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The Concentration of Nutrients in Tissues of Plantation-Grown Eastern Cottonwood (*Populus deltoides* Bart.)

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SUMMARY AND CONCLUSIONS

Nutrient concentrations were determined for 10 tissues from each of 24 cottonwood trees that ranged in age from four to 16 years. Highest concentrations occurred in the most physiologically active tissues; i.e., stemtips, current branches and foliage. Tree age had little influence on the variation in nutrient concentration of tissues.

Some differences in concentrations of nutrients in foliage were associated with differences in chemical properties of the soils. Concentrations of P, Ca and Mg were above proposed critical levels for cottonwood, but concentrations of N were slightly below the critical level. The concentration of K in the foliage varied with the level of exchangeable K in the soil. However, the range of observed variation was not reflected in the productivities of the several plantation soils.

Gradients in nutrient concentrations along the length of stems occurred in both stemwood and stembark. Concentrations in stems were highest near the apex and lowest at the base, and the greatest rates of change were in the portion of the stem within the living crown. The gradients were most evident for N, P and K. Concentration gradients in stembark were similar in pattern to those in stemwood except for Ca, which was highest at the base of stems.

Coefficients of correlation of nutrient concentrations among tissues generally were low. Thus, the nutrient concentration of any single tissue cannot reliably serve as a predictor of nutrient levels in other tissues.

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Knowledge of chemical composition is essential for estimating the nutrient uptake of cottonwood plantations and the nutrient removals imposed by cropping. This information is vital because of the high nutrient demand and rapid growth rates of the species (Carter and White, 1971a).

The chemical status of plant tissues has been used to estimate site quality in cottonwood (White and Carter, 1968) and to assess growth and nutrient requirements of the species (Gilmore, 1976). However, the literature lacks information about the inorganic composition of trees and the concentration relationships among the various tree parts, and there is a growing need to increase the reference data in this area (Aldrich, 1967). Therefore, a study was designed and conducted to characterize the chemical composition of plantation-grown cottonwood trees on alluvial sites in the Mississippi River Valley.

The plantations studied ranged from four to 16 years of age and are located in Bolivar, Issaquena and Warren Counties in Mississippi and Chicot County in Arkansas (Table 1). The plantations in Bolivar, Issaquena and Chicot Counties are on the Commerce (Typic Fluvaquents) and Robinsonville (Typic Udifluvents) soil series in the floodplain of the Mississippi River. The plantations in Warren County are on the Adler soil series (Aquic Udifluvents) in a drainage of the loessial bluffs. The average site index of the plantations is 38 meters at 30 years. The plantations exhibited satisfactory early establishment and received intensive culture during their development, including early cultivation and frequent thinnings. The planting stock for all plantations consisted of cuttings from unselected populations.

Table 1. Age and average dimensions of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley, by identity and location of plantations.

Identity	Location	Age	Number of Trees	Dimensions	
				DBH	Height
		-years-		-cm-	-m-
Catfish	Bolivar Co., MS	4	3	16	13
Leavenworth	Chicot Co., AR	6	3	19	18
Catfish	Bolivar Co., MS	9	3	23	22
Fitler	Issaquena Co., MS	9	3	26	23
Fitler	Issaquena Co., MS	12	4	28	26
Warren	Warren Co., MS	15	4	31	29
Warren	Warren Co., MS	16	4	36	32

PROCEDURE

Destructive Sampling of Trees

A 24-tree sample was selected from seven plantations that differed by age and/or location, using a mean tree technique described by Mueller (1976). The trees were harvested in August 1975 and ranged in size from 16 to 36 cm in diameter and from 13 to 32 m in height (Table 1).

