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TRENDS IN THE NITROGEN, PHOSPHORUS, POTASSIUM AND CALCIUM CONTENT OF THE LEAVES OF SOME FOREST TREES DURING THE GROWING SEASON

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Information regarding the movement of nutrient elements to or from the leaves of forest trees is of importance from several points of view. Besides being of academic interest to plant physiologists and botanists, such information is of material value to foresters concerned with either tree nutrition or the rôle played by various species in soil upbuilding or deterioration. Preliminary investigations (Mitchell, 1935) indicate that some of the chemical aspects of site quality may be evaluated on the basis of leaf analysis. And there is some evidence (Mitchell and Finn, 1935) that silvical data regarding the relative feeding power of various tree species for soil nutrients may be similarly obtained. Granting that these fundamental problems can be profitably approached in this way, through leaf analyses, there remains the question of sampling technique.

It is well known that the concentration of the various nutrient elements in tree leaves changes with the age of the leaf as well as with site quality or species. Therefore, if accurate quantitative comparisons (of nutrient content) are to be made, the time of leaf collection must be either standardized, or some correction made for the influence of this factor. In the following report the physiological data regarding nutrient translocation are discussed with special reference to this phase of the sampling problem.

Data were obtained on both the concentration and the absolute quantity of nitrogen, phosphorus, potassium and calcium in the leaves of seven commercially important species (red, white and chestnut oak, sugar and red maple, shagbark hickory and Norway spruce) at five different times during the growing season. Observations were also made of the dry weight increase, and changes in the moisture content of the leaves. The absolute amount of N, P, K or Ca in an average leaf at any given time was calculated as the product of nutrient concentration (as a per cent of dry weight) and leaf mass. Although many somewhat similar studies have been reported, few others have included data on changing leaf mass or, consequently, the total quantity of the various elements in the leaves at different times. Without such absolute values it is impossible to determine, with any degree of accuracy, either the direction or magnitude of nutrient migration at various times during the growing period.

DETAILS OF EXPERIMENT

During the summer of 1935 leaf samples were taken on May 27, June 26, July 26, August 26, and September 25 from single trees of each of the seven species listed in Table 1. All trees were within 600 yards of the Black Rock Forest Laboratory and all on essentially the same type of soil, a Gloucester stony loam as mapped by Crabb and Morrison (1914). Considerable care was exercised in sampling leaves for there is some evidence to show that

TABLE 1

Species and Approximate Age of Trees From Which Leaf Samples Were Taken.

Species	Approximate Age
White Oak (*Quercus alba* L.)	55
Chestnut Oak (*Quercus montana* Willd.)	35
Red Oak (*Quercus borealis* Michx.)	60
Shagbark Hickory (*Hicoria ovata* (Mill.) Britton)	35
Sugar Maple (*Acer saccharum* Marsh.)	20
Red Maple (*Acer rubrum* L.)	20
Norway Spruce (*Picea abies* L.)	45

chemical composition may vary with location on the tree, not only as regards elevation, but exposure (north or south) as well. Rather than attempt to obtain a representative sample of the entire leaf mass of each tree on each sampling date, it was thought best to standardize on a given location on each tree and take all samples therefrom. Limbs of a convenient height on the south side of each tree were selected and marked with tags. Successive samples were composed of leaves taken at random from branches of the marked limbs. In the case of Norway spruce only needles of the current year's growth were collected. As a very small portion of the total leaf mass of each limb was removed at a time, these minor losses probably caused no abnormal variations in the nutrient flow. In no case were leaves taken which had been subject to insect or fungus attack, or damaged in any way that might affect either their weight or nutrient content.

Leaves of each sample were counted and bagged in the field, brought to the laboratory and weighed in the fresh state within one-half hour after collection, and then dried to constant weight at $+70°C$. After reweighing (dry) all leaves were ground in a Wiley mill to pass through a 0.55 mm. mesh screen. The moisture content of all samples was determined and expressed as a per cent of dry weight, and the dry weight of the average leaf in each sample of deciduous leaves was calculated. Because of their small size and great number no attempt was made to determine the average weight of individual spruce needles.

Duplicate determinations of each sample were made for nitrogen, phosphorus, potassium and calcium, usually considered the four most important nutrient elements because they are more apt to be deficient in natural soils than the others. A modification (Mitchell, 1934, p. 28) of the Pregl (1930) micro-Kjeldahl technique was used to determine nitrogen. Following perchloric acid digestion phosphorus and potassium were determined colorimetrically, the former by the method of Fiske and Subbarow (1925), and the latter by the Hoffman and Jacobs (1931) method. Calcium was determined according to the usual gravimetric procedure in which calcium is precipitated as the oxalate, and the
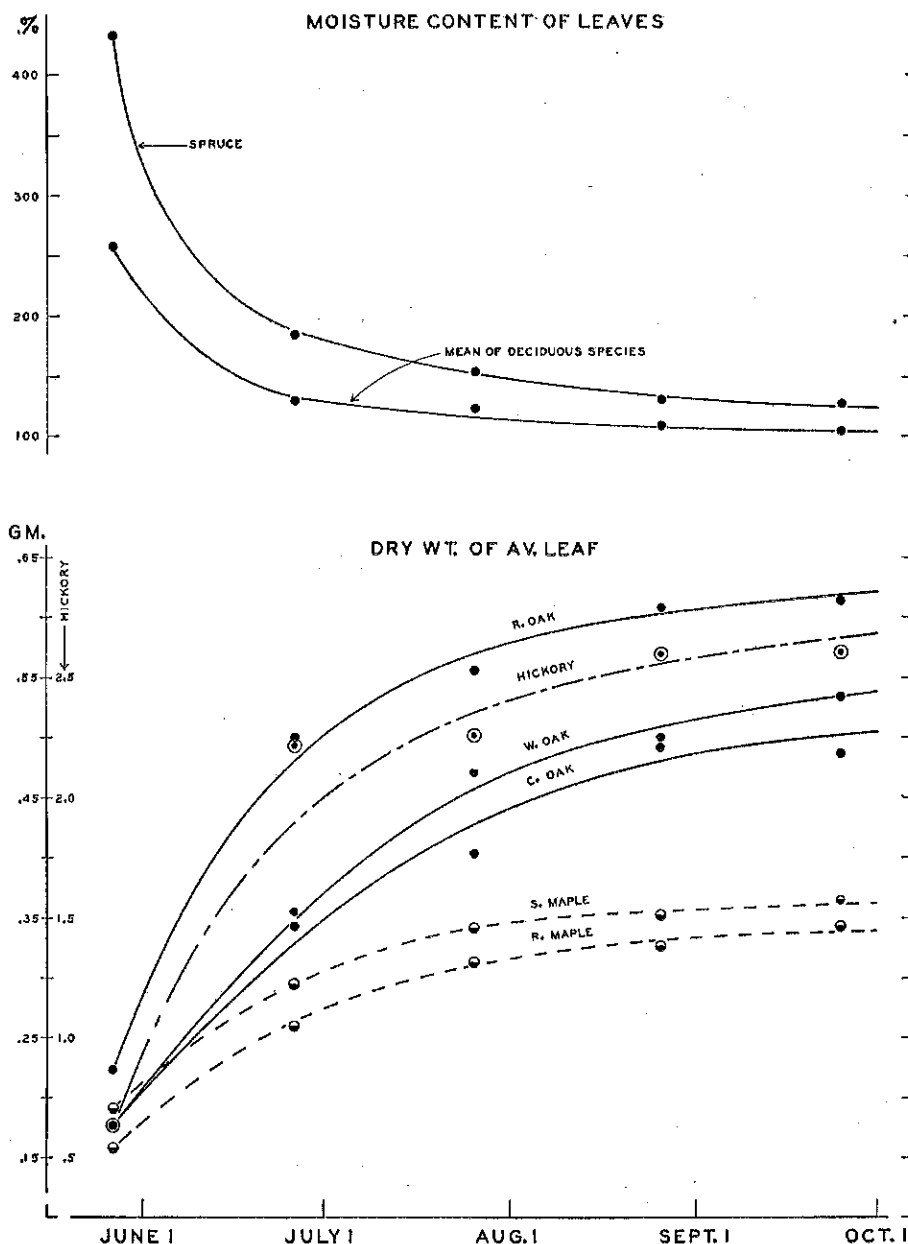
MOISTURE CONTENT OF LEAVES

DRY WT. OF AV. LEAF

FIG. 1.—Average trends in the moisture content, and the dry weight increase of the leaves of some forest trees during the growing season.

oxalate converted to the oxide by strong ignition. The data on dry weights, moisture contents and chemical analysis are summarized in Table 2.

DISCUSSION OF RESULTS

DRY WEIGHT INCREASE OF LEAVES

Leaves of the various species increased in dry matter from June 1 to October 1 by the following approximate amounts: hickory, 340%; oaks, 190%; and maples, 100% (Fig. 1; Table 2, col. 4). Although leaf sampling is somewhat crude at best, deviations of observed data from the smooth curves shown in Fig. 1 are relatively small (see comparisons, Table 2, cols. 4 and 5). The rate of increase in dry matter was, in each case, greatest during the first two months and then dwindled to

almost nothing in September. But, according to the above percentages, the growth rate apparently varied somewhat with species. As will be shown later these differences in the rate of dry weight increase are of particular interest because of their influence upon trends in nutrient concentration. From June 1 to October 1 leaves of the oaks and especially hickory increased considerably more than did those of the maples. This may be attributed to the fact that maple leaves start to develop three to four weeks earlier, and are therefore partly through their period of most rapid growth by the time hickory and oak leaves begin to form. If a 30-day correction is made for differences in time of initial growth, the trends are more comparable. Thus, sections of the maple growth curves from June 1 to September 1 are quite similar in both slope and general shape to those of hickory and the oaks from July 1 to October 1 (see Fig. 1).

