoided some of them may have gotten into the various collections.

*It has been proven since by Dr. E. M. Harvey that maltose is not present in apple wood but instead the glucoside phloridzin. American Journal of Botany 10:288-293, 1923 and Oregon Agr. Exp. Sta. Bul. 215, 1925.

The material for chemical analysis consisted of leaves in various stages of yellowing, of dropped leaves, and of non-bearing spurs and 1-, 2-, and 3-year-old branches. The persisting leaves were taken from both spurs and branches and analyzed separately. In order to secure uniform samples of dropped leaves, five representative branches on each tree were covered with mosquito netting bags, 30 by 60 inches, to catch all leaves that fell. Twenty-five spurs were collected from 3- and 4-year wood of each of the chosen trees, which formed a composite lot for each variety. At the same time five shoots to include 1- to 3-year-old wood were cut from each tree and the wood of various ages separated at once for preservation and subsequent chemical analysis. These shoots were selected for uniformity and an approximate length of 20 inches. At the time of the last collections it was necessary to take twigs of a more variable length because of scarcity of material. All collections were made between 7 and 10 a. m. and preserved with dispatch.

The dates of collecting samples in the respective years were as follows: (*1927*) Attached leaves, October 7 and 26, November 4 and 14; abscissed leaves, October 26, November 4, and 14; spurs and twigs, October 7 and 26, November 4 and 14, December 7. (*1928*) Attached leaves, October 12 and 27, November 10; abscissed leaves, October 26, November 10 and 26; spurs and twigs, October 12 and 27, November 10 and 26, December 28. It will be noted that in 1928 the last collection of wood material was considerably later than in the previous year.

Weather is an important factor, determining undoubtedly in a large measure the time and rate of autumnal reabsorption of organic substances from the leaves into the structural parts of the apple tree. The fall of 1927 was very mild with a precipitation above normal both in October and November. The first month was rather sunny, the second more or less cloudy. Heavy frosts occurred on November 2 and 3, a "killing freeze" (22° F.) on November 6. Apple leaves remained green and seemed to function normally much later than usual. Very little yellowing of foliage occurred till the November freezes made the leaves turn brown rather rapidly. The fall of 1928 was characterized by a mild October with normal amount of rain and sunshine. November, too, was warm but quite cloudy. The first frost occurred on November 4 and two real freezes on November 25 (19° F.) and November 26 (21° F.). Thus, in general, the falls of 1927 and 1928, though by no means alike, were somewhat similar in respect to weather conditions.

Preservation of Samples and Analysis.—After separating into the requisite parts, composite samples of each type of material were cut into small pieces and dried at once in an oven with forced ventilation at 75° C. Drying of leaves was usually complete in 1½ to 2 hours, of woody tissues in 5 to 6 hours*. When fully dry the material was ground in a Wiley mill till the tissues passed through a 60-mesh sieve. The powder was allowed to take up hygroscopic moisture and then preserved for chemical analysis. All chemical data are based on this "air dry" ground material.

The nitrogen analyses were made in the laboratories of the Department of Agricultural Chemistry. The official Kjeldahl-Gunning-Arnold method was used. Carbohydrates were analyzed in our laboratory and include determinatons of total sugars, starch and hemicellulose. The methods employed in carbohydrate analysis need not be given here. They have been described fully in another publication of the Department of Horticulture of the Missouri Agricultural Experiment Station.**

PRESENTATION OF RESULTS

The chemical data presented herewith, in tabular and graphic forms, are grouped so as to show most conveniently and clearly the end-season trend in chemical changes of leaves and adjoining organs. While the actual concentration of the determined forms of nitrogen and carbohydrates is given separately for each variety and date of sampling, the average record of the three varieties is emphasized. It seems to express more typically the movement of these organic substances during the period under consideration.

Autumnal Migration of Nitrogen.—The percentages of total nitrogen in leaves from two positions, in spurs and 1-, 2- and 3-year-old wood are given for the two years in Tables 1 and 2 and presented graphically

TABLE 1.—TOTAL NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	1.65	.90	.75	.63	.48
Delicious	1.69	1.04	.90	.66	.64
Stayman	1.76	1.02	.88	.66	.64
Average	1.70	.99	.84	.65	.59
October 26					
Grimes	1.53	.98	.77	.60	.50
Delicious	1.57	1.14	.91	.73	.61
Stayman	1.61	1.13	.83	.60	.49
Average	1.57	1.08	.84	.64	.53
November 14					
Grimes	1.45	1.01	.86	.63	.55
Delicious	1.46	1.17	.91	.66	.56
Stayman	1.62	1.21	.95	.74	.60
Average	1.51	1.13	.91	.68	.57
December 7					
Grimes	----	1.12	.83	.55	.52
Delicious	----	1.34	.86	.69	.55
Stayman	----	1.25	.92	.68	.54
Average	----	1.24	.87	.64	.54

*An efficient oven for drying plant material. Proc. Amer. Soc. Hort. Sci. 1928:338-341.
**Mo. Agr. Exp. Sta. Res. Bul. 90.

TABLE 2.—TOTAL NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 12						
Jonathan	1.616	1.467	.923	.885	.590	.496
Grimes	1.640	1.640	-----	.774	.630	.535
Delicious	1.691	1.716	1.008	.815	.572	.491
Average	1.649	1.607	.965	.824	.597	.507
October 27						
Jonathan	1.430	1.447	.937	.935	.657	.504
Grimes	1.536	1.495	.942	.817	.606	.460
Delicious	1.590	1.548	.971	.766	.579	.493
Average	1.518	1.496	.950	.839	.614	.485
November 10						
Jonathan	1.275	1.220	1.038	.925	.659	.514
Grimes	1.264	1.174	1.058	.870	.672	.543
Delicious	1.152	1.036	1.035	.963	.671	.547
Average	1.230	1.143	1.043	.919	.667	.534
November 26						
Jonathan	-----	-----	1.093	.962	.670	.577
Grimes	-----	-----	1.074	.950	.703	.551
Delicious	-----	-----	1.116	.967	.704	.589
Average	-----	-----	1.094	.959	.692	.572
December 28						
Jonathan	-----	----	1.123	1.046	.710	.552
Grimes	-----	-----	1.125	.940	.676	.554
Delicious	-----	-----	1.130	.974	.744	.597
Average	-----	-----	1.129	.986	.706	.567