Stems of the sample trees were severed into 1.2 m bolts, and *stemwood* and *stembark*[1] subsamples were obtained from 5-cm thick disks cut from the middle of each bolt. The stemwood samples were wedge shaped and extended outward from the stem pith to assure representative samples of stem cross sections. No separation was made of the wood and bark tissues in the material remaining (i.e., *stemtips* of varying length) after the last bolt was cut from each stem. Living branches were separated into three portions based on age as follow:

1. *older branches*---those initiated three or more years earlier and without current branches;
2. *intermediate branches*---those one to two years old and with current branches and
3. *current branches*---those produced during the season when sampled and with foliage.

The living branches were sampled by dividing the crown into upper, middle and lower sections and separating the branches of each section into older, intermediate and current portions. Each branch portion was subsampled in each crown section on the basis of its contribution to the total weight of that portion for the entire crown. These subsamples were composited to obtain a single sample of each branch portion. The older and intermediate branch portions were separated into wood and bark tissues. The *dead branches* were sampled in a similar manner. A *foliage* sample was obtained by compositing subsamples proportionally to the weight of each crown section.

Therefore, each tree was represented by the following ten tissues:

stemwood
stembark
stemtip
older branchwood
older branchbark
intermediate branchwood
intermediate branchbark
current branches
dead branches
foliage.

Each tree was represented by a single sample of each tissue, except for stemwood and stembark for which the number of samples varied. About one half of the total stemwood and stembark samples were analyzed, and these were distributed evenly along the length of the stem. A total of 702 samples were analyzed---236 stemwood, 274 stembark and 192 other tissues.

Laboratory Analysis

Tissues were prepared for chemical analysis by grinding in a Wiley mill to pass a 20-mesh sieve. Total N of wood tissues was determined by a macro-Kjeldahl procedure, and a semimirco-Kjeldahl procedure was used for non-woody tissues. Samples were analyzed for P, K, Ca and Mg after dry ashing at 500° C for four hours. Total P was determined by the vanadomolybdate procedure (Jackson, 1958), total K, Ca and Mg by atomic absorption spectroscopy (Issac and Kerber, 1971). The concentration of nutrients was expressed as a percentage of oven-dry weight (75° C).

Statistical Analaysis and Calculations

Data were analyzed as a completely random design, using analysis of variance to test for differences among the plantations for given tissues and nutrients. Differences in nutrient concentration among tissues also were tested, using the 24 sample trees as replicates in the analysis of variance. Means were separated by Student-Newman-Keuls' test to permit meaningful comparisons among ages, locations and soil series.

Gradients in nutrient concentration along the length of stems were regressed with the reciprocal of distance from the stem apex as the independent variable. The quadratic and cubic forms of the independent variable also were tested. The resulting equation for each nutrient contained only the terms that were significant at the 5% probability level. The stemtips were not included in the regression; therefore, the data ranged from the stem base to less than 1.2 m from the apex.

A weighted mean nutrient concentration for each tree was calculated for the stemwood, stembark, stem and living branches. The weighted mean concentration of each nutrient in each tree component or combination of components was nutrient content divided by dry weight of the component or combination.

[1]Bark is used in a broad context and the samples consisted of all tissues that were separated easily from the stemwood.

RESULTS

Nutrient Concentrations of Tissues

Nutrient concentrations within a tree vary by tissue (Table 2). The general ranking of nutrient concentrations in tissue categories is *other* > *bark* > *wood*, except that Ca concentration is highest in *bark*. For specific tissues, foliage has the highest nutrient concentrations, followed by *stemtips* and *current branches*. The rank of nutrient concentrations in wood and bark is *intermediate branches* > *older branches* > *stems*. Nutrient concentration of *bark* is more uniform than that of *wood*. The concentra-

Table 2. Weighted mean concentrations of selected nutrients in tissues of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley.

