

THE MINERAL NUTRIENT REQUIREMENTS OF FOREST TREES

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Substantial increases in tree growth following the application of mineral fertilizers have been reported from a number of countries, and it is now generally recognized that many soils under forest cover or available for reforestation are deficient in mineral nutrients. Whether fertilizing on the scale appropriate to the management of large areas is economically worthwhile is still somewhat controversial, but there is little doubt that with increasing awareness of the advantages to be gained from a more intensive silvicultural program, the potential benefits of fertilizing are receiving serious attention. The immediate problem is to decide whether the establishment or growth of a tree crop on a particular site is indeed limited by nutrient deficiencies and if so, what and how much fertilizer to apply. At the same time, because of the present lack of data, some knowledge of the total mineral nutrient demand of the forest stand on the soil is also desirable in view of the not inconsiderable amounts of nutrients removed from the site in logging.

As far as deficiencies are concerned, actual fertilizer trials in the field will of course most readily provide the answer but such trials are costly and time consuming; furthermore, they suffer from the disadvantage that the results are generally limited to the site and species under investigation at the particular time. Nor has soil analysis provided more than a general guide to the problem of tree nutrient requirements. As a result of the differentiation of distinct horizons, often differing appreciably in composition and rooting capacity, most forest soils are markedly heterogenous; this, together with the long periods of growth concerned and the well known limitations of conventional extraction procedures, severely limits the value of this approach.

An alternative approach is provided by studying the actual mineral composition of the tissues of the trees themselves, in particular the composition of the foliage since this is usually considered as providing the most sensitive indicator of the sufficiency or otherwise of the nutrient supply to the trees. This foliar diagnostic approach has been widely applied to agricultural and horticultural crops and earlier investigations, especially those of Mitchell (1939) and Mitchell and Chandler (1939), have confirmed its potential value in the study on the mineral nutrient requirements of forest trees. However, for a consistent and successful application of this technique, an understanding of the relationship between tree growth and the mineral composition of the foliage, both in relation to supply and other factors affecting this relationship, is essential. Failure to appreciate this and the limitations imposed on diagnostic interpretations has, in many cases, led to false conclusions and often invalid criticism.

As it is most simply and commonly interpreted, foliar diagnosis is based on the assumption that a deficiency in a particular nutrient is reflected in a subnormal content of that nutrient in the foliage or in an abnormal balance with respect to other nutrients or in both of these. This assumption implies the existence of a *normal or minimum* foliar content, and in the choice of standards of comparison a popular approach has been to select well grown specimens of the species and age concerned. However, it is well known that even in the same tree the composition of the foliage is not constant but varies according to its location on the crown, its age (*i.e.*, in conifers bearing more than one year's needles), and the time

of the year. Hence, in applying the concept of normal composition it is essential that the sample of foliage be so defined as to allow for a valid comparison between individuals. It is now more or less generally accepted that the most suitable time for sampling is when the variation in leaf composition with time is at a minimum, thus, just before yellowing in deciduous trees and sometime after the end of the growing season in conifers. Somewhat less attention has been paid to the location and age of the foliage although this would appear to be of considerable importance. Presumably the most suitable sample should reflect to the greatest degree differences between trees of varying nutritional status and vigor. According to recent investigations of Leyton and Armson (1956) on Scots pine of varying heights in an even aged plantation, this condition is provided only by current needles from the terminal or uppermost lateral shoots; in this particular case, older needles or those taken from lower down the crown revealed little consistent change in composition with tree vigor and it is possible that many of the reported failures to relate growth to foliar composition can be attributed to incorrect sampling.

A major objection to the use of healthy well grown trees as standards of comparison is that the foliage of a selection of such trees, even when sampled under identical conditions, may differ appreciably in composition because of the phenomenon of *luxury consumption*, i.e., nutrient uptake in excess of actual growth requirements without any apparent influence on growth. Under these circumstances simple comparisons between individuals may lead to errors in diagnosis.