It is believed that the trends shown in Fig. 1, although based in each case on samples from a single limb, express fairly accurately the increase in total leaf mass on trees of the different species. Weights on supplementary samples taken from time to time indicated that neither elevation (distance from the ground) nor exposure (north or south) had any appreciable effect upon the rate of dry weight increase.

MOISTURE CONTENT OF LEAVES

Data on the moisture content of the various leaves at different times during the summer were obtained (Table 2, col. 6). Trends are shown in Fig. 1. As there were no significant differences between the various hardwood species only mean values for the entire group were plotted (Fig. 1). But it is apparent that spruce needles had a higher moisture content than the leaves of any of the hardwood species. This is probably due to morphological differences between spruce needles and the deciduous leaves.

According to the data presented in Fig. 1, trends in moisture contents were exactly opposite to those of dry weight increase. As with all plants the leaves were most succulent during the period of rapid growth. Thus, because of the high moisture content early in the season, the fresh weight of the average leaf was about as great on July 1 as at the end of the summer. This probably accounts for the rather general belief that leaves "grow" but little after the initial early spring spurt.

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TABLE 2

Dry weight, and the moisture, nitrogen, phosphorus, potassium and calcium content of the leaves of seven forest tree species at five different times during the 1935 growing season.

Species [1]	Date Sampled	Number of Leaves Collected	Dry Wt. Av. Leaf in Mg.[2]		Moisture Content as % Dry Wt.	Nitrogen Content [4]		Phosphorus Content [4]		Potassium Content [4]		Calcium Content [4]	
			Experimentally Determined	Calculated [3]		$N\%$	$(7) \times (5) = N_{mg}$ [5]	$P\%$	$(9) \times (5) = P_{mg}$ [5]	$K\%$	$(11) \times (5) = K_{mg}$ [5]	$Ca\%$	$(13) \times (5) = Ca_{mg}$ [5]
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
White Oak	May 27	31	177	177	236	3.992	7.07	0.339	0.60	1.385	2.45	0.668	1.18
	June 26	49	343	348	113	2.700	9.40	0.160	0.56	0.987	3.44	0.793	2.76
	July 26	36	470	457	108	2.597	11.87	0.138	0.63	0.871	3.98	0.877	4.01
	Aug. 26	57	499	508	98	2.445	12.42	0.130	0.66	0.774	3.93	1.064	5.41
	Sept. 25	23	534	534	93	2.262	12.08	0.135	0.72	0.760	4.06	1.096	5.85
Chestnut Oak	May 27	25	176	176	252	3.500	6.16	0.325	0.57	1.525	2.68	0.581	1.02
	June 26	40	355	328	135	2.576	8.45	0.190	0.62	1.297	4.25	0.842	2.76
	July 26	26	403	428	128	2.464	10.55	0.161	0.69	1.025	4.39	0.968	4.14
	Aug. 26	35	491	480	107	2.199	10.55	0.167	0.80	0.991	4.76	1.521	7.30
	Sept. 25	30	486	502	107	2.215	11.12	0.159	0.80	1.050	5.27	1.158	5.81
Red Oak	May 27	66	223	223	267	3.750	8.36	0.363	0.81	1.500	3.35	0.410	0.91
	June 26	31	500	482	136	3.000	14.46	0.167	0.81	1.340	6.46	0.511	2.46
	July 26	31	555	570	128	2.844	16.21	0.155	0.88	1.215	6.93	0.631	3.60
	Aug. 26	26	607	602	123	2.776	16.71	0.157	0.95	1.241	7.47	0.755	4.55
	Sept. 25	22	614	618	113	2.733	18.89	0.154	0.95	1.190	7.35	0.810	5.01
Shagbark Hickory	May 27	17	629 [6]	629	335	3.785	23.81 [6]	0.352	2.21 [6]	1.665	10.47 [6]	1.470	9.25 [6]
	June 26	9	2,222	1,900	132	2.089	39.69	0.125	2.38	1.090	20.71	1.683	31.98
	July 26	7	2,257	2,360	115	2.012	49.84	0.124	2.93	0.981	23.15	2.085	49.21
	Aug. 26	8	2,587	2,550	93	2.012	51.31	0.121	3.09	1.075	27.41	2.158	55.03
	Sept. 25	6	2,600	2,670	91	1.566	41.81	0.103	2.75	0.547	14.61	2.334	62.32
Sugar Maple	May 27	37	192	192	237	2.467	4.74	0.293	0.56	1.440	2.77	0.732	1.41
	June 26	35	295	295	140	1.913	5.64	0.247	0.73	0.950	2.80	1.285	3.79
	July 26	31	341	341	126	1.874	6.39	0.240	0.82	0.804	2.74	1.176	4.01
	Aug. 26	33	352	355	111	1.794	6.37	0.238	0.85	0.808	2.87	1.403	4.98
	Sept. 25	25	365	362	114	1.755	6.35	0.235	0.85	0.804	2.91	1.477	5.35
Red Maple	May 27	43	158	158	216	2.161	3.41	0.286	0.45	1.120	1.77	0.751	1.19
	June 26	25	260	265	119	1.870	4.96	0.228	0.60	0.670	1.77	1.090	2.89
	July 26	30	313	310	126	1.901	5.89	0.229	0.71	0.569	1.76	0.897	2.78
	Aug. 26	34	326	332	113	1.900	6.31	0.229	0.76	0.566	1.88	0.935	3.10
	Sept. 25	35	343	338	107	1.855	6.27	0.225	0.76	0.560	1.89	1.267	4.28
Norway Spruce	May 27	...	...	...	433	2.832	...	0.365	...	1.550	...	0.395	...
	June 26	...	...	...	184	1.682	...	0.210	...	0.911	...	0.603	...
	July 26	...	...	...	153	1.677	...	0.176	...	0.858	...	0.733	...
	Aug. 26	...	...	...	130	1.670	...	0.171	...	0.880	...	0.721	...
	Sept. 25	...	...	...	127	1.611	...	0.168	...	0.780	...	0.686	...

[1] Scientific equivalents of common names are given in Table 1.

[2] Petioles removed.

[3] These values were obtained from the smooth curves in Fig. 1. No attempt was made to determine the weight of individual Norway Spruce needles.

[4] Nitrogen, Phosphorus, Potassium and Calcium are expressed in this Table as elements and not as the oxides —P_2O_5, K_2O and CaO. It is certain that few if any of these oxides occur as such in plant tissue. And since gravimetric procedures—in which plant ash constituents are weighed as oxides—are no longer the rule, there remains no valid reason for continuing to calculate comparative analyses by introducing into the calculations a variable factor such as the number of oxygen atoms with which each element will combine.

[5] Leaf sampling is somewhat crude at best and certain leaf irregularities, particularly in leaf weights, are to be expected. But to avoid magnifying such deviations further, leaf weights read from the smoothed curves in Fig. 1 were used, in preference to the "found" weights, in calculating the milligrams of N, P, K and Ca in the average leaf at any given time. Average trends based upon the data computed in this way are believed to be truer estimates of what actually takes place.

[6] Hickory leaves are compound, weigh more, and, therefore, have a higher N, P, K and Ca content, in milligrams, than the leaves of any of the other species studied.

But, due largely to increments in total ash and carbohydrate which more than balance the moisture decrease, the total leaf mass, expressed as dry matter, increases considerably after July 1. This increase is not accompanied by an increase in surface area which preliminary measurements show to be relatively constant after mid-summer.

Variations in the Chemical Composition of Leaves

It is well known that the concentration of mineral nutrients in the conducting vessels of a tree is greatest in the early spring. About this time there is a movement of these nutrients up the bole and through the various limbs, branches, twigs and into the newly-formed leaves. The forces concerned with the upward transfer, and the rôle of phloem and xylem in the conduction of

Schütz (1909), Serex (1917), Palladin (1923), Seiden (1926), Combes (1926), Quartaroli (1929), McHargue and Roy (1932), Alway, Maki and Methley (1934) [1] and Sampson and Samisch (1935). Although some minor discrepancies are apparent, due possibly to differences in climate, species or experimental technique, a review of the literature reveals numerous similarities. It is generally agreed, for example, that the concentration of ash, silica, manganese and calcium in tree leaves (on per cent dry matter basis) increases as the season advances; that the concentration of magnesium, copper, and crude fiber tends to remain constant; but that the concentration of nitrogen, phosphorus, potassium and sulphur decreases. Results of the present study are in agreement with those of a majority of previous investigations as regards trends in the nitrogen, phosphorus,

TABLE 3

Average dry weight, and the nitrogen, phosphorus, potassium and calcium content of the leaves of three oak and two maple species at different times during the growing season.