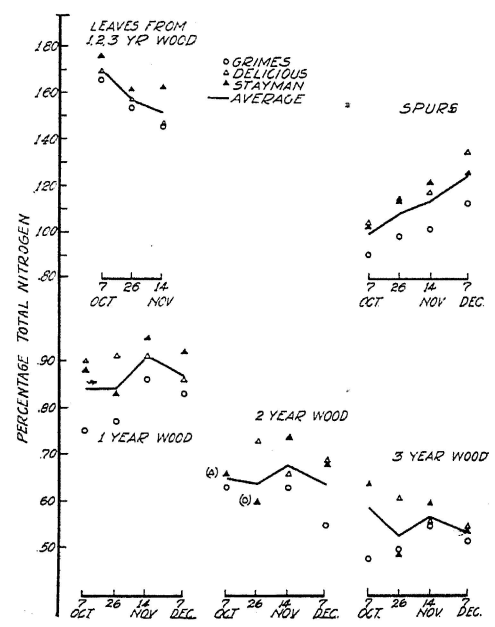

Fig. 1.—Total nitrogen in leaves, spurs and 1- to 3-year-old branches, 1927.

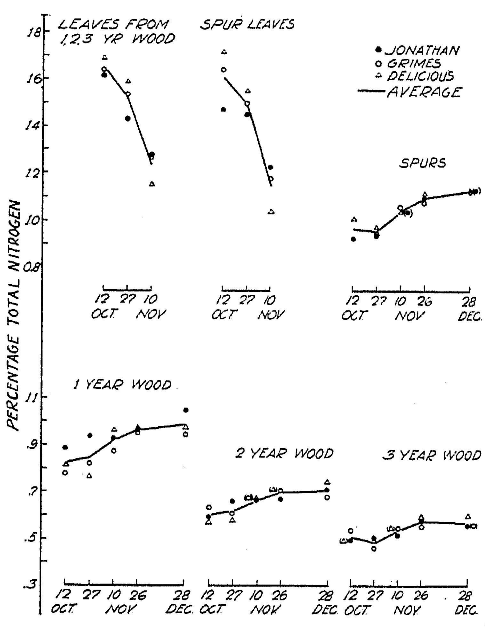

Fig. 2.—Total nitrogen in leaves, spurs and 1- to 3-year-old branches, 1928.

in Figures 1 and 2. Whether on twigs or spurs, the leaves show a rapid and equal decrease in total N, especially preceeding their normal dropping (November). This decline seems to be almost entirely due to a decrease in the water insoluble fraction, since most of the nitrogen in the leaf is in a combined or protein form. The curves for total and water insoluble nitrogen in leaves are quite similar for both years and all varieties (Figures 1-4). Temperature undoubtedly is an important factor tending to accelerate the evacuation of nitrogen from this temporary

TABLE 3.—WATER INSOLUBLE NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	1.51	.78	.60	.43	.34
Delicious	1.54	.87	.68	.50	.48
Stayman	1.63	.96	.64	.52	.49
Average	1.56	.87	.64	.48	.44
October 26					
Grimes	1.34	.85	.65	.44	.35
Delicious	1.41	.92	.76	.55	.41
Stayman	1.57	.92	.66	.57	.34
Average	1.44	.89	.69	.52	.36
November 14					
Grimes	1.31	.84	.73	.47	.44
Delicious	1.31	.97	.76	.62	.49
Stayman	1.49	.98	.80	.57	.53
Average	1.37	.93	.76	.55	.49
December 7					
Grimes	----	.95	.76	.48	.43
Delicious	----	1.13	.80	.62	.49
Stayman	----	1.18	.78	.51	.47
Average	----	1.09	.78	.54	.46

TABLE 4.—WATER INSOLUBLE NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 12						
Jonathan	1.450	1.381	.843	.669	.482	.435
Grimes	1.530	1.534	.762	.581	.462	.388
Delicious	1.571	1.600	.809	.614	.472	.388
Average	1.517	1.505	.805	.621	.472	.403
October 27						
Jonathan	1.350	1.360	.857	.794	.556	.422
Grimes	1.432	1.383	.814	.679	.457	.378
Delicious	1.532	1.436	.798	.689	.502	.381
Average	1.435	1.359	.823	.721	.505	.393
November 10						
Jonathan	1.136	1.079	.910	.808	.556	.454
Grimes	1.046	.985	.896	.729	.517	.444
Delicious	.958	.885	.942	.820	.535	.467
Average	1.046	.983	.916	.786	.536	.455
November 26						
Jonathan	-----	-----	.952	.828	.605	.443
Grimes	-----	-----	.922	.722	.523	.432
Delicious	-----	-----	.928	.803	.540	.453
Average	-----	-----	.934	.786	.556	.442
December 28						
Jonathan	-----	-----	1.026	.935	.641	.440
Grimes	-----	-----	.938	.787	.528	.416
Delicious	-----	-----	.990	.849	.638	.488
Average	-----	-----	.985	.857	.602	.448

organ. A cool atmosphere will hasten the process, a severe freeze will stop it entirely by killing the protoplasm and hastening the abscission of leaves. Removal of nitrogen from leaves of these apple trees was more complete in 1928 than in 1927 (Tables 3 and 4, and Figures 3 and 4). This evidently should be ascribed more to temperature than any other factor, whether internal or external to the tree.

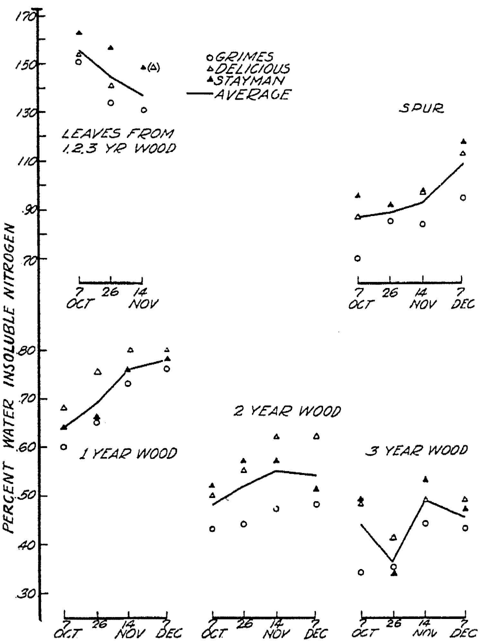

Fig. 3.—Water insoluble nitrogen in leaves, spurs and 1- to 3-year-old branches, 1927.