More reliable data on optimum nutritional conditions have been obtained experimentally by growing trees in cultures with an adequate supply of all nutrients other than the one in question and by following the response in growth and in foliar composition to increasing supplies of that nutrient. In this way Mitchell (1939) demonstrated, for white pine seedlings, a curvilinear relation (diminishing returns) between supply and growth and between growth and the concentration of the limiting nutrient in the foliage dry weight. Similar relations have been established for older specimens of a number of tree species in the field, e.g. by Mitchell and Chandler (1939) for various hardwoods, by Tamm (1956) for Scots pine, and by the author for Sitka spruce and Corsican pine (fig. 1 and 2). Generally there is evidence for the occurrence of maximum growth (under the prescribed experimental conditions) at a particular optimum concentration characteristic of the nutrient and species concerned, e.g., in the above cases of spruce and pine at optimum P concentrations of 0.13 and 0.15 percent, respectively. At higher concentrations there is a tendency for growth to fall, though this is probably due to the influence of high levels of supply on the uptake of other nutrients rather than to a so-called toxic effect of high concentrations in the foliage per se.

A qualification to the relationships established above is suggested by observations of an initial fall in concentration with increasing supply and growth giving a sigmoid shaped curve (Steenbjerg, 1954). In the case of micro-nutrients for example, this may be brought about by a disproportionately large response in growth to a small increase in supply. Though similar phenomena have been occasionally claimed for the major elements, no evidence of these has yet been put forward for forest tree species, especially under field conditions.

From the nature of the curve relating growth to foliar composition, it is evident that over a large part of the deficiency range and *only within this range*, growth and concentration of a limiting nutrient are linearly and positively related, or at least the regression of one on the other yields only a significant linear component. If the converse were equally valid, it would mean that the establishment of a positive linear correlation between growth and the concentration of a particular nutrient in the foliage would signify a deficiency in that nutrient. Such correlations have indeed been found on a number of occasions where proof of a deficiency has subsequently been established. For example, in the case of Sitka spruce growing on a

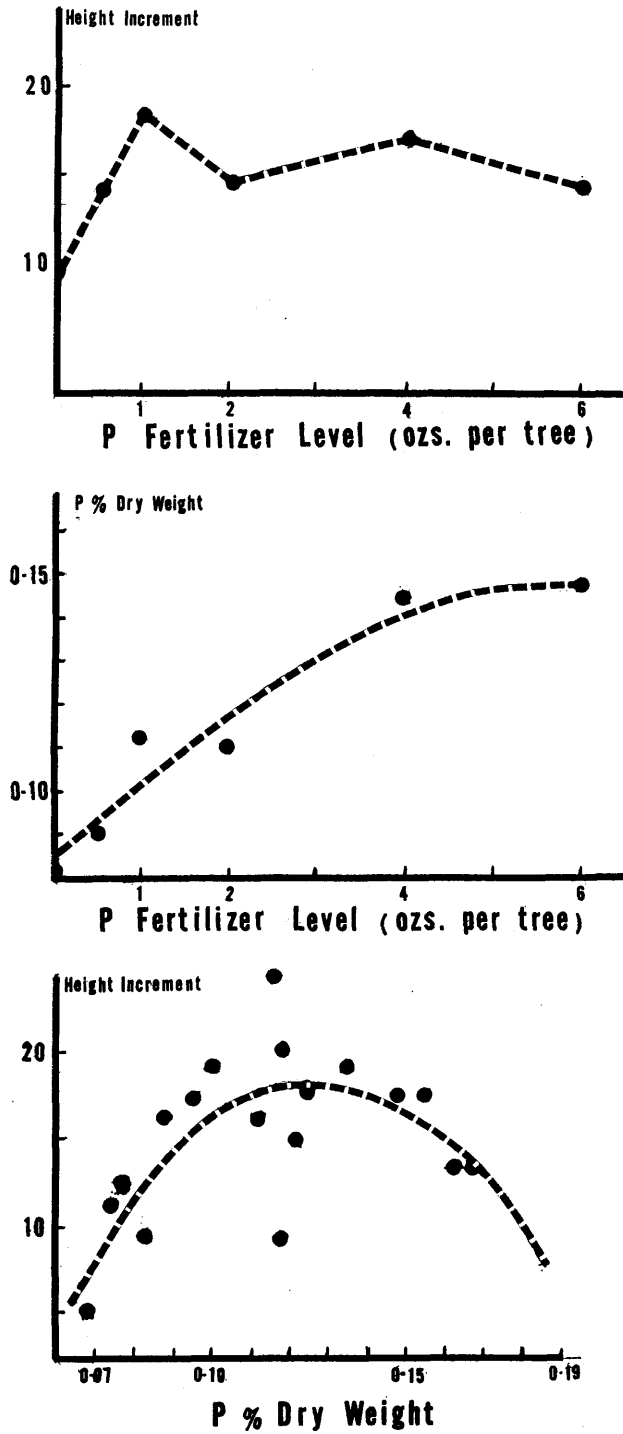


FIGURE 1. Sitka spruce. Relationship between phosphate supply, height increment, and P content of current needles (% D. Wt.).