Species	Date Sampled	Dry Wt. of Av. Leaf in Mg.	Nitrogen Content		Phosphorus Content		Potassium Content		Calcium Content [a]	
			N%	N_{mg}	P%	P_{mg}	K%	K_{mg}	Ca%	Ca_{mg}
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Average of Oaks [1]	May 27	192	3.747	7.19	0.342	0.66	1.470	2.82	0.539	1.04
	June 26	386	2.759	10.65	0.172	0.67	1.208	4.66	0.652	2.52
	July 26	485	2.635	12.78	0.151	0.73	1.037	5.03	0.754	3.66
	Aug. 26	530	2.473	13.11	0.151	0.80	1.002	5.31	0.909	4.82
	Sept. 25	551	2.403	13.25	0.149	0.82	1.000	5.51	0.953	5.25
Average of Maples [2]	May 27	175	2.314	4.05	0.289	0.51	1.280	2.24	0.741	1.30
	June 26	280	1.891	5.30	0.237	0.67	0.810	2.27	1.187	3.32
	July 26	326	1.887	6.14	0.234	0.76	0.686	2.23	1.036	3.37
	Aug. 26	343	1.847	6.34	0.233	0.80	0.687	2.36	1.169	4.02
	Sept. 25	350	1.805	6.32	0.230	0.81	0.682	2.39	1.372	4.80

[1] White, red and chestnut oak. Averages based on data in Table 2.
[2] Sugar and red maple. Averages based on data in Table 2.
[a] Because of exceedingly discordant results with chestnut oak (see calcium content for Sept. 1 in Fig. 3) the data from this species were not used in calculating the following averages.

inorganic solutes, are controversial questions that need not be discussed here. This study is concerned with the changes that take place within the leaves from the time they are formed until they drop in the fall. In the following discussion this period will be divided into two intervals, the one preceding and the one following that time at which the leaves start to yellow in the early fall. The former, which will be considered first, very nearly corresponds to the period of dry weight increase.

Changes During the Period of Dry Weight Increase.— Available data show that the concentration of nitrogen and various ash constituents in the leaves of deciduous trees may alter considerably as the leaves increase in age. But it should be emphasized that so long as the leaves are growing—increasing in dry matter—changes in the concentration of the various elements do not necessarily indicate movement of mineral nutrients to or from the leaves. Of previous investigations having a direct bearing upon this subject the following may be cited: Wehmer (1892), Riesmüller (see Palladin), Schulze and

potassium and calcium concentration of leaves. Experimental data (from Table 2, cols. 7-14) are shown in Figs. 2 and 3.

It is apparent (Figs. 2 and 3) that although the nitrogen, phosphorus and potassium concentration of all leaves decreased as the season advanced, the absolute quantity of these elements tended to increase. As regards calcium, both the concentration and the absolute amount of this element in all leaves showed an increase. To facilitate further discussion and description of the various illustrations the symbols $N_\%$, $P_\%$, $K_\%$ and $Ca_\%$ will be used to denote the concentration (as a per cent of dry weight) of these elements in leaves, and N_{mg}, P_{mg}, K_{mg} and Ca_{mg} to represent the milligram content.

Since the absolute amount of N, P, K and Ca in the leaves of all species except hickory was greater on

[1] According to the authors the headings to Table 3 (Alway, Maki and Methley, 1934) should be corrected to read, left to right, as follows: Date, Ash, CaO, MgO, P_2O_5, K_2O, Na_2O, SO_3 and N.

October 1 than at the beginning of the season, these data tend to show that there was no "backward" translocation of these elements during this period. In the literature that has been examined there is no conclusive evidence of nutrient movement out of the leaves so long as they are alive and growing, although some plant physiologists and botanists have interpreted decreases in nutrient concentration to mean backward (into twigs,

Data presented by Palladin (*loc. cit.*), based upon Riesmüller's analyses, show that the potassium concentration of beech leaves decreased considerably from May to November, but that during the period of *growth* there was no decrease in the absolute quantity of this element in samples of 1,000 leaves harvested at intervals of one month. Results of several other interesting experiments are discussed by Palladin, all of which indicate that
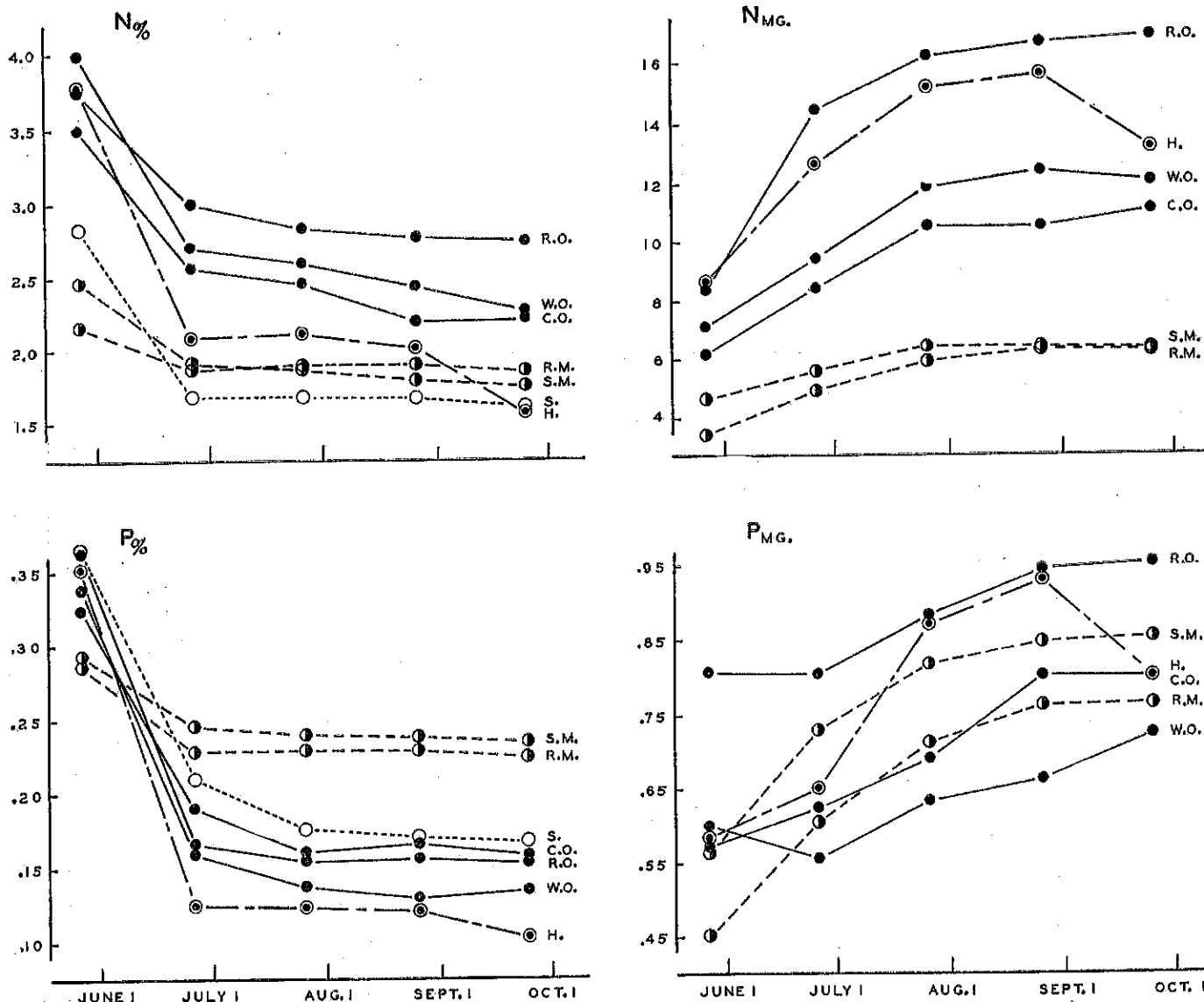
FIG. 2.—The nitrogen and phosphorus content, as per cent and milligrams per leaf, of the leaves of some forest trees at different times during the growing season.

branches and stem) translocation. But conclusions based upon variations in percentage values ignore the diluting or concentrating powers of changing leaf mass and, as has been shown (Fig. 1), the leaves of most species continue to grow until early fall. It is therefore apparent that changes in concentration are, in themselves, no evidence of nutrient migration. This was pointed out by Wehmer as early as 1892, and has since been referred to by many others (Palladin, 1923; Combes, 1926; Raber, 1928; McHargue and Roy, 1932; Mitchell, 1935; and Sampson and Samisch, 1935).

there is an increase rather than a backward movement of the various nutrients during the period of growth.

It will be observed (Figs. 2 and 3) that the N, P and K concentrations of all species decreased quite rapidly during the early summer, but that after mid-summer, and especially during September, $N_\%$, $P_\%$ and $K_\%$ tended to be relatively constant. The following explanation, which seems to agree with the observed data, is suggested. During the period of most rapid leaf growth the rate of dry weight increase exceeded the rate of N, P and K flow into the leaves, and the net

result was a "dilution" of these elements, apparent in the decreasing percentage values. As the growth rate fell off and became equal to the rate of N, P and K flow, the dilution process tended to cease, causing the concentration values (per cent nutrient content) to remain constant so long as the two rates were equal. Trends of the several variables, based upon averages of oaks and maples only, are shown in Figs. 4 and 5 (data from