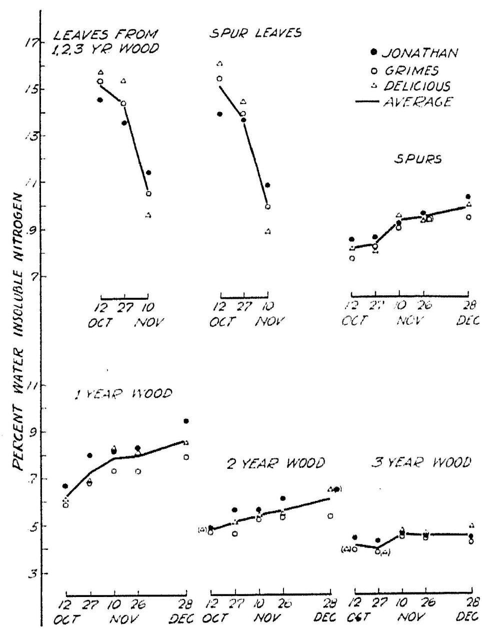

Fig. 4.—Water insoluble nitrogen in leaves, spurs and 1- to 3-year-old branches, 1928.

The water soluble fraction of nitrogen, the form in which it is moved out of the leaf, exhibits comparatively small and irregular changes. This is clearly evident in Tables 5 and 6. The graphical representations of these data (Figures 5 and 6) appear to be exaggerated, having been drawn on a scale five times as large as that used to represent total and water insoluble N. Temperature, sunlight and other environmental factors undoubtedly determine the rate of hydrolysis, concentration and movement of soluble N at any particular time and per time unit.

TABLE 5.—WATER SOLUBLE NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	.14	.12	.15	.20	.14
Delicious	.15	.17	.22	.16	.16
Stayman	.13	.06	.24	.14	.15
Average	.14	.12	.20	.17	.15
October 26					
Grimes	.19	.13	.12	.16	.15
Delicious	.16	.22	.15	.18	.20
Stayman	.15	.21	.17	.12	.15
Average	.17	.19	.15	.15	.17
November 14					
Grimes	.14	.17	.13	.16	.09
Delicious	.15	.20	.15	.04	.07
Stayman	.13	.16	.15	.17	.07
Average	.14	.18	.14	.12	.08
December 7					
Grimes	---	.17	.07	.07	.09
Delicious	---	.21	.06	.07	.06
Stayman	---	.07	.14	.17	.07
Average	---	.15	.09	.10	.07

TABLE 6.—WATER SOLUBLE NITROGEN, IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 12						
Jonathan	.166	.085	.080	.216	.108	.061
Grimes	.110	.106	----	.193	.168	.147
Delicious	.120	.116	.199	.201	.100	.103
Average	.132	.102	.139	.203	.125	.104
October 27						
Jonathan	.080	.087	.080	.141	.101	.081
Grimes	.104	.112	.128	.138	.149	.082
Delicious	.058	.112	.173	.077	.077	.112
Average	.081	.103	.127	.119	.109	.092
November 10						
Jonathan	.139	.141	.128	.117	.103	.060
Grimes	.218	.189	.162	.141	.155	.099
Delicious	.194	.151	.128	.143	.136	.080
Average	.184	.160	.139	.134	.131	.079
November 26						
Jonathan	-----	-----	.134	.134	.065	.134
Grimes	-----	-----	.152	.228	.180	.119
Delicious	-----	-----	.188	.164	.164	.136
Average	-----	-----	.158	.175	.136	.129
December 28						
Jonathan	-----	-----	.097	.111	.069	.112
Grimes	-----	-----	.187	.153	.148	.138
Delicious	-----	-----	.140	.125	.106	.109
Average	-----	-----	.141	.129	.108	.119

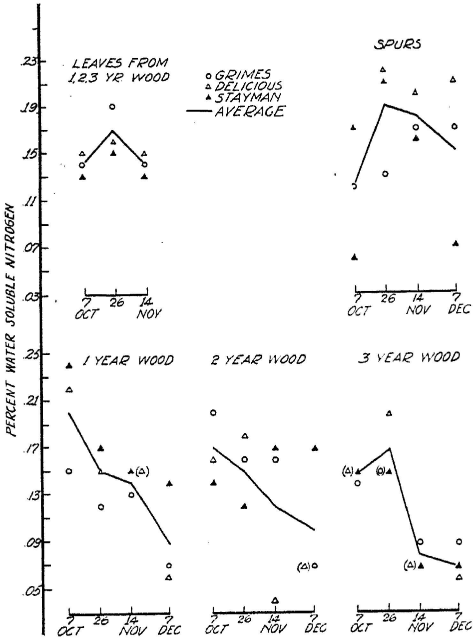

Fig. 5.—Water soluble nitrogen in leaves, spurs and 1- to 3-year-old branches, 1927.

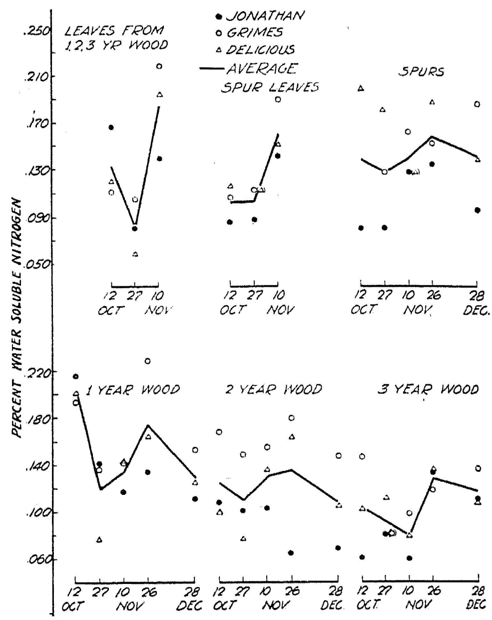

Fig. 6.—Water soluble nitrogen in leaves, spurs and 1- to 3-year-old branches, 1928.

The longer the leaves remain attached to the tree the more complete will be the removal of nitrogen. This is apparent from an examination of Tables 7 and 8, giving nitrogen concentration in fallen leaves.