heathland site in Britain, significant linear relationship between tree height or mean needle weight and the nitrogen concentration in the foliage were confirmed as reflecting a nitrogen deficiency by subsequent responses in growth to nitrogenous fertilizers (fig. 3; also Leyton, 1954). On the other hand, because of mutual interrelations between nutrients, false correlations of this kind are also possible. A particularly interesting example of these was provided by an investigation into the nutritional relationships of young even-aged Japanese larch trees growing on a heterogenous site and showing considerable variation in height growth. In this case (Leyton, 1956) significant linear relations were established between tree height and the concentrations of the nutrients N, P, K, and Ca in the foliage. However, from the analysis of the multiple regression of height on these

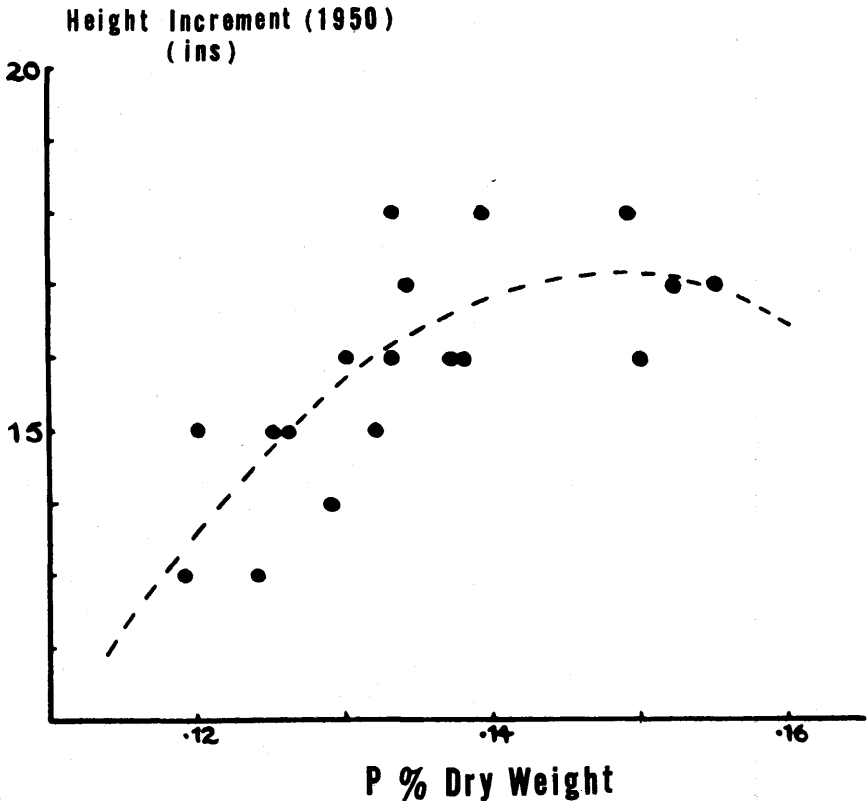


FIGURE 2. Corsican pine. Relationship between height increment and P content of current needles (% D. Wt.).

nutrient factors, it was found that only N, and to a lesser extent K, made significant contributions to the regression and that the apparent relation of growth to P and Ca arose out of significant internal relations between these and the significant nutrient factors. Subsequent fertilizer trials revealed the existence of marked N deficiencies and lesser K deficiencies in these trees, thus confirming the deductions based on analysis of the nutritional relationships (Leyton, 1957).