the leaves. Since maples start earlier they approach this period sooner than either hickory or the oaks. So, if a 30-day correction is made for differences in the time of initial leaf growth, the $N_\%$ and $P_\%$ trends of the various species are, as with trends in dry weight increase, more comparable. Sections of the maple $N_\%$ and $P_\%$ curves (Fig. 4) from June 1 to September 1 are quite comparable to those of the oaks from July 1 to October
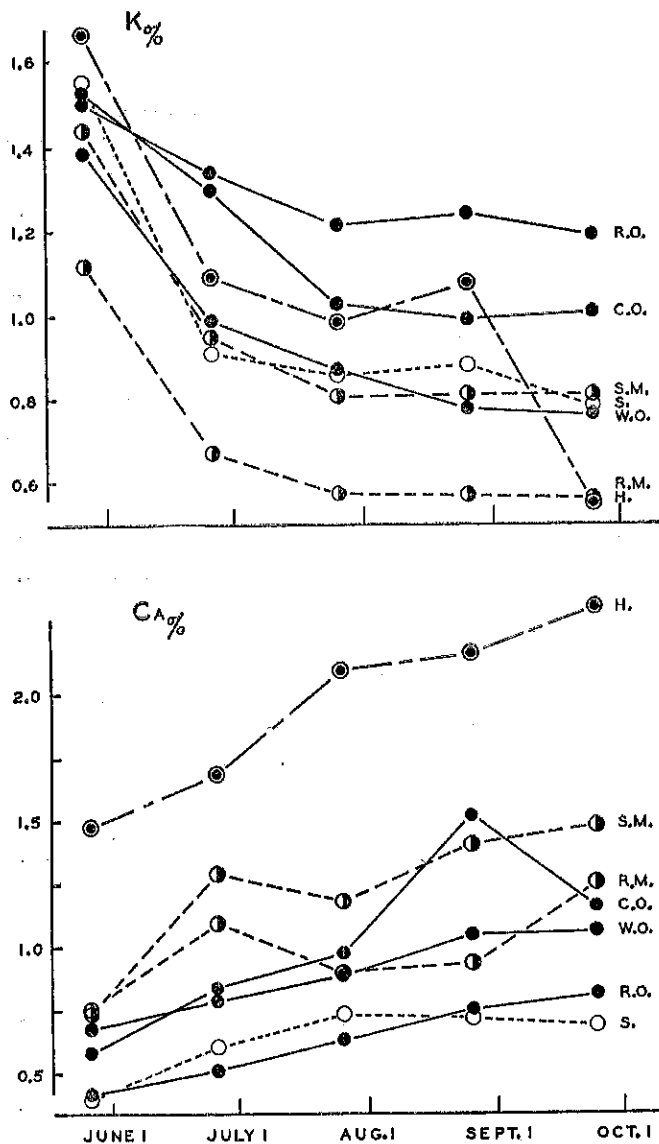

FIG. 3.—The potassium and calcium content, as per cent and milligrams per leaf, of the leaves of some forest trees at different times during the growing season.

Table 3). A study of these figures reveals the interrelations of the different variables better than any amount of written description.

Trends in $N_\%$ and $P_\%$ were not identical for all species. During June, for example, the rate of decrease in the concentration of these two elements was significantly greater for hickory and the oaks than for the maples (Figs. 2 and 4). This was probably due to differences in the time of initial growth. As pointed out above the greatest changes in nutrient concentration take place during the period of most rapid dry weight increase of
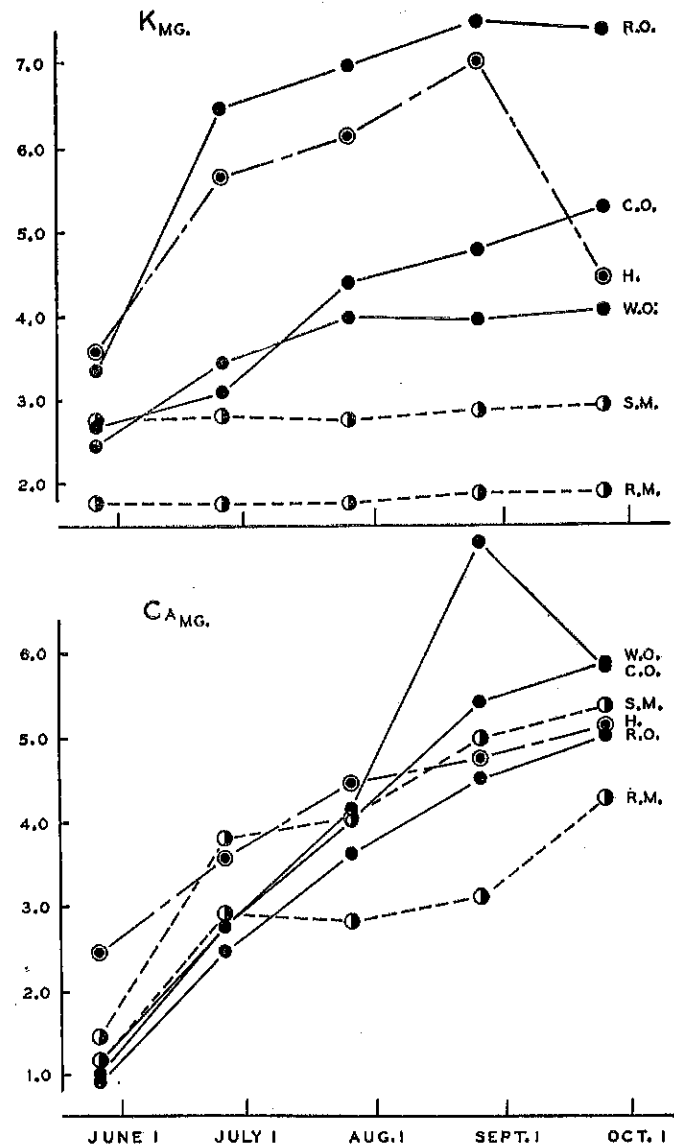
1. It is evident that many interesting points may be obscured, and the accuracy of trends affected, by the tendency of some investigators to group, and express only as a mean, the data for all trees irrespective of species.

$K_\%$ and $Ca_\%$ trends seem to be about the same for all deciduous species (Figs. 3 and 5). The absolute amount of potassium in the leaves of maples apparently increased but little between June 1 and October 1. This may account for the similarity (in $K_\%$ trends) between the maples and oaks. According to the data presented

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the movement of calcium into the leaves of all species proceeded at approximately the same rate during the entire growing season. Thus, unlike any of the other elements studied, the relation between leaf age and calcium concentration is a linear increase of approximately the same slope for all deciduous species. Because of

variations in nutrient concentration do not necessarily indicate translocation. No data were obtained on changing needle mass or, consequently, the absolute amount of the various mineral elements in the spruce needles at different times. For this reason no conclusions can be drawn regarding the movement of mineral

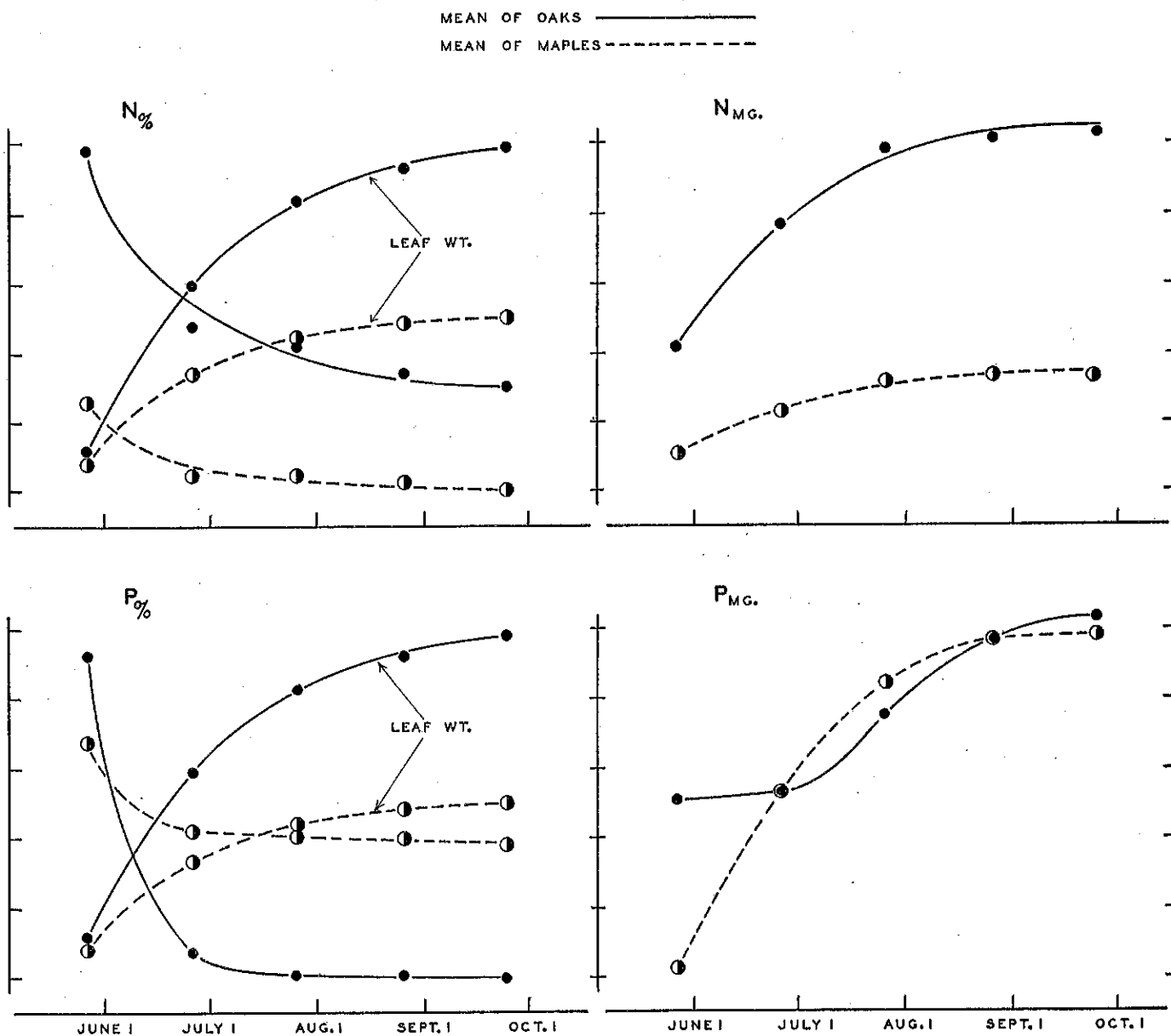MEAN OF OAKS ————————
MEAN OF MAPLES — — — — — — —

Fig. 4.—Average trends in the nitrogen and phosphorus content, as per cent and milligrams per leaf, and the dry weight increase of the leaves of oaks and maples during the growing season.

certain irregularities in the experimental data, due possibly to errors in sampling or analysis, the Ca variations are probably best shown as the average trends in Fig. 5.