TISSUE	NUTRIENT N	P	K	Ca	Mg
	%				
	WOOD				
Stems	0.08 f* (0.004)	0.021 f (0.0014)	0.14 de (0.011)	0.16 g (0.016)	0.025 e (0.0012)
Older Branches	0.19 f (0.012)	0.038 f (0.0015)	0.14 de (0.008)	0.23 g (0.010)	0.038 e (0.0025)
Intermediate Branches	0.39 e (0.024)	0.085 de (0.0084)	0.30 d (0.013)	0.44 f (0.025)	0.057 de (0.0041)
Dead Branches	0.32 e (0.020)	0.036 f (0.0030)	0.09 e (0.012)	0.94 e (0.078)	0.079 d (0.0072)
	BARK				
Stems	0.57 d (0.029)	0.069 e (0.0023)	0.66 c (0.034)	1.96 c (0.057)	0.143 c (0.0098)
Older Branches	0.77 c (0.033)	0.100 d (0.0051)	0.71 c (0.034)	2.19 b (0.075)	0.166 bc (0.0121)
Intermediate Branches	0.85 c (0.029)	0.128 c (0.0059)	0.72 c (0.029)	2.24 b (0.106)	0.146 c (0.0077)
	OTHER				
Stemtips	1.22 b (0.113)	0.194 a (0.0108)	1.29 a (0.121)	0.98 e (0.089)	0.177 bc (0.0138)
Current Branches	0.91 c (0.035)	0.197 a (0.0096)	1.06 b (0.030)	1.73 d (0.087)	0.195 b (0.0154)
Foliage	1.88 a (0.046)	0.167 b (0.0047)	1.27 a (0.077)	2.44 a (0.071)	0.364 a (0.0233)

*Means in a column not followed by a common letter differ ($P \leq 0.05$) as determined by Student-Newman-Keuls' test. Numbers in parentheses are the standard errors of the means.

tion of nutrients for all tissues is in the order Ca > N ≥ K > Mg ≥ P.

Stems---Concentrations of N, P and K generally decline with plantation age (Table 3), but the highest K concentration is in the trees from the nine-year-old plantation at Fitler. Ca concentrations are very uniform across plantation ages, and no meaningful trends in Mg concentration are evident.

Living branches---Some differences in N and K concentrations are significant (5% level), but the variation does not appear to be associated with plantation age (Table 4). Concentrations of P, Ca and Mg do not differ significantly by plantation age.

Foliage---No variation in N, P and Ca could be attributed to plantation age (Table 5). However, foliage of trees from the two Warren County plantations (Adler soil series) is higher in Mg and lower in K than that of the other plantations (Commerce and Robinsonville soil series). Thus, foliage more nearly reflects the chemical properties of soil than do the other tissues.

Foliar concentrations of P, Ca and Mg exceed the critical levels proposed by White and Carter (1968) for cottonwood on alluvial soils in Alabama (Table 6). Foliar N concentrations in trees on all soil series is slightly below the critical level, but foliar K of trees on the Adler soil series is well below the critical level.

Correlations of Nutrient Concentrations Among Tissues [2]

The correlation coefficients for nutrient concentrations of foliage and other tissues generally are low (Table 7). About two thirds of the correlation coefficients are significant for K and Mg. Correlation coefficients are lower for N, P and Ca and only one is significant.

Table 3. Weighted mean concentrations of selected nutrients in the stems (i.e., wood and bark) of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley, by age and identity of plantations.

Age	Identity	NUTRIENT				
		N	P	K	Ca	Mg
yrs		%				
4	Catfish	0.19 a* (0.012)	0.038 a (0.0009)	0.25 ab (0.088)	0.38 a (0.003)	0.040 ab (0.0007)
6	Leavenworth	0.16 b (0.009)	0.037 a (0.0033)	0.25 ab (0.038)	0.36 a (0.021)	0.037 b (0.0033)
9	Catfish	0.13 bc (0.012)	0.023 b (0.0003)	0.18 b (0.009)	0.38 a (0.023)	0.037 b (0.0033)
9	Fitler	0.14 bc (0.012)	0.027 ab (0.0033)	0.29 a (0.026)	0.40 a (0.047)	0.040 ab (0.0012)
12	Fitler	0.12 c (0.006)	0.022 b (0.0025)	0.19 b (0.009)	0.38 a (0.021)	0.032 b (0.0025)
15	Warren	0.11 c (0.006)	0.022 b (0.0003)	0.16 b (0.018)	0.39 a (0.011)	0.045 ab (0.0029)
16	Warren	0.13 bc (0.005)	0.025 b (0.0050)	0.17 b (0.010)	0.40 a (0.018)	0.055 a (0.0064)