Table 7.—Nitrogen in Abscissed Leaves, in Percentages of Dry Weight —1927

Variety	Total Nitrogen	Water Insoluble N.	Water Soluble N.
October 7			
Grimes	1.11	.91	.20
Delicious	1.22	1.03	.19
Stayman	1.54	1.43	.11
Average	1.29	1.12	.17
October 26			
Grimes	.86	.66	.20
Delicious	1.10	.99	.11
Stayman	1.00	.91	.09
Average	.98	.85	.13
November 14			
Grimes	.87	.78	.09
Delicious	.99	.89	.10
Stayman	1.02	.92	.10
Average	.96	.86	.10

Leaves that had dropped normally early in the season (collected on October 7, 1927) contained on the average for the three varieties, 1.29% nitrogen, while leaves of the late collection (November 14, 1927) contained only 0.96% N. The more or less corresponding figures for 1928

TABLE 8.—NITROGEN IN ABSCISSED LEAVES, IN PERCENTAGES OF DRY WEIGHT —1928

Variety	Total Nitrogen	Water Insoluble N.	Water Soluble N.
October 27			
Jonathan	1.191	1.120	.079
Grimes	1.136	.740	.313
Delicious	1.393	1.259	.134
Average	1.240	1.024	.175
November 10			
Jonathan	1.054	.984	.070
Grimes	.976	.937	.049
Delicious	1.199	1.122	.077
Average	1.076	1.014	.065
November 26			
Jonathan	.837	.646	.171
Grimes	.782	.701	.081
Delicious	.843	.775	.068
Average	.821	.707	.107

are: October 27, 1.24% and November 26, 0.82%. It will be noted that practically all of this nitrogen was still in the water insoluble form. This, together with the fact that the rainfall is usually low at this time of the year in Central Missouri, makes it very probable that there was practically no "leaching" of N from the abscissed leaves. Other evidence to this effect will be presented further on.

The most interesting feature of the nitrogen data of dropped leaves is the very large amount of N remaining even in those leaves that absciss very late (Tables 7 and 8, Figures 7 and 8). The nitrogen content of apple leaves begins to decrease soon after growth is completed and continues at an accelerating rate till the foliage drops (Thomas[28]). Still only a part of the total N content of the leaf seems to migrate back into the tree. Comparing the amount of N of still attached green leaves with that of dropped and completely dry ones, we find these approximate differences, constituting the percentage that apparently had been translocated into the woody structure, preparatory to the final abscission of these leaves: (*1927*) October 7, loss of N in fallen leaves, 24%; October 26, loss of N, 40%; November 14, loss of N, 38%. (*1928*) October 27, loss of N in fallen leaves, 22%; November 10, loss of N, 22%; November 26, loss of N, 33%. The end-season figures approach quite closely those of Ramann[21] and Lincoln[15], although the latter's data are from much younger and climatically better situated pear trees.

It is quite evident, therefore that though a large proportion of the nitrogen content of apple leaves is reabsorbed into the tree, approximately ½ to ¾ of it is lost, at least temporarily, by way of the dropped leaves. To what extent, and when, this finds its way back into the tree by way of the soil and the root system is a problematic question.

That the nitrogen decrease in senescent leaves is an actual migration into the branches is indicated clearly by a parallel and correspondingly

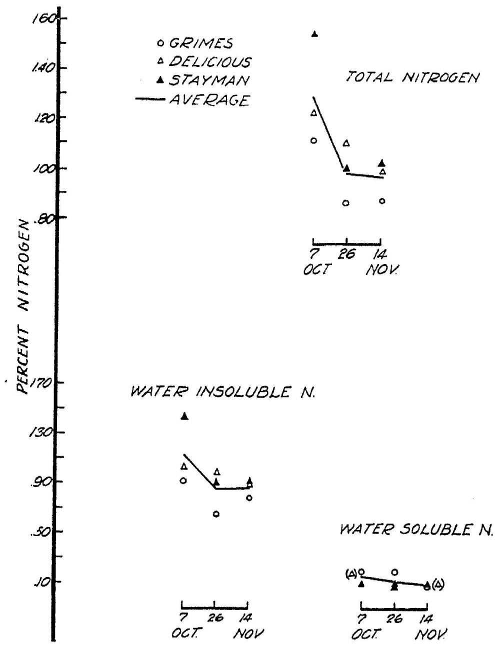

Fig. 7.—Nitrogen in abscissed leaves, 1927.

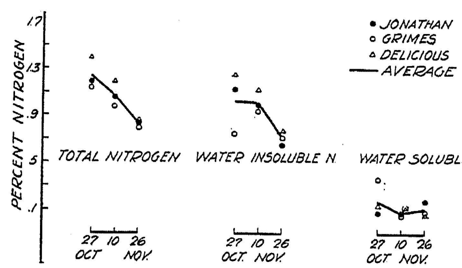

Fig. 8.—Nitrogen in abscissed leaves, 1928.

autumnal increase in percentage of total nitrogen of the spurs and 1- to 3-year-old branches (Tables 1 and 2, Figures 1 and 2). The greatest percentage increase is exhibited by spurs and one year-old-twigs. But since the older parts of the branches represent in aggregate more tissue, the actual quantity of nitrogen present may be far greater than in the last year's growth. Undoubtedly nitrogen entering the 1-year-old tissue is translocated later into older wood and probably into the root system. This has been definitely found by Combes[4-8] and others to be the case with young forest trees. The decline in total nitrogen concentration in twigs between November 14 and December 7, 1927, (Figure 1) may indicate such a migration of N in the tree. The general seasonal decrease in percentage of the soluble fraction of N in the twigs points to a decrease in volume of nitrogen that may be passing through. With the approach of winter there is, of course, a continuous reduction in the amount of foliage remaining on the tree and thus the source of nitrogen is diminishing rapidly. Fluctuations in concentration of soluble N in all analyzed woody tissues seem to indicate (Figures 5 and 6) the direct effect of environmental factors, primarily the weather, on the rate of nitrogen reabsorption and movement within the tree. This has been observed among others, by Richter[23]. Variability between the samples may also account for a part or for some of these differences and irregularities.

Autumnal Migration of Carbohydrates.—While the end-season removal of nitrogen from apple leaves and its migration into the tree can be determined with reasonable certainty, the gathering of proof on a similar movement of carbohydrates is beset with considerable difficulties. This has been emphasized by several other investigators[11, 12, 3, 9]. The formation of carbohydrates through photosynthesis is affected by several environmental factors, while the polymerization and hydrolysis of these substances is subject to wide fluctuations, primarily those caused by changes in temperature and light.