Aside from minor differences the N%, P% and K% trends for Norway spruce (current year's growth) were quite similar to those of the deciduous species studied (Figs. 2 and 3). But, unlike any of the deciduous species, the concentration of calcium in spruce needles tended to decrease after about August 1. However,

nutrients to or from the needles of spruce during the growing season.

Translocation During the Period of Changing Leaf Color.—Experimental evidence presented in the foregoing discussion indicates that there is no movement of the various nutrient elements out of the leaves so long as they are living or growing organs. There is evidence, however, of such a migration just previous to the death of the leaves. Apparently this translocation begins about the same time that leaves turn from green to

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the autumnal colors characteristic of the species. The leaves of hickory, which usually start to yellow three to four weeks before those of oaks and maples, were green when sampled late in August, but were obviously dead and in full autumnal color by the next sampling date. It was during this period—one month—that leaves of

ducting system of the tree during September. The leaves of oaks and maples, which remained green through September, evidenced no significant changes during this month. However, leaves of these species sampled after leaf fall (about November 1) showed marked decreases in N, P and K. These results are not

MEAN OF OAKS ———————
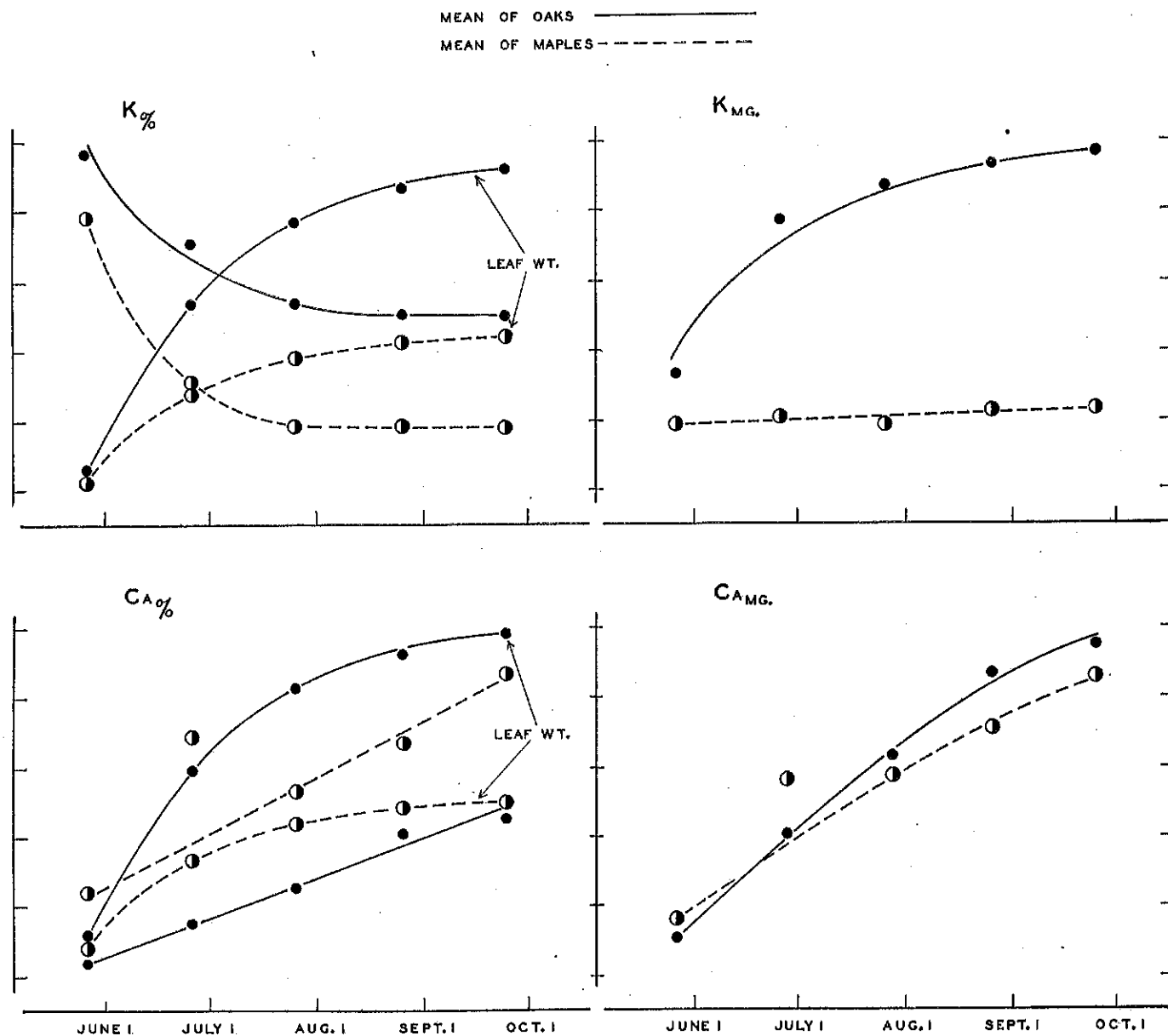MEAN OF MAPLES — — — — — — — —

FIG. 5.—Average trends in the potassium and calcium content, as per cent and milligrams per leaf, and the dry weight increase of the leaves of oaks and maples during the growing season.

this species showed marked decreases in the concentration of nitrogen, phosphorus and potassium (see Figs. 2 and 3). Since decreases in $N_\%$, $P_\%$ and $K_\%$ were accompanied by like decreases in the milligram content,[2] there can be little doubt that relatively large quantities of these elements were translocated back into the con-

[2] For comparison with other species the higher milligram content values of the heavier (compound) hickory leaves were plotted against reduced ordinate scales in Figs. 2 and 3. See Table 2, cols. 8, 10, 12 and 14 for actual data.

given in Table 2, since the leaves remained on the ground some time before the analyses were made. Therefore the indicated decreases in nutrient content were not all attributable to translocation, for there undoubtedly was some leaching while the leaves remained on the ground (see Lunt, 1933 and 1935). Unfortunately no analyses were made during or immediately following leaf fall. However, the data of Alway, Maki and Methley (1934) show very clearly what takes place at this time.

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Alway *et al.* (1934) sampled and analyzed leaves from nine species at five different times during the 1933 growing season: June 1, July 1, August 1, September 1 and ("freshly fallen") October 11-16. Leaves of every species—Norway and silver maple, red, white and bur oak, basswood, American elm, box elder and green ash—showed marked decreases in N and P concentration during the five or six weeks previous to leaf fall. On the basis of an average for all species, the same was true of K (no individual K values were given). Since it is certain that the leaves grew little if any during this interval, the decreasing percentages may, in this case, be safely interpreted as indicating nutrient migration. There may have been some leaching, even before the

TABLE 4

The nitrogen and phosphorus content of the leaves of some forest trees growing at Minneapolis, Minnesota, compared with similar analyses of the same and different species growing at Cornwall, New York.[1]

Species and Location	Date Sampled	P_2O_5 % [3]	P% [3]	N%
(1)	(2)	(3)	(4)	(5)
Average of 3 Oaks (Minneapolis, Minn.)	June 1	0.603	0.263	2.953
	July 1	0.483	0.211	2.486
	Aug. 1	0.446	0.195	2.276
	Sept. 1	0.446	0.195	2.160
	Oct. 11-16	0.273	0.119	0.963
Average of 3 Oaks [2] (Cornwall, N. Y.)	May 27	....	0.342	3.747
	June 26	....	0.172	2.759
	July 26	....	0.151	2.635
	Aug. 26	....	0.151	2.473
	Sept. 25	....	0.149	2.403
Average of 2 Maples (Minneapolis, Minn.)	June 1	0.640	0.279	2.905
	July 1	0.580	0.253	2.675
	Aug. 1	0.460	0.201	2.480
	Sept. 1	0.465	0.201	2.385
	Oct. 11-16	0.175	0.076	0.525
Average of 2 Maples [2] (Cornwall, N. Y.)	May 27	....	0.289	2.314
	June 26	....	0.237	1.891
	July 26	....	0.234	1.887
	Aug. 26	....	0.233	1.847
	Sept. 25	....	0.230	1.805
Green Ash (Minneapolis, Minn.)	June 1	....	....	2.670
	July 1	....	....	1.870
	Aug. 1	....	....	1.920
	Sept. 1	....	..	1.250
	Oct. 11-16	....	....	0.630
Shagbark Hickory [2] (Cornwall, N. Y.)	May 27	....	....	3.785
	June 26	....	....	2.089
	July 26	....	....	2.112
	Aug. 26	....	....	2.012
	Sept. 25	....	....	1.566

[1] Minneapolis, Minnesota data after Alway, Maki and Methley (1934).

[2] Data from Table 2.

[3] Phosphorus is expressed as P_2O_5 in Table 2, *Alway et al., loc. cit.* These values are shown in col. 3 of the above table for comparison with the P% equivalents in col. 4. Calculation as P_2O_5 gives the impression of more phosphorus than is actually present.

leaves fell. The data of Combes (1926) suggest this possibility. But the majority of the loss can undoubtedly be attributed to nutrient translocation.