*Means in a column not followed by a common letter differ ($P \leq 0.05$) as determined by Student-Newman-Keuls' test. Numbers in parentheses are the standard errors of the means.

[2] *Correlations of nutrient concentration of foliage to that of other tissues are presented in Table 7 as examples of the correlations found among all tissues. Correlation coefficients for other tissues may be obtained from the authors upon request.*

Table 4. Weighted mean concentrations of selected nutrients in the living branches (i.e., all branch tissues except dead) of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley, by age and identity of plantations.

Age	Identity	NUTRIENT				
		N	P	K	Ca	Mg
yrs		%				
4	Catfish	0.47 ab*	0.077 a	0.51 a	0.82 a	0.080 a
		(0.045)	(0.0025)	(0.035)	(0.058)	(0.0029)
6	Leavenworth	0.42 ab	0.082 a	0.49 a	0.94 a	0.081 a
		(0.040)	(0.0009)	(0.042)	(0.151)	(0.0071)
9	Catfish	0.35 b	0.056 a	0.37 abc	0.99 a	0.088 a
		(0.040)	(0.0022)	(0.051)	(0.071)	(0.0203)
9	Fitler	0.58 a	0.073 a	0.47 ab	1.06 a	0.083 a
		(0.067)	(0.0130)	(0.072)	(0.155)	(0.0134)
12	Fitler	0.39 b	0.073 a	0.38 abc	0.86 a	0.064 a
		(0.042)	(0.0058)	(0.030)	(0.053)	(0.0048)
15	Warren	0.32 b	0.065 a	0.25 c	0.76 a	0.089 a
		(0.020)	(0.0047)	(0.009)	(0.038)	(0.0070)
16	Warren	0.44 ab	0.071 a	0.31 bc	0.86 a	0.102 a
		(0.030)	(0.0059)	(0.022)	(0.085)	(0.0120)

*Means in a column not followed by a common letter differ ($P \leq 0.05$) as determined by Student-Newman-Kuehls' test. Numbers in parentheses are the standard errors of the means.

Table 5. Mean concentrations of selected nutrients in the foliage of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley, by age and identity of plantations.

Age	Identity	NUTRIENT				
		N	P	K	Ca	Mg
yrs		%				
4	Catfish	2.00 a*	0.187 ab	1.81 a	2.37 a	0.313 b
		(0.088)	(0.0177)	(0.127)	(0.134)	(0.0285)
6	Leavenworth	1.86 a	0.193 a	1.41 b	2.31 a	0.317 b
		(0.163)	(0.0145)	(0.086)	(0.242)	(0.0233)
9	Catfish	1.79 a	0.143 b	1.50 b	2.37 a	0.287 b
		(0.201)	(0.0033)	(0.118)	(0.153)	(0.0328)
9	Fitler	1.80 a	0.147 b	1.38 b	2.75 a	0.320 b
		(0.170)	(0.0033)	(0.079)	(0.061)	(0.0173)
12	Fitler	1.90 a	0.160 ab	1.39 b	2.53 a	0.255 b
		(0.073)	(0.0081)	(0.065)	(0.183)	(0.0029)
15	Warren	1.74 a	0.160 ab	0.82 c	2.18 a	0.480 a
		(0.040)	(0.0066)	(0.098)	(0.112)	(0.0238)
16	Warren	2.02 a	0.182 ab	0.81 c	2.58 a	0.522 a
		(0.013)	(0.0055)	(0.076)	(0.212)	(0.0545)

*Means in a column not followed by a common letter differ ($P \leq 0.05$) as determined by Student-Newman-Kuehls' test. Numbers in parentheses are the standard errors of the means.