The important problem remains as to how far relationships between tree growth and foliar composition, of the kind discussed above, are affected by other factors such as environment and tree age. Are the optimum concentrations found

in the above examples peculiar to the particular experimental conditions under which they were determined or are they of wider application? In those cases where the availability of a particular nutrient is the sole factor determining growth, the relationship between supply, growth, and concentration is uniquely determined; under natural conditions such a situation is largely hypothetical since, in the field at least, growth is invariably influenced to a greater or lesser extent by many factors other than the availability of a single nutrient. In many cases, especially on very infertile soils, responses in tree growth may be obtained to increased sup-

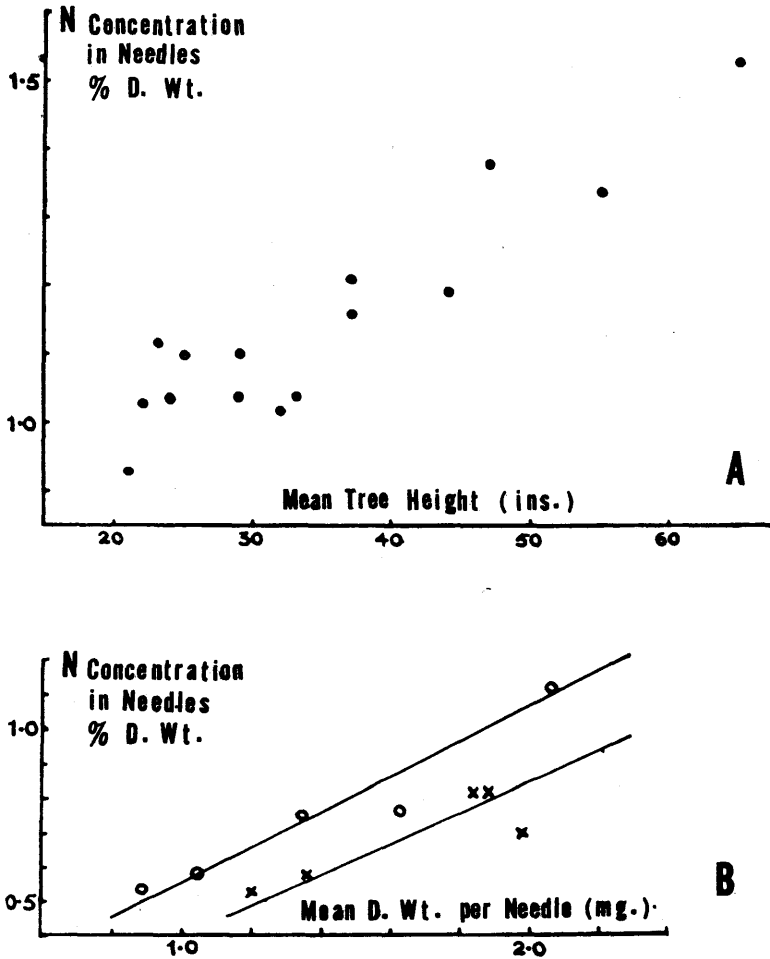


FIGURE 3. Sitka spruce on heathland. A. Relationship between mean tree height and N content of current needles (% D. Wt.). B. Relationship between mean needle dry weight and N content. x-x, control plots. o-o, treated with P fertilizer.

plies of different nutrients revealing the existence of multiple deficiencies. An example of this was provided by the case of the Japanese larch mentioned above and the relationships involved could be analyzed by multiple regressions. This approach suggested that in terms of their concentration in the needle dry weight, each nutrient could be considered independently as making their separate contri-

butions to growth and furthermore that there was for each nutrient an optimum concentration independent of the influence of other factors (Leyton, 1957). These findings support earlier conclusions of Mitchell and Chandler (1939) that although the actual amount of growth at a particular concentration of a limiting nutrient in the foliage varied with site, maximum growth on different sites corresponded to more or less the same optimum concentration. Further support for this argument is provided by various other investigations. In the case of Japanese larch an optimum N concentration in the needles of about 2.8 percent dry weight has been established independent of fertilizer influences (Leyton, 1957) whilst the results of an independent investigation on seedlings of this species provided with different amounts of N and P (van Goor, 1953) suggest that maximum growth occurs at much the same value. This investigation also reveals an optimum P concentration of about 0.4 percent and it hardly seems coincidental that in a recent countrywide survey of the P status of young transplants of this species, in relation to their growth and response to P fertilizers (fig. 4), a similar optimum