Additional information regarding the time at which the backward translocation of nutrient elements takes place can be obtained by comparing the Alway *et al.* data with those of the present study. The necessary data from Table 2 (Alway *et al., loc. cit.*) are reproduced, with permission of the authors, in Table 4, and various comparisons are made in Fig. 6. Because of climatic differences certain corrections are necessary. For example, according to the U. S. Weather Bureau reports, the growing season is somewhat shorter at Minneapolis, Minnesota, than at Cornwall-on-Hudson, New York. At the former place the leaves of most trees fell about October 15, in the autumn of 1933 (see Alway *et al., loc. cit.*). But at Cornwall, in the autumn of 1935, the leaves from trees used in the present study did not fall until November 1. The difference in the time of leaf fall at the two places, and for the years of the respective experiments, appears to be about 15 days. With this 15-day correction made, as in Fig. 6, the similarity of trends is striking, especially for the latter part of the season. The agreement is not as good for the early part of the summer. This, however, is to be expected, for the growing season at Minneapolis does not start as early in the spring as at Cornwall. But we are interested chiefly in what takes place in the autumn, so no attempt was made to "compress" the entire (New York) growing season to a comparable basis.

According to available information (personal communication) the leaves of oaks and maples started to yellow at Minneapolis about September 15, while at Cornwall there was no yellowing until after October 1. In neither case was there any significant change in N, P and K concentration for the month previous to this time. But it is evident (Fig. 6; Alway *et al., loc. cit.,* Table 2) that both oaks and maples lost considerable N, P and K during the period in which the leaves were changing color—dying. It is perhaps more significant that hickory at Cornwall and ash at Minneapolis, two species whose leaves ordinarily start to yellow three to four weeks sooner than oaks or maples, both showed marked nutrient losses approximately one month sooner than the oaks and maples of the respective locations (Figs. 2 and 3; Alway *et al., loc. cit.,* Table 2). In Fig. 6 the nitrogen concentration trends of these two species are compared with each other, and with similar trends for oaks and maples.

QUANTITATIVE COMPARISONS

In the foregoing discussion comparison of the mineral concentration in the leaves of the different species at any given time has been purposely avoided. Successive analyses of leaves from a single tree of each species or, better still, several species of the same genera, are apparently sufficient to show characteristic *trends* in mineral nutrient content during the growing season (Fig. 6). But such data, since each species is represented by only a single tree, are insufficient as a basis for comparing the nutrient intake of the different

species. Even though all trees sampled occur on essentially the same site, it is possible that the apparent differences in nutrient absorption, as reflected in the leaves, may be due to some peculiarity of the individual or its local environment, and not characteristic of the species in general. It so happens that the phosphorus

cussed in another paper), in which numerous analyses were made of the leaves of the three species of oaks growing together on a wide variety of sites, indicate that the reverse is usually true. However, the high N content of this red oak—higher than any sampled to date—is easily explained. This particular tree is
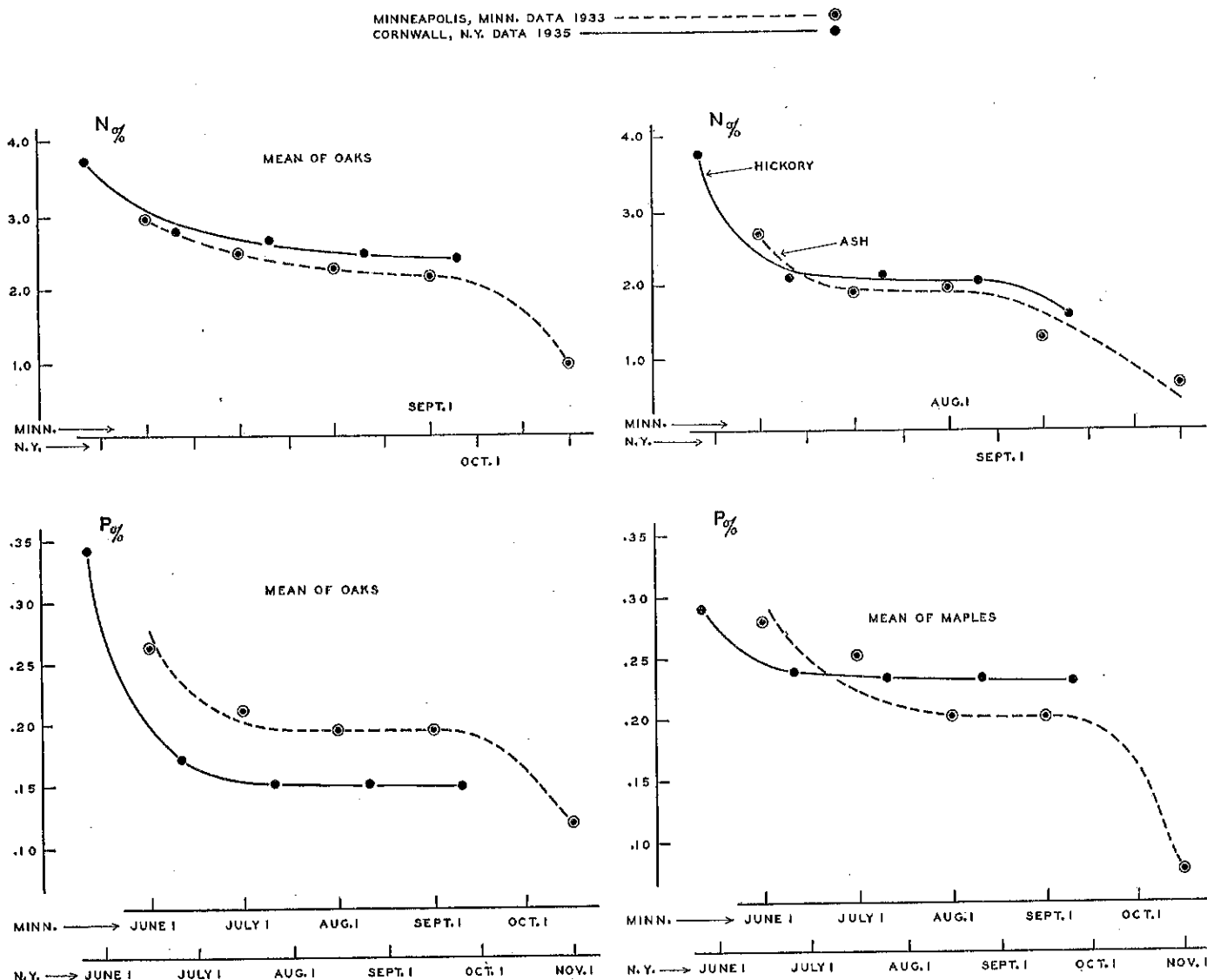
FIG. 6.—Trends in the nitrogen and phosphorus content of the leaves of some forest trees growing at Minneapolis, Minnesota, compared with those of the same and different species growing at Cornwall, New York. The Minneapolis data, from Table 2, Alway, Maki and Methley (1934), are compared with the Black Rock Forest data in Table 4, p. 38.

intake of the maples and oaks sampled in this experiment is, in each instance, quite typical, but such is not the case with nitrogen.

According to the data presented (Figs. 2 and 4) the phosphorus concentration of the maple leaves just previous to yellowing was considerably higher than that of the oaks. This is in line with previous observations based upon more numerous data (Mitchell and Finn, 1935). But it is not characteristic of red oak for its leaves to have a higher nitrogen content than those of white and chestnut oak, as the data (Fig. 2) seem to indicate. The results of recent experiments (to be dis-

located in the corner of a pasture, and beneath it is a water trough where cows congregate to drink. The abundant fertilizer which this tree now receives is very much in evidence. But such is not always the case, since soil fertility differences are seldom so apparent. Therein lies the danger of basing quantitative comparisons on data obtained from *single* trees of each species. It is interesting, however, that although the general level of N is higher in the leaves of red oak than in those of the other two oaks, the trends during the summer are very similar. And the higher N and K content of the red oak leaves is further proof of the

sensitivity of leaf analysis as an indicator of soil nutrient supply (Mitchell, 1935).

EVIDENCE OF MINERAL NUTRIENT MOVEMENT FROM LEAVES TO ROOT

Evidence has been presented to show that relatively large amounts of nitrogen, phosphorus and potassium disappear from tree leaves during the period of yellowing. But since neither stems nor roots were analyzed, the question arises as to whether these losses are attributable to translocation or to leaching. In the preceding discussion it has been assumed, on the basis of data presented by Combes (1926), that most of the nutrients lost by yellowing leaves tend to move back into the conducting system of the tree. This is the opinion of most plant physiologists, although based in many instances on results obtained with species other than trees.

Combes (1926) was perhaps the first to present conclusive evidence of nitrogen transfer from the leaves to the stem and roots of tree species. In one experiment the nitrogen content of horse chestnut, beech and chestnut leaves, yellowing naturally on the trees, was compared with that of leaves yellowing on branches removed when the leaves were green. Bases of the detached branches were kept in water during the experiment, and the leaves were exposed in the open air. Successive analyses showed that leaves yellowing normally on the trees lost much of their nitrogen—absolute amounts were calculated—whereas those yellowing on the detached branches lost very little, due to leaching or translocation, even though they were attached to a branch through which the N would normally move. In another experiment the leaves, stems, and roots of young beech and oak trees were analyzed for N at various times during the period of yellowing. It was found that nitrogen lost by the leaves during yellowing accumulated first in the stems and then in the roots. Since nitrogen was calculated in absolute amounts as well as in terms of concentration, these results, unlike those where N is expressed only in terms of concentration, may be accepted as positive evidence of N movement out of the leaves, through the stem and into the roots. The net increment of N in the stem and roots was very nearly, but not quite, equal to the N lost by the leaves. This suggests a small loss due to leaching while the leaves were yellowing on the trees.