The sugar content of apple leaves that undergo senescence seems to be augmented rapidly (Tables 9 and 10, and Figures 9 and 10). That a large proportion of it may be removed before abscission is completed is indicated by the almost equal decrease in sugar content in the dropped leaves collected on November 14, 1927, (Table 15 and Figure 15).

TABLE 9.—TOTAL SUGAR (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT —1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	2.63	1.89	1.25	0.99	1.61
Delicious	2.93	1.13	1.24	.96	.89
Stayman	2.93	1.47	1.50	.98	1.20
Average	2.83	1.50	1.33	.98	1.23
October 26					
Grimes	4.3	3.68	2.08	2.88	1.80
Delicious	5.0	3.20	2.53	2.68	1.93
Stayman	3.4	3.88	2.80	2.60	2.20
Average	4.23	3.58	2.46	2.72	1.97
November 14					
Grimes	10.4	3.95	3.00	2.53	1.93
Delicious	9.5	3.95	2.23	1.36	1.98
Stayman	9.38	3.68	2.80	2.60	2.53
Average	9.76	3.86	2.67	2.16	2.14
December 7					
Grimes	----	11.35	9.50	3.40	2.90
Delicious	----	9.93	10.30	2.80	3.58
Stayman	----	10.00	8.78	3.58	3.08
Average	----	10.42	9.52	3.26	3.18

TABLE 10.—TOTAL SUGARS (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT —1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 12						
Jonathan	6.75	5.40	5.50	5.25	4.92	4.38
Grimes	5.70	4.30	4.47	4.09	3.60	2.01
Delicious	4.92	4.68	4.17	3.70	3.50	2.38
Average	5.82	4.79	4.71	4.35	4.01	2.92
October 27						
Jonathan	7.40	6.60	3.77	5.79	3.67	3.56
Grimes	6.60	5.37	3.26	4.22	3.45	2.89
Delicious	6.79	5.79	3.92	3.89	3.80	2.78
Average	6.93	5.92	3.65	4.63	3.64	3.08
November 10						
Jonathan	7.39	6.47	4.89	4.40	4.82	3.70
Grimes	9.42	6.47	4.90	5.10	3.89	3.87
Delicious	7.09	6.54	5.62	4.53	3.53	2.50
Average	7.97	6.49	5.14	4.68	4.08	3.36
November 26						
Jonathan	----	----	5.34	6.07	4.97	5.25
Grimes	----	----	6.39	4.36	4.50	2.97
Delicious	----	----	6.02	5.27	4.69	4.02
Average	----	----	5.92	5.23	4.72	4.08
December 28						
Jonathan	----	----	8.82	7.27	6.89	11.75
Grimes	----	----	7.08	6.71	5.38	4.85
Delicious	----	----	7.80	5.88	4.92	3.91
Average	----	----	7.90	6.62	5.73	6.84

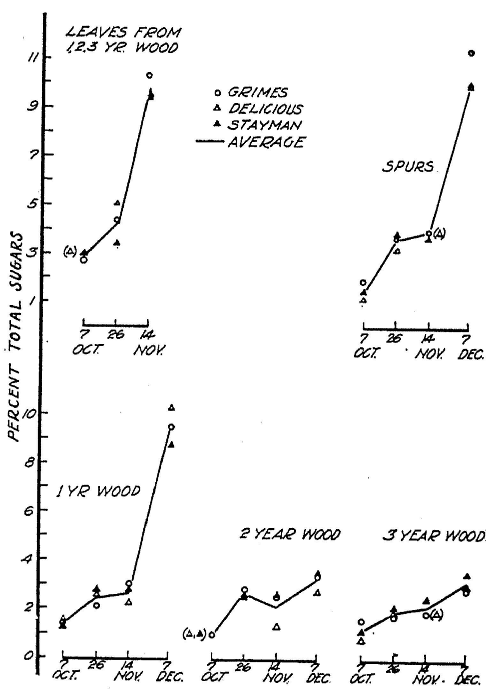

Fig. 9.—Total sugars (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1927.

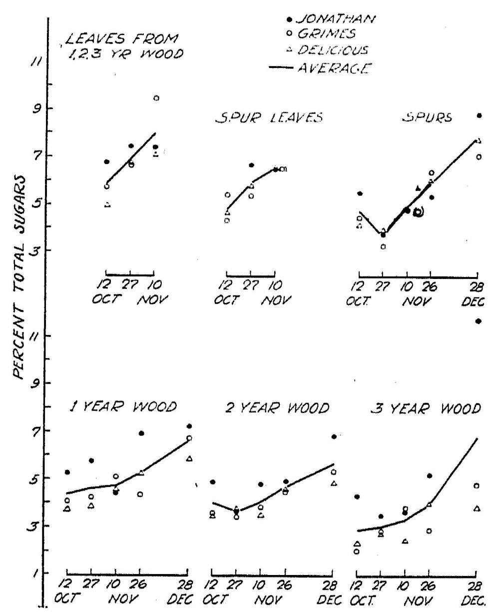

Fig. 10.—Total sugars (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1928.

But fallen leaves gathered on earlier dates of the same year were actually higher in sugar content than the corresponding green leaves. Moreover, the 1928 figures of percentages of total sugars in either green or dropped leaves do not indicate such a reverse relationship (Tables 10 and 16, and Figures 10 and 16).

In 1927 the concentration of starch in leaves was equally as marked late in the season as that of sugars, but not so in 1928 (Table 11, Figure 11 and Table 12, Figure 12). Evidently then the difference between the two years is greater than that of a possible seasonal trend. Leaves that had dropped still contained from 3 to 5% starch (Figures 15 and 16).