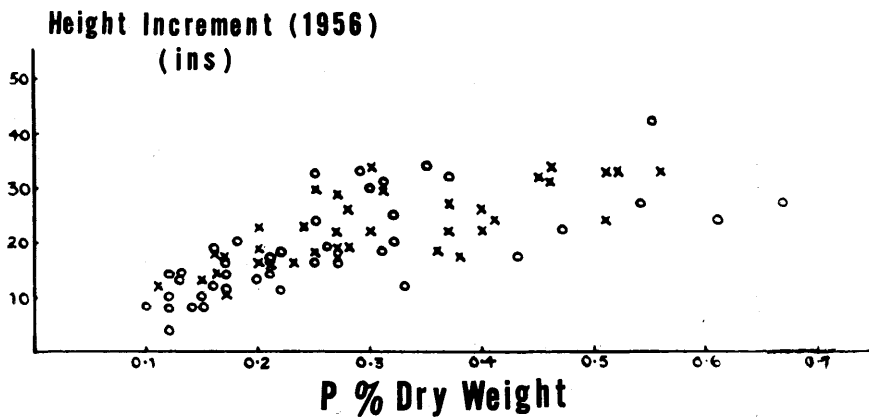


FIGURE 4. Japanese larch. P50 phosphate trials. Relationship between current height increment and P content (% D. Wt.). 0—0, controls. x—x, treated with P fertilizer.

value is suggested. It is perhaps of no less significance that in recent trials on older trees with P concentrations of this order, no response has been obtained to the application of P fertilizers (Leyton, 1957). Similarly, in an investigation on Sitka spruce (fig. 5), evidence is suggested for an optimum N concentration of about 1.6 percent whilst in other trials on this species with values below this, essentially linear relations between growth and N concentrations have been established (fig. 3).

On the evidence available, therefore, there would appear to be some justification for assuming that the concept of optimum nutrient concentrations for a particular species holds over a range of environmental conditions and age, though of course the actual amount of growth made will tend to vary according to other factors influencing growth. At the same time it will be appreciated that from a practical point of view the forester is concerned not so much with optimum levels (about which growth varies little with changes in nutrient supply) as with lower levels which correspond to definite deficiency conditions. Much attention has therefore been paid to the possible establishment of minimum or critical concentrations below which a response to the appropriate fertilizer can be expected with reasonable certainty. For adult trees in the field such information has been obtained from fertilizer trials in which growth responses can be related to the

concentration of a particular nutrient in the foliage. It must be emphasized, however, that in view of the nature of the response curve, there is probably no precise critical concentration but a range of concentrations below which growth increases rapidly with increasing supply and concentration and above which there is little change. From the data available in the literature to date, critical and optimum concentrations for a number of tree species have been summarized in table 1 below.

TABLE 1
Deficiency and optimum levels of foliage N, P, and K concentrations (% dry weight)

Species	Deficiency			Optimum			Authority
	N	P	K	N	P	K	
<i>Pinus sylvestris</i>	(S)			3.0			Gast (1937)
<i>Pinus sylvestris</i>	(F)	1.2-1.3	.08				Tann (1954)
<i>Pinus strobus</i>	(S)	.70-1.33	.10-.28	.82-1.02	3.26	.67-1.72	Mitchell (1939)
<i>Pinus strobus</i>	(F)			.34			Heiberg & White (1951)
<i>Pinus resinosa</i>	(F)			.34			Heiberg & White (1951)
<i>Pinus corsicana</i>	(F)				.15		Leyton (1954)
<i>Picea abies</i>	(F)	.80-1.0	.06				Tamm (1954)
<i>Picea abies</i>	(F)			.13-.21			Heiberg & White (1951)
<i>Picea glauca</i>	(F)			.13-.21			Heiberg & White (1951)
<i>Picea sitchensis</i>	(F)			1.5-1.6	.14		Leyton (1954)
<i>Larix leptolepis</i>	(F)			2.8	.40		Leyton (1957)
<i>Betula</i> spp	(F)	1.8-2.1	.08-.10				Tamm (1954)
<i>Populus tremuloides</i>	(F)	2.0		2.6-2.8			Mitchell & Chandler (1939)
<i>Acer saccharum</i>	(F)	1.75		2.8-2.9			Mitchell & Chandler (1939)
<i>Fraxinus americana</i>	(F)	2.01		2.8-2.9			Mitchell & Chandler (1939)
<i>Tilia americana</i>	(F)	2.32		3.1-3.2			Mitchell & Chandler (1939)

(S) Seedling. (F) Established trees in field.