Table 6. Proposed critical levels of nutrients for cottonwood foliage and foliar levels of these nutrients on the Commerce, Robinsonville and Adler soil series.

Nutrient	Proposed Critical Level*	Soil Series	
		Commerce and Robinsonville	Adler
	%		
N	2.00	1.87	1.88
P	0.17	0.17	0.17
K	1.30	1.50	0.82
Ca	2.20	2.47	2.32
Mg	0.18	0.30	0.50

* White and Carter (1968) specify crown position for their critical levels. Since the foliar concentrations of this study are a weighted mean for all crown positions, an error in comparison can be a maximum of 3% for N and P, 6% for K and Mg, and 12% for Ca based upon the difference they reported between upper and lower crown concentrations.

Differences in Nutrient Concentrations Along the Stem

Nutrient concentrations in stemwood are highest near the apex and lowest at the base (Figure 1). The gradients are steepest in the portion of stems within the tree crowns and almost flat in the lowest portion. The gradients generally are steeper for four-year-old trees than for older trees, and the coefficients of determination are highest for the youngest trees.

Concentration gradients in stembark are similar in pattern to those of stemwood except for Ca, which is highest at the base of the stems (Figure 2). The coefficients of determination generally are lower for stembark than for stemwood.

Table 7. The coefficients of correlation of the nutrient concentration in the foliage to that of the other tissues of 24 sample trees from cottonwood plantations in the Lower Mississippi River Valley.

Tissue	Foliage				
	N	P	K	Ca	Mg
			Wood		
Stems	0.23	0.28	0.27	0.16	0.19
Older Branches	0.21	0.27	0.61**	0.14	0.66**
Intermediate Branches	0.04	0.02	-0.11	0.14	0.53**
			Bark		
Stems	0.33	0.10	0.76**	0.44*	0.61**
Older Branches	0.26	0.34	0.60**	0.39	0.28
Intermediate Branches	0.31	0.26	0.34	0.19	0.46*
			Other		
Stemtips	0.18	0.08	0.77**	0.14	-0.34
Current Branches	0.22	0.15	0.44*	0.32	0.88**
Foliage	1.00	1.00	1.00	1.00	1.00

* Significant at the 5% probability level.
** Significant at the 1% probability level.