The data of Combes show that the migration period of N covers about two months, and that the outward flow becomes more rapid toward the end. This agrees with the decreasing N trends of ash and hickory, as shown in Fig. 6.

THE INFLUENCE OF NITROGEN AVAILABILITY UPON THE TIME AT WHICH LEAVES YELLOW

Apparently the external (soil) nitrogen supply, through its influence upon internal (leaf) N concentration, controls to a certain extent the time at which tree leaves begin to yellow in the fall. A brief summary of a recent experiment—to be discussed fully in another paper—will illustrate. Four quarter-acre plots were established in an even-aged stand of mixed hardwoods in the spring of 1935. One plot served as a control, and the others were supplied varying amounts of nitrogen fertilizer (Mitchell and Hosley, 1936). The leaves of ash and hickory on the control plot started to yellow about September 1, whereas those on the fertilized plots remained green until October 15. As might be expected in view of previous discussion, analyses showed that N, P and K started to migrate from the leaves of ash and hickory on the control plot soon after the leaves began to yellow on September 1. Although it does not necessarily follow, leaves of these same species growing on the nitrogen fertilized plots evidenced no loss of N, P and K until after their leaves started to yellow about October 15—six weeks later. Since all other factors of site were identical, the six-week difference in the time at which leaves of the same species started to yellow and lose nutrient elements through translocation, can be explained only the basis of nitrogen availability. The results of similar experiments, in which plots were fertilized with varying amounts of phosphorus and potassium, indicate that the time of yellowing is not influenced by the available supply of either of these elements.

Additional evidence of this effect of nitrogen is available. In the autumn of 1935 notes were made on the time of initial yellowing of trees growing in a wide range of soils on the Black Rock Forest. The previous year most of these soils were evaluated for nitrogen supplying power on the basis of leaf tests. When the data on N supply and date of yellowing were grouped into elevation classes, so as to eliminate the influence of this factor on local climate, a good correlation was found between nitrogen availability and the time of yellowing: the higher the nitrogen supply, the longer the leaves of the various species remained green. No study of nutrient movement was made. Observations made during trips through the northern tier of Pennsylvania counties in the fall of 1934 and the fall of 1935 are also of interest in this connection. Within a limited range in elevation, the leaves of species growing on poor, rocky slope sites appeared to yellow two to three weeks sooner than the same species on the deeper, and probably more fertile, valley soils. Although such general observations are by no means conclusive, they do tend to confirm conclusions drawn from the controlled fertilizer experiment.

Supplements of nitrogen above the minimum necessary for survival probably accelerate tree growth more than equal amounts of any other single nutrient element. It is well known that within the critical range of supply, nitrogen increments stimulate the *rate* of dry weight increase. But since relatively high nitrogen supplies appear to keep the leaves green longer, and possibly functioning longer, part of the *total increment* attributable to nitrogen in any single season may be due to prolonging the *length* of the growing period.

It is difficult to explain why, as the data seem to indicate, high nitrogen supplies defer the movement of mineral nutrients from the leaves in the autumn. The

chief difficulty is that so little is known about the forces concerned with the translocation of inorganic solutes. Autumnal growth of tree roots is well known. It is possible, therefore, that the downward movement of mineral nutrients is in response to some attracting force set up by the growing roots. On the other hand the downward migration of nutrients may be the cause rather than the result of autumnal root development.

Relative Mobility of Mineral Elements

It appears that during the period of yellowing certain mineral elements are translocated to a greater extent than others. Although some apparent discrepancies may be found in the literature, the trends for certain elements are fairly well established. Available data indicate, for example, that during the period of yellowing there is an outward movement of potassium, nitrogen and phosphorus from the leaves, whereas there is little or no change in the calcium, silicon or magnesium content at this time (Figs. 2, 3, and 6; Wehmer, 1892; Riesmüller, cited by Palladin; Schulze and Schütz, 1909; Palladin, 1923; Combes, 1926; Raber, 1928; McHargue and Roy, 1932; Alway, Maki and Methley 1934; and Sampson and Samisch, 1935). Some of these studies include no data on absolute quantities of nutrients. But since, as shown in Fig. 1, leaves grow little if any after they start to yellow, variations in nutrient concentration can, during this period, be interpreted as indicating changes in the absolute amount of the various elements present.

The relative stability, complexity and solubility of the inorganic and organic compounds formed in the leaf by the various elements probably determine which are translocated, and to what extent. Thus, although the physiological rôle of potassium is not definitely known (Miller, 1931, p. 255), experimental evidence (Kostyts-chew and Eliasberg, 1920; André and Demoussy, 1927; Janssen and Bartholomew, 1929) indicates that this element occurs in plants in forms readily soluble in water, and that it is one of the most mobile of the essential mineral nutrients. It is significant, therefore, that during the period of yellowing hickory leaves lost, through translocation or leaching, more potassium than either nitrogen or phosphorus (see Figs. 2 and 3). These two elements, N and P, although it is generally believed that they are less mobile than K, apparently do occur in leaves in forms quite readily transferable. A considerable amount of the phosphorus—necessary for the formation of lecithin, the nucleoproteins and nucleic acid—in plants is soluble in water (Ames and Boltz, 1912; Hartwell et al., 1917; Peterson and Peterson, 1926). Nitrogen enters into the structure of chlorophyll, amino acids, protein, alkaloids, and the protoplasm of the plant, and is seldom found in very great amounts as ammonia, nitrates or nitrites. Nevertheless, the experiments of Schulze and Schütz (1909), Combes (1926) and Alway et al. (1934) suggest that the nitrogen in the leaves of tree species is relatively mobile.

Apparently the compounds formed by calcium and silicon in the leaves of trees are relatively insoluble.

This probably explains why, as the data seem to indicate, these two elements are not transported out of the leaves during the period of yellowing. Although in plants such as cabbage up to 60 per cent of the Ca is soluble in cold water, it is known that in many other species of plants and possibly in tree leaves, much of the calcium is deposited as calcium pectate and calcium oxalate, both of which are practically insoluble in water. Silicon is a common constituent of tree leaves and, according to available information, is usually found deposited in the cell walls. In ash analysis of tree leaves silicon invariably occurs, and makes up practically all, of the insoluble residue. Magnesium is one of the constituents of chlorophyll, which disintegrates as the leaves yellow, and is also quite abundant in various soluble forms in the green leaf. It is difficult, therefore, to explain the apparent immobility of this element on the basis of solubility.

The Value of Leaf Analysis

As suggested in the introduction there is reason to believe that much valuable information regarding tree nutrition and the chemical aspects of site can be obtained from leaf analysis. Available data indicate a high degree of correlation between the external (soil) supply of nitrogen, phosphorus, potassium and calcium, and the concentration of these elements in the sap, foliage and other parts of tree seedlings and mature trees; also that, within certain critical ranges, and when other growth factors are not limiting, tree and seedling growth varies in proportion to the internal nutrient concentration (Aldrich-Blake, 1930; Gast, 1936; Mitchell, 1934, 1935 and unpublished data; Mitchell and Finn, 1935; Mitchell and Hosley, 1936). Since tree species apparently absorb mineral nutrients in proportion to the available supply, the nutrient content of the foliage or some other part of a tree growing in a given soil complex should be a good index to the mineral supplying power of that soil. Agriculturists have for many years been utilizing this principle of proportional nutrient absorption to determine the fertilizer requirements of various crop plants (see Mitchell, 1934, pp. 5-9 for a discussion of the literature).

Artificial fertilization of forest crops is not being advocated since, aside from nursery fertilization, such a practice is probably not economic at present in this country. But it is suggested that the chemical aspects of different sites can be evaluated and compared on the basis of leaf analysis. The advantage is that the question of "availability," which always arises in connection with either direct or so-called extraction methods of soil analysis, is satisfactorily solved. It must be conceded that any nutrients absorbed are necessarily available and, perhaps more important, available to the plant that absorbed them from a given soil complex. The significance of the latter point becomes apparent in view of recent experiments showing that different species of trees vary in ability to extract nitrogen and phosphorus from identical substrates (Mitchell and Finn, 1935; Mitchell, unpublished data).

Chemical fertility evaluations based upon leaf analyses

are not confined to any particular soil zone or horizon, and they are selective only in so far as the tree roots are selective in their absorption of nutrients. The chemical composition of the foliage on a single tree is influenced by, and is therefore a measure of, conditions in the entire soil volume penetrated by its roots. Mineral nutrients are extracted, not from an arbitrarily fixed zone, but from the soil horizon or horizons which the roots of a particular tree species naturally occupy in any given soil complex. Nutrient intake, as measured by the internal concentration of the leaves, depends upon the external supply and the absorbing power of the roots. It is doubtful if the extraction properties of chemical solutions in the laboratory imitate the latter, especially since most tree species are mycotrophic and may obtain large quantities of mineral nutrients through their symbiont fungi.

Leaf tests give promise of providing the silviculturist, and especially the ecologist, with a very useful tool. It is believed, therefore, that in any intensive study of forest soils, both soil and leaf samples should be taken: the former to determine physical conditions, and the latter to evaluate nutrient availability.

SAMPLING TECHNIQUE

The value of quantitative comparisons depends to a great extent upon the care used in taking leaf samples. The concentration of nutrient elements in tree leaves may vary with factors other than the available external (soil) supply. A knowledge of these factors is therefore essential if accuracy in sampling is to be attained. Of such factors, leaf age is perhaps the most important and will be discussed first.