TABLE 11.—STARCH (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	2.94	6.60	7.44	6.09	2.69
Delicious	2.83	7.30	9.19	7.16	6.38
Stayman	2.78	4.50	7.11	4.81	4.68
Average	2.85	6.10	7.91	6.02	4.58
October 26					
Grimes	1.44	5.88	8.50	6.05	6.15
Delicious	1.26	6.39	6.98	7.34	8.43
Stayman	1.40	6.59	5.30	5.26	5.10
Average	1.37	6.28	6.93	6.21	6.56
November 14					
Grimes	5.19	5.64	6.75	3.11	3.00
Delicious	4.30	5.14	4.03	3.56	3.98
Stayman	5.40	5.71	6.45	4.41	3.83
Average	4.96	5.49	5.74	3.70	3.60
December 7					
Grimes	----	5.56	6.09	4.10	4.18
Delicious	----	5.95	5.48	4.06	3.99
Stayman	----	5.03	6.29	3.83	3.60
Average	----	5.51	5.95	3.99	3.92

TABLE 12.—STARCH (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
Oct ber 12						
Jonathan	1.90	1.88	7.40	6.02	5.98	5.67
Grimes	2.08	2.05	7.02	5.00	4.52	3.15
Delicious	3.30	2.89	5.46	5.38	5.66	3.67
Average	2.43	2.27	6.63	5.47	5.39	4.16
October 27						
Jonathan	2.08	1.51	7.52	5.90	5.26	5.10
Grimes	1.44	2.33	8.78	8.07	7.96	6.57
Delicious	2.36	1.48	5.35	8.63	7.72	6.33
Average	1.96	1.77	7.22	7.53	6.98	6.00
November 10						
Jonathan	1.98	1.96	7.42	7.72	5.85	6.11
Grimes	2.82	2.68	5.80	5.96	6.29	5.85
Delicious	1.52	1.78	6.65	5.78	4.77	5.25
Average	2.11	2.14	6.62	6.49	5.64	5.74
November 26						
Jonathan	----	----	4.42	5.22	5.05	4.60
Grimes	----	----	3.92	3.80	4.16	3.60
Delicious	----	----	4.92	5.52	4.93	4.10
Average	----	----	4.42	4.85	4.71	4.10
December 28						
Jonathan	----	----	3.29	4.07	2.81	3.07
Grimes	----	----	3.95	3.75	2.06	2.10
Delicious	----	----	1.88	3.53	2.17	2.03
Average	----	----	3.04	3.78	2.35	2.40

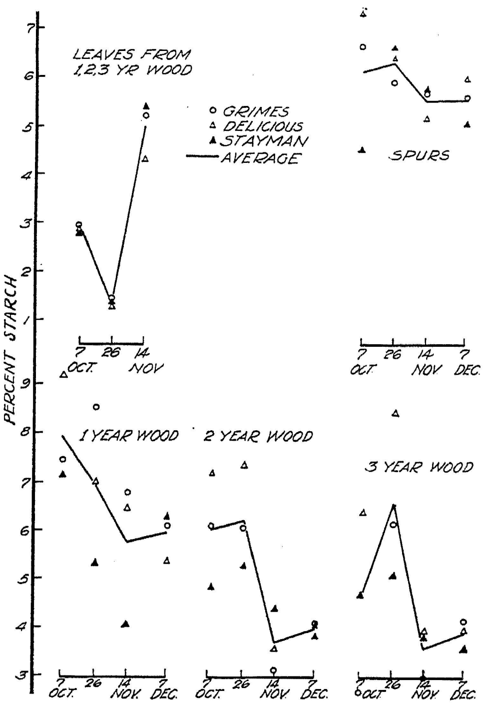

Fig. 11.—Starch (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1927.

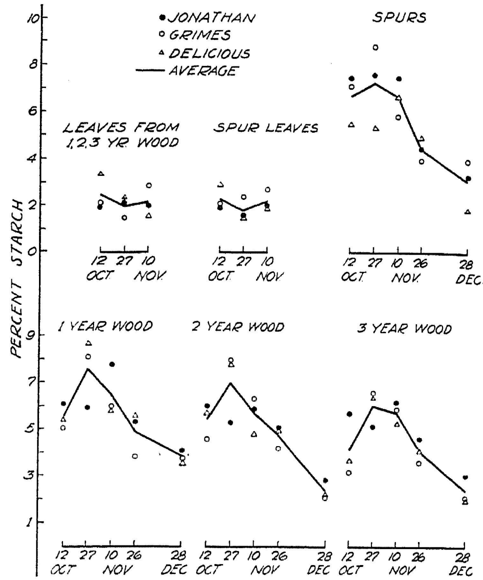

Fig. 12.—Starch (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1928.

There was an increase in percentage of so-called hemicellulose in both years till about the middle of November, followed by a decline later (Tables 13 and 14 and Figures 13 and 14). It is doubtful whether

TABLE 13.—HEMICELLULOSE (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Leaves from 1, 2, 3 yr. wood	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 7					
Grimes	10.05	26.15	23.51	25.08	25.90
Delicious	9.54	15.11	16.30	22.05	16.51
Stayman	11.39	18.00	14.90	19.94	22.84
Average	10.66	19.75	18.23	22.35	21.75
October 26					
Grimes	11.45	27.91	13.95	25.30	20.33
Delicious	13.40	27.54	27.00	22.18	21.90
Stayman	11.95	26.95	29.80	27.95	22.70
Average	12.27	27.46	23.68	25.14	21.64
November 14					
Grimes	10.00	27.51	26.01	26.98	28.53
Delicious	10.00	23.29	27.34	27.59	27.91
Stayman	16.45	22.86	24.30	26.76	26.23
Average	12.15	24.55	25.88	27.11	27.55
December 7					
Grimes	-----	24.83	26.44	27.51	25.21
Delicious	-----	22.95	22.96	14.80	23.35
Stayman	-----	25.69	21.63	24.28	25.21
Average	-----	24.49	23.67	22.19	24.59

TABLE 14.—HEMICELLULOSE (AS DEXTROSE), IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Leaves from 1, 2, 3 yr. wood	Spur Leaves	Spurs	1 yr. wood	2 yr. wood	3 yr. wood
October 12						
Jonathan	16.98	16.38	22.87	27.11	21.56	23.10
Grimes	16.32	16.47	21.85	25.50	23.70	21.41
Delicious	16.42	17.52	22.70	24.17	21.78	22.51
Average	16.57	16.79	22.47	25.59	22.35	22.34
October 27						
Jonathan	18.47	20.85	21.87	20.45	26.58	22.22
Grimes	18.37	18.57	19.13	27.77	24.15	26.48
Delicious	19.70	19.50	26.17	21.37	25.02	26.83
Average	18.85	19.64	22.39	23.20	25.25	26.18
November 10						
Jonathan	15.95	17.55	27.72	23.11	17.31	24.55
Grimes	17.47	17.10	22.62	23.21	21.82	21.91
Delicious	16.37	17.05	20.18	21.36	24.45	22.55
Average	16.60	17.23	23.51	22.56	21.19	23.00
November 26						
Jonathan	-----	-----	20.17	27.77	22.90	26.23
Grimes	-----	-----	20.32	22.95	24.80	25.72
Delicious	-----	-----	19.47	21.93	24.27	28.80
Average	-----	-----	19.99	24.22	23.99	26.92
December 28						
Jonathan	-----	-----	23.32	19.47	21.90	27.92
Grimes	-----	-----	22.80	26.45	24.06	25.42
Delicious	-----	-----	20.68	20.72	23.22	22.83
Average	-----	-----	22.27	22.21	23.06	25.39