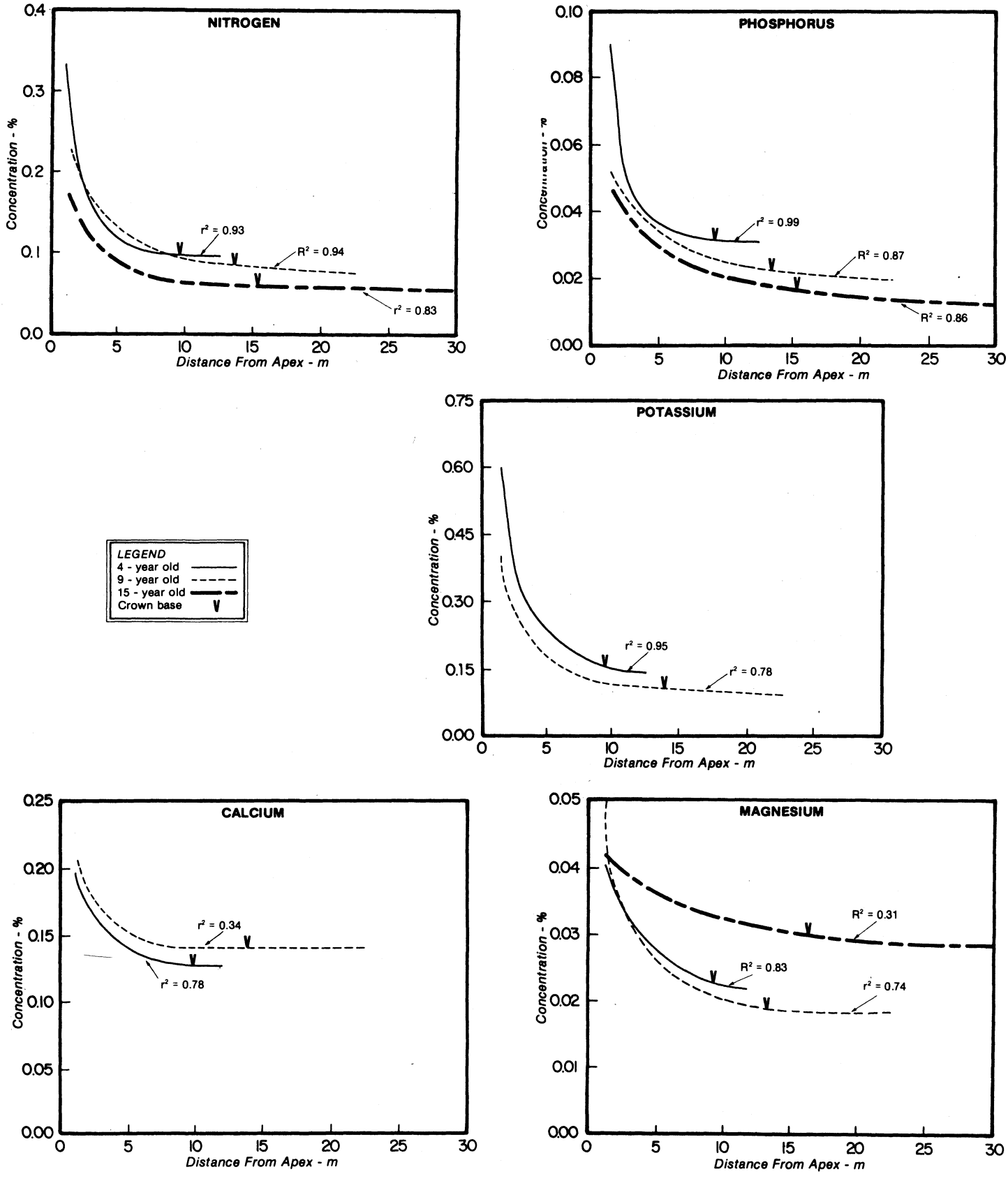

Figure 1. The relationship of nutrient concentration in the stemwood to distance from the stem apex for the 4-, 9-, and 15-year old plantations. The K and Ca concentrations do not vary significantly with distance for the 15-year old plantation and are not shown.