In view of the still limited experimental proof of the constancy of the above values under all conditions, however, an unreserved acceptance of these limits is unwarranted.

In an alternative approach to the problem of foliar diagnosis, a number of investigations have stressed the importance for growth of a correct balance between nutrients in the foliage and especially in the case of the ratios N/P, N/K, and K/P, have proposed optimum values, a departure from which has been considered responsible for depressed growth. Investigations into the nutritional relations of Japanese larch (Leyton, 1957) have indeed disclosed an association of maximum growth with certain optimum values for such ratios and somewhat similar relationships have been established for Sitka spruce. There is also some evidence that these optimum values are of more general application insofar as N/P values calculated for Japanese larch in different parts of Britain correspond with each other and with values quoted by van Goor (1953) for seedlings of this species, namely 12.6, 14.7, and 9-12 respectively. When these values are compared with other estimated N/P optima, ranging from 12 to 15 for Scots pine (Boszormenyi, 1956), rubber (Beaufils, 1956) and oil palm (Prevot and Ollagnier, 1954), some

speculation as to a possible underlying common relationship in plant nutrition is unavoidable, especially when the various estimated optima for the N/K and K/P ratios also show some agreement. On the other hand, a careful inspection of the origin of these ratios would suggest that, rather than possessing some individual physiological significance, they merely offer an alternative reflection of relationships based on concentrations (Leyton, 1957).

Physiologically, there can be little doubt that neither the concentration nor the balance of nutrients in the foliage provide more than a reflection of the complex interaction between various nutrients and the metabolic responses resulting in growth. The fact that in most cases we are dealing with foliage at the end of the growing season when back translocation of mobile N, P, and K would presum-

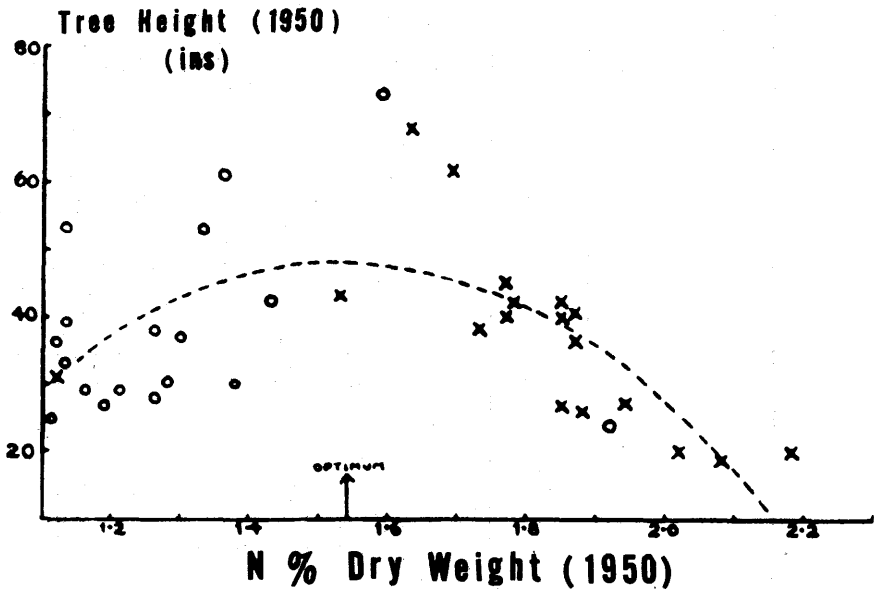


FIGURE 5. Sitka spruce on heathland. Relationship between tree height and N content of current needles (% D. Wt.). 0—0, controls. x—x, with surrounding heath vegetation removed by scalping.

ably have taken place, serves to emphasize the empirical nature of this approach in the study of tree nutrition. Nevertheless, if the physiological significance of these relationships is at present beyond our knowledge, their apparent consistency provides at least a valuable working basis for the determination of the nutrient requirements of trees. From a diagnostic point of view a stage has now been reached where foliar analysis, carried out with proper regard to sampling, would provide a reasonably consistent guide, not only to the nature and extent of a particular deficiency limiting growth, but also to the interpretation of many field observations. Because of the influence of other environmental factors like temperature and moisture on growth, data on foliar composition generally provide little information as to the extent of a growth response to a given increase in nutrient supply; of necessity this must be a limitation of all approaches other than actual field trials at the time in question.

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