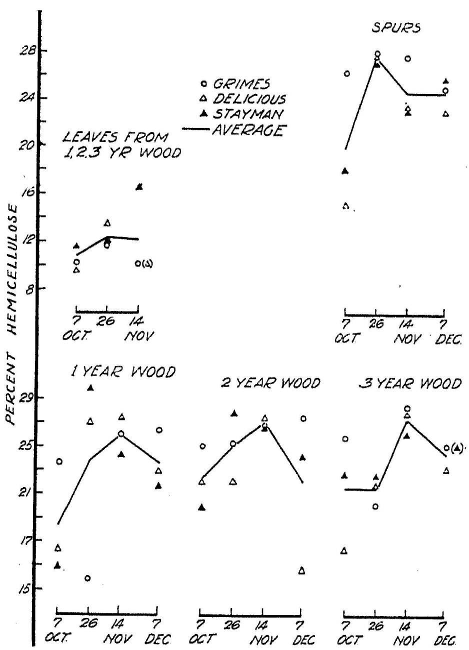

Fig. 13.—Hemicellulose (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1927.

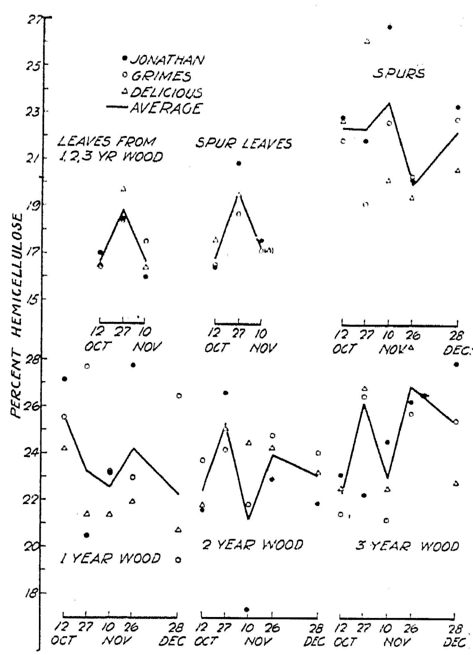

Fig. 14.—Hemicellulose (as Dextrose) in leaves, spurs and 1- to 3-year-old branches, 1928.

this has any particular significance or has a direct relationship to fall migration of carbohydrates. Most of the dropped leaves contained equally high concentrations of hemicellulose (Tables 15 and 16, and Figures 15 and 16).

TABLE 15.—CARBOHYDRATES (AS DEXTROSE) IN ABSCISSED LEAVES, IN PERCENTAGES OF DRY WEIGHT—1927

Variety	Total Sugars	Starch	Hemicellulose	Total Carbohydrates
October 26				
Grimes	7.05	5.10	6.19	18.34
Delicious	11.08	5.38	9.35	25.81
Stayman	10.80	5.38	6.05	22.23
Average	9.64	5.29	7.20	22.13
November 4				
Grimes	8.00	5.64	6.05	19.69
Delicious	11.08	4.91	8.99	24.98
Stayman	8.70	5.60	4.91	19.21
Average	9.26	5.38	6.65	21.29
November 14				
Grimes	4.73	3.75	19.41	27.71
Delicious	2.38	3.94	21.31	27.63
Stayman	3.20	3.83	17.36	24.39
Average	3.42	3.84	19.36	26.57

TABLE 16.—CARBOHYDRATES (AS DEXTROSE) IN ABSCISSED LEAVES, IN PERCENTAGES OF DRY WEIGHT—1928

Variety	Total Sugars	Starch	Hemicellulose	Total Carbohydrates
October 27				
Jonathan	2.65	----	17.56	-----
Grimes	3.96	3.07	20.95	27.98
Delicious	3.87	4.25	20.17	28.29
Average	3.49	3.44	19.56	28.13
November 10				
Jonathan	4.82	3.70	18.35	26.87
Grimes	3.57	2.78	16.10	22.45
Delicious	4.14	2.56	20.12	26.82
Average	4.18	3.01	18.19	25.38
November 26				
Jonathan	3.00	0.98	20.65	24.63
Grimes	4.42	1.00	18.77	24.19
Delicious	3.85	2.08	20.45	26.38
Average	3.76	1.35	19.96	25.07

Another source of information on the autumnal removal of carbohydrates from leaves is found in analyses of those structural parts of the tree to which the leaves are attached. It will be seen from Tables 9 and 10, Figures 9 and 10, that concomitantly with the seasonal increase in sugars in leaves there was a similar increase in these plastic substances in spurs and branches. Now as there is a corresponding decrease in starch concentration at this time in all the considered woody structures (Tables 11 and 12 and Figures 11 and 12), it is more than likely that the weather had more to do with these drastic changes in form of carbohydrates in the apple than any other factor. With the onset of cold

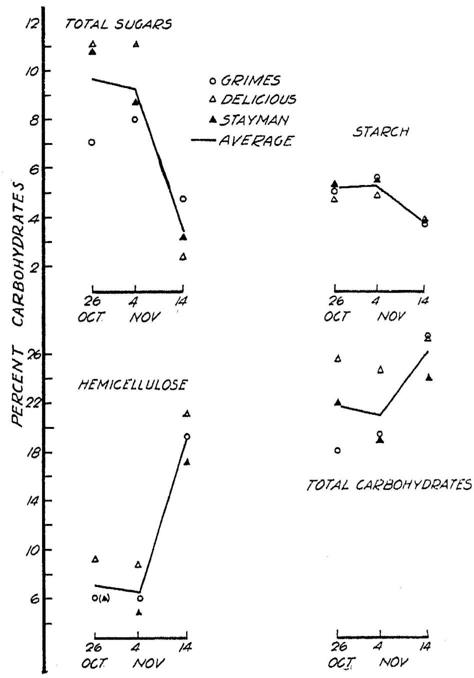

Fig. 15.—Carbohydrates (as Dextrose) in abscissed leaves, 1927.