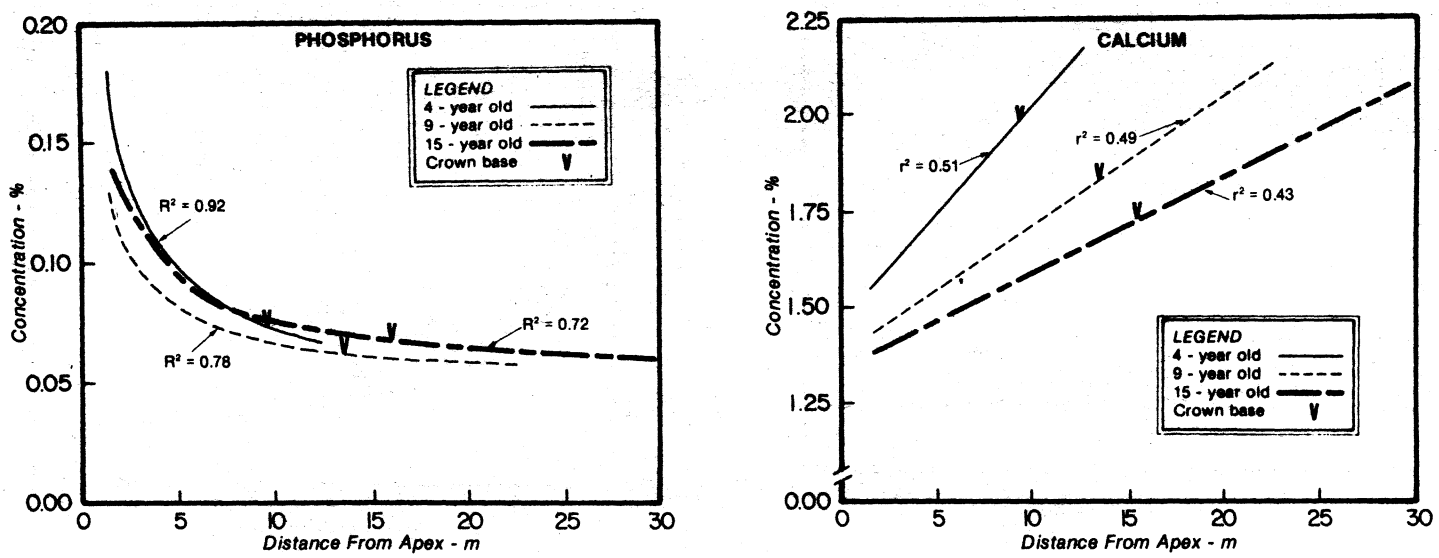

Figure 2. The relationship of P and Ca concentration in the stembark to distance from the stem apex for the 4-, 9-, and 15-year old plantations.

DISCUSSION

Variation in Nutrient Concentration Within a Tree

Nutrient concentrations within a tree vary by kind and age of tissues. Although bark and wood are both produced by the lateral meristem, they differ both morphologically and chemically. Nutrient concentrations always are higher in bark than in the adjacent wood tissue.

The greatest difference in nutrient concentration in bark and wood is for Ca, and the smallest is for P, which may reflect a difference in retention of these nutrients. The bark-to-wood concentration ratios range from 2 to 12 and generally correspond to those reported for cottonwood by Carter and White (1971b). The bark-to-wood ratios generally are lower for Ca and Mg and higher for N, P and K than for other species, such as willow, sweetgum, red oak and ash (Choong et al, 1976).

The concentrations of nutrients within a tree are generally highest in tissues with high metabolic activity and a high proportion of living cells. In contrast, the lowest concentrations are in tissues with low metabolic activity and a low proportion of living cells. Thus, the highest nutrient concentrations are in the foliage and in new tissues that are being formed near the meristem, and the lowest concentrations are in the wood tissues at the base of the stem. In short, concentrations of mobile nutrients (N, P and K) decrease with an increase in tissue age. A portion of the N, P and K is mobilized and translocated into other tissues during tissue senescence, while Ca remains relatively immobile (Baker and Blackmon, 1977). This translocation is a mechanism for nutrient conservation and efficiency.

Translocation of N, P and K in a tree results in radial gradients of nutient concentration, because the stem cross section contains tissues of different ages. The radial gradients occur in both stemwood and stembark, and concentrations of mobile nutrients in stemwood are highest near the cambium and lowest near the pith (Wardell and Hart, 1973). A sharp decrease in concentration of N, P and K has been observed in the transition of sapwood to heartwood in various species (Wright and Will, 1958; Orman and Will, 1960; Merrill and Cowling, 1966). Radial gradients in bark have received less attention in the literature, but Choong et al. (1976) found generally higher concentrations in inner bark than in outer bark.

Radial gradients were not determined in this study. However, radial gradients are reflected in the concentration changes along the stem, since tissue ages and proportions vary with stem position. Gradients along the length of the stem are most evident for N, P and K and least apparent for Ca and Mg.