Data from the present and other experiments indicate that the concentration of nitrogen, phosphorus, potassium and certain other elements in tree leaves decreases with leaf age—quite rapidly in early summer during the period of greatest dry weight increase—but becomes relatively constant for the two or three weeks previous to yellowing. It has also been shown (Figs. 2, 3, and 6) that just previous to yellowing, leaves contain the greatest total quantity of the various nutrient elements. Backward translocation apparently does not start until the leaves begin to change color. It appears, then, that for quantitative comparisons of nitrogen and ash content, the best time to make leaf collections is during the two or three weeks preceding yellowing, when the total mineral content is near maximum, and the concentration is relatively constant. At the Black Rock Forest in an average year experience has shown that the best time to sample such species as ash and hickory is from August 15 to September 1. Oaks and maples are usually sampled during the last two weeks in September. But since the time at which leaves start to yellow varies with local climate, species and nitrogen supply, these dates are applicable only to localities with soil and climatic conditions similar to those at the Black Rock Forest. It is simple, however, to work out similar dates for any given region or species. Local residents usually know to

within a week or two the time at which the various species ordinarily start to color.

Although the data presented show that the mineral and nitrogen content of leaves is maximum just previous to yellowing, after which the backward translocation starts, there is some evidence that this migration removes only about half of the amounts originally present in the leaves. It also appears that species which are able to absorb large quantities of nitrogen and phosphorus from a given soil complex, retain in their leaves, after translocation, greater amounts of these elements than species of lower nutrient extractive ("feeding") powers (Mitchell, unpublished data). If this is true it may be possible to compare species for relative "feeding power" on the basis of samples taken immediately after leaf fall. But until more data are available on this subject such comparisons, as well as site evaluations, should be based upon results obtained from leaves sampled during the two or three weeks preceding yellowing. However, if it is desired to compare deciduous species for the amount of mineral nutrients they deposit on the forest floor with the annual leaf fall, it is probably best to obtain leaf samples just previous to, or immediately after leaf fall. If taken sooner, translocation may still be taking place, and the analyses will indicate amounts greater than will actually reach the soil; if samples are composed of leaves which have remained on the ground very long, the results are apt to be low because of loss due to leaching (see Lunt, 1933 and 1935).

Another point to be considered is the time of day at which to take leaf samples. The investigations of Frank and Otto (1891), Schulze and Schütz (1909), Otto and Kooper (1910), Chibnall (1924) and Miller (1926) show the nitrogen content of tree leaves, and the leaves of many other plants, to be slightly, but significantly, higher at night than in the morning. However, since the difference between samples taken at the two extremes, twelve hours apart, is relatively small, no great error would be incurred if sampling times differed by only four or five hours. But comparison of samples taken at extremes should be avoided. It might be well to standardize on mid-day as a convenient sampling time, and limit the collection interval to from two to three hours before and after noon.

There is much difference of opinion as to whether samples should be composed of leaves from a single, or from many different locations on each tree. In most cases samples taken according to the latter procedure are supposed to be representative of the total leaf mass. Such a sample, if truly representative, is highly desirable. There are, however, several factors which may affect the accuracy of this method of sampling. Seiden (1926) presents data to show that the ash content of tree leaves varies with elevation (distance from ground), and there is some evidence that exposure (north or south) influences the nutrient concentration of leaves. Because of these factors there is reason to doubt whether a truly representative sample (of the entire leaf mass) can be obtained unless all foliage is removed, thoroughly mixed, and then subdivided. It is obvious that such a procedure is impractical except for very careful ex-

perimental work. The short cut to this method, in which leaves are taken at random from many different elevations and exposures, may not produce a sample that is sufficiently representative of the *entire* leaf mass to justify the extra work involved.

A sampling method favored by some investigators is that which requires leaves from single limbs of a standardized elevation on each of four exposures, *i. e.*, north, south, east and west. Such a sample is not assumed to be representative of the entire leaf mass, since leaves are taken from only four places on each tree. For the same reason this method is more rapid than those requiring leaves from many different elevations and exposures. This method, although somewhat slower than that in which leaves are taken from only a single location on each tree, has one apparent advantage over the latter procedure. It seems there is little or no lateral transfer of inorganic solutes in tree species (Miller, 1931, p. 695). Available data indicate that mineral nutrients absorbed by roots on one side of a tree are moved to, and used by, that portion of the bole and the limbs, branches, twigs and leaves directly above those roots. Thus, if soil conditions vary significantly from one side of a tree to another, a sample composed of leaves from four exposures should be a better index to the nutrient absorption of the entire root system than a sample taken from a single limb on any one exposure.

If leaf tests are to be of practical value to foresters a rapid method of sampling must be devised. Because of the time and expense of climbing, or moving an extension ladder to many different locations on each tree, as would be necessary if the sample is to represent the *entire* leaf mass, it is exceedingly doubtful if this method will be generally used. This leaves two methods to be considered: the one in which leaves are taken from a single standardized location on each tree, and the one requiring leaves from single limbs of a standardized elevation on each of four exposures. Neither procedure is assumed to produce a sample representative of the entire leaf mass, although it is possible that they may. The former is by far the faster method, but the latter, since there is little or no lateral transfer of inorganic solutes, is supposed to yield a sample more representative of the nutrient absorption of the entire root system. However, the extra work of sampling three more locations on each tree may not be justified on the basis of increased accuracy. Although this question cannot be settled until more data are available, it is doubtful if, in a majority of cases, soil conditions vary sufficiently from one side of a tree to another so that, since there is no "equalization" by lateral movement, the mineral content of the leaves on one side would differ greatly from those on any other.

The practice of taking leaves from a single standardized location on each tree is certainly more rapid than any of the other methods discussed, and is believed to be sufficiently accurate for practical purposes. Although samples taken in this way may not correspond exactly with the average for all foliage on each tree, they do afford a rapid means of making relative comparisons of trees of the same or different species on various sites.

Furthermore, available data indicate that samples taken from a standardized location (near the top of the crown on the south exposure) on each tree deviate only slightly in nutrient content from samples composed of leaves taken from fifteen or twenty locations on the same trees.

If samples are to be taken from a single place on each tree, the question of location arises. In the fertilization experiments at the Black Rock Forest all samples are taken from a limb near the top of the crown on the south side of each tree. A five-man crew equipped with two ladders and two extension pruners can take as many as 200 such samples in four hours. In all cases within critical ranges of nutrient supply a good correlation has been found between the external (soil) supply and the nutrient concentration of leaves sampled in this way (Mitchell, 1935; Mitchell and Finn, 1935, and unpublished data). This particular location was decided upon because of the possible influence of varying degrees of shade upon the nutrient concentration of leaves. The light received by leaves on the lower branches of trees in a fully stocked stand would be variable. For the same reason only trees of the dominant and codominant crown classes are sampled.

The number of trees of a single species to be sampled on a given area, if an evaluation of the chemical aspects of site is desired, will depend upon the deviations of individual samples from the mean of all trees sampled. Under conditions prevailing at the Black Rock Forest a mean based upon analysis of samples from fifteen individuals scattered over an area of one acre has been found to be statistically significant as an indicator of the available nutrient supply. On some areas where soil conditions are more uniform the standard error of the mean of fewer samples has been acceptable.

SUMMARY AND CONCLUSIONS

Leaf samples were taken on May 27, June 26, July 26, August 26 and September 25 from single trees of each of the following species: white, red and chestnut oak, red and sugar maple, shagbark hickory and Norway spruce. The moisture content and the dry weight of the average leaf in each sample were determined. All samples were analyzed for N, P, K and Ca. Results of analyses were expressed as milligrams per average leaf, as well as in terms of concentration (per cent dry matter basis). Only changes in the former (absolute amounts) constitute evidence of movement of these elements to or from the leaves.

It was found that leaves of the deciduous species studied continued to increase in weight as long as they remained green. The rate of dry weight increase was greatest during the first two months after the leaf buds burst, and dwindled to almost nothing in the month preceding initial yellowing. Trends in the moisture content were exactly opposite to those of dry weight increase.

The *concentration* of N, P and K in the leaves of all species decreased quite rapidly during the period of greatest leaf growth, but tended to become relatively constant for the month previous to initial yellowing. In

every case the calcium concentration increased steadily during the entire growing period.

The *absolute amount* of N, P, K and Ca in the leaves increased as the season advanced, reaching a maximum just previous to the time at which the leaves turned from green to the autumnal colors characteristic of the species. After yellowing the absolute amounts of N, P and K decreased, indicating a movement of these elements out of the leaves. There was no loss of Ca either before or after yellowing.

Although there appears to be a movement of N, P and K out of the leaves and back into the conducting system of the tree, starting about the time the leaves begin to yellow (die), the experimental evidence presented in this and other reports referred to in the text indicates that there is no such migration so long as the leaves are alive and growing. Decreases in mineral *concentration* during the period of leaf growth, which are sometimes interpreted as indicating mineral nutrient migration, are due to the "diluting" effect of rapidly increasing leaf mass and, taken alone, are not evidence of translocation.

It is believed that much valuable information regarding tree nutrition and the chemical aspects of site quality can be obtained from leaf analysis. The best time to collect leaf samples for quantitative comparison of nitrogen and ash content is during the two or three weeks preceding yellowing, when the total mineral content is near maximum, and the concentration is relatively constant. The exact time will vary with species, nitrogen supply and local climate, since these factors all influence to some extent the time at which leaves start to yellow.

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