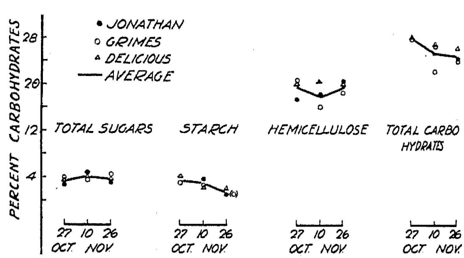

Fig. 16.—Carbohydrates (as Dextrose) in abscissed leaves, 1928.

and freezing temperatures, starch very likely is hydrolyzed into sugars simultaneously in all parts of the apple tree including the older wood*. This, of course, is a common phenomenon in many other plants.

When the figures representing the starch data for both years are superimposed upon those for hemicellulose (Figures 11 to 14) there is a suggestion of a reverse relationship between the concentration of these two forms of carbohydrates. Subject to influence of weather, there is a possibility that in apple tissues starch may be changed to hemicellulose and related compounds and that the latter, under certain conditions, in turn may be transformed into starch†.

In conclusion, it must be stated, that our present evidence on the autumnal movement of carbohydrates from leaves into the structural parts of the apple tree is suggestive but by no means certain. It is of course, understood that this has no direct relationship with the known periodic or diurnal transfer of carbohydrates from normally functioning leaves to other parts of a tree—a subject matter not considered here. The reader will appreciate the fact also that our present accepted methods of analysis for higher carbohydrates are indeed very gross and by no means satisfactory.

DISCUSSION AND APPLICATION

The information presented in this report makes it certain that nitrogen, and probably other soil nutrients, are absorbed from apple leaves preceding their exfoliation. The removal of N from the leaf is due primarily to a decrease in the water insoluble fraction. Nitrogen migrates into the spurs and branches where it may be laid down temporarily in the form of reserve proteins. Eventually it is translocated to the older wood and possibly to the root system.

Weather conditions, especially temperature, seems to determine to a considerable extent the initiation and speed of this movement. Cool weather may hasten it, while a killing frost will destroy the process. Hence, under environmental conditions obtaining in the Central States, it is doubtful whether there is such a thing as a "normal" senescence and abscission of leaves of fruit trees. Heavy freezes occurring more or less unexpectedly, the amount of nitrogen that will be removed from the leaves will differ from year to year. It is of interest to note in this connection that leaves that drop more or less "normally" early in the fall lose less of their N content than those that absciss later. This difference may amount to as much as 100%.

*This is supported by still unpublished data obtained by the senior author.

†For further discussion of this subject see Plant Physiology 4:2:251-264, 1929.

When leaves have been killed by freezing before yellowing occurs and have been removed by wind or other agencies from the immediate vicinity of the tree, then the nitrogen content of such trees may be markedly deficient. As a result weaker growth and a smaller set of fruit may be expected the following year. This deficiency in the nitrogen reserves may be corrected by application of a readily available nitrogen fertilizer either in the fall or before growth starts in the spring.

Abscissed apple leaves contain about 1% nitrogen on dry weight basis. Considering the total quantity of the foliage, it will be evident that a great deal of nitrogen is lost by the tree each fall. It is of importance to know what becomes of the N contained in this litter of dry foliage. Leaves disintegrate rather rapidly, consequently much of this nitrogen will find its way back into the tree through the usual channel, the soil and the root system. If the weather is favorable, this may happen quite promptly in the same fall or early winter, at least in the more southern latitudes. Here then we have a natural "fall fertilization" of fruit trees. With less favorable conditions for disintegration of the dead foliage, especially in the more northern states where the ground freezes early and promptly, the nitrogen within the leaf debris will not be returned to the tree till the following spring. This, too, constitutes a more or less normal "spring fertilization" with a certain amount of nitrogen. Thus our rather popular recommendations of nitrogen application to fruit trees, including the so-called "split application" may be but an extension and duplication of a naturally occurring phenomenon. One should be mindful of the fact, however, that a varying portion of this N may be lost in diverse ways. The largest amounts of carbohydrates present in the dead leaves may play a role by furnishing a proper C/N ratio for the efficient function of certain forms of soil bacteria, the causal agents bringing about the reduction of the more complex nitrogen compounds to substances simple enough to be water soluble and available to fruit trees.

Another feature which may have some bearing on orchard practices is the accumulation of nitrogen in the twigs and branches during the fall. At the time of leaf abscission the spurs and one-year-old wood seem to increase in nitrogen content first, followed by a similar increase in the older portions of the branch, the stem and roots. This movement of N from the peripheral regions to the more central structural parts of the tree may not be completed till late in the season, possibly during early winter. Consequently pruning of dormant trees should be delayed till the later part of winter or early spring period. This will tend to conserve the nitrogen reserves of a tree and thus help to maintain its vitality.

Non-bearing trees making vigorous growth might be made to bear by practicing summer or fall pruning to curtail the nitrogen reabsorption from the leaves and thereby widen the nitrogen-carbohydrate ratio, which presumably initiates or determines reproductive activities.

SUMMARY

From the data presented and the disclosure of other investigators, the facts seem rather well established that the nitrogen and carbohydrate content of the leaves and adjoining organs of the apple tree undergo the following autumnal changes:

1. Nitrogen content of the leaves decreases from the time active growth ceases till complete defoliation occurs. The removal of nitrogen is greater from the yellowed leaves than the green ones collected at the same time. This difference, in our investigations, amounted to 22 to 40%, depending upon time of abscission. Leaves that remain attached to the tree longer will release their N content more completely.

2. The percentage of nitrogen in non-bearing spurs and twigs increases rather uniformly during the period of dropping of leaves. Later in the fall much of this absorbed N is moved to older wood and probably to the root system of the tree.

3. The nature and seasonal trend in migration of carbohydrates from the foliage to the woody structures of the apple has not been established. With the onset of cold weather starch and possibly other more complex carbohydrates are hydrolyzed simultaneously into sugars in all peripheral regions of the tree. With changes in temperature condensation may again take place. Modifications induced by weather often are of greater amplitude than a possible seasonal trend.

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