Concentration gradients of N, P, K and Mg in stembark are similar to those in stemwood but differ for Ca. The Ca concentration in bark increases linearly from the apex to the base of the stem, and the

gradients are similar to those described in Montery pine (Orman and Will, 1960). The higher concentration of Ca in the lower stem is attributed in part to the retention of Ca in the cell walls, to the weight loss accompanied by the translocation of N, P, K and other cell materials during senescence and to leaching and decomposition of exposed outer bark.

Correlations of K and Mg concentrations in foliage to K and Mg concentrations in other tissues are significant, but concentrations of N, P and K in foliage vary independently of concentrations in other tissues. The generally poor correlations among tissues indicate that the concentration of a nutrient in a particular tissue does not necessarily reflect the concentration of that nutrient in other tissues, even if the tissues are closely associated. A similar relationship has been demonstrated by Cain (1953) in deciduous fruit trees.

Variation in Nutrient Concentration Among Trees

Trees within a plantation generally are uniform in the nutrient concentration of their tissues, as indicated by the small differences in weighted means and the low coefficients of variation. However, wide variations may occur occasionally within a plantation, and this probably can be attributed in part to differences in soil properties, to the genetic variation in trees and to their interaction. Differences in rooting depth of trees also may account for some differences in nutrient concentrations (Walker, 1955).

The effect of plantation age is most apparent in the concentration of N, P and K in the stemwood and stembark, and these concentrations generally decline with increases in age. Plantation age did not influence the nutrient concentrations in tissues produced during the same growing season (i.e., the foliage and current branches).

Much of the variation in nutrient concentration among plantations can be attributed to differences in the soil chemical properties. The greatest differences in this study were in the K and Mg concentration of trees from the Adler and the Commerce and Robinsonville soil series. Average exchangeable K and Mg to a depth of 120 cm is 0.085 and 1.84 meq/100 g for K and Mg, respectively, for the Adler soil series, and 0.364 and 4.25 meq/100 g for the Commerce and Robinsonville soil series (Broadfoot, 1976). These differences in the K and Mg levels in the soil are reflected in the low K and high Mg concentrations in some tissues of trees from the plantations on the Adler soil series. The tissue sensitivity to differences in soil chemical properties is in the order of foliage, current branches and bark.

The interaction of K and Mg has been frequently observed in nutritional studies. Most studies have found that low foliar levels of Mg are induced by fertilizing with K (Boynton and Burrell, 1944; Emmert, 1961). Also, K deficiency in tissues may be induced by heavy applications of Mg, but this has been observed less frequently (Ulrich and Ohki, 1966). Causes of the interaction of K and Mg are not well understood, but it appears that these occur in the plant rather than in the soil. Epstein (1972) postulates that the phenomenon may be due to competitive effects in the translocation of K and Mg within the plant.

Foliar Critical Levels

The low K concentration in the foliage in plantations on the Adler soil series does not indicate low site quality. The average site index of the Adler soils is 38 meters at 30 years, which is about the same as for the Commerce and Robinsonville soil series (Broadfoot, 1960). Reuther et al. (1958) found that foliar levels of K can vary over a relatively wide range with no observable effect on fruit tree productivity. Therefore, care must be exercised in using foliar analysis for estimating the nutritional status of the trees or site quality.

Implications for Sampling

To provide the resolution required for estimating nutrient accumulation and removal, the sampling procedure should recognize the major components of the tree---foliage, branches and stem. However, variations in nutrient concentrations within foliage, branches and stem components increase the difficulty of obtaining representative samples; therefore, subdivisions in addition to those used in this study are necessary for more critical evaluations. This problem is especially evident in the branch and stem components. Plantation age apparently can be ignored in sampling the ephemeral tissues of trees (e.g., foliage and current branches).

Differences in soil chemical properties can contribute to differences in nutrient concentrations in tissues. These differences occur over sites of comparable quality and are most pronounced in the foliar levels of K and Mg. Therefore, an adequate sample requires recognition of variation in soil chemical properties.

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