

FERTILIZATION OF STAGNATED SITKA SPRUCE PLANTATIONS
ON NORTHERN VANCOUVER ISLAND

BY

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Fertilization of Stagnated Sitka Spruce Plantations
on Northern Vancouver Island

ABSTRACT

Extensive areas of Sitka spruce plantations established during the last 15 years on the CH-phase of the salal-moss ecosystem association on northern Vancouver Island are presently exhibiting symptoms of severe chlorosis and growth check. Investigations into the poor performance of these plantations are described in this thesis. Comparisons of the soil nutrient levels between this poorly productive CH-phase and the adjacent highly productive HA-phase were made. In addition, fertilization screening trials were established in order to identify possible limiting nutrients and determine the potential responsiveness of Sitka spruce to fertilization.

Soil samples were collected over an age sequence of cutovers from both phases in order to compare differences in the soil nutrient status and to determine the effects of time since harvesting on N mineralization rates.

Significantly greater amounts of total and available P and total, KCl extractable, and mineralizable N ($p=.01$) were found in the mineral soil and humus of the HA-phase. The mineral soil of the HA-phase also had

significantly higher ($p=.05$) concentrations of exchangeable K. In addition, this phase had a significantly lower ($p=.01$) C/N ratio. Although significant differences were noted in the mineral nutrient composition of the two phases, in all cases (with the possible exception of mineralizable N), the absolute differences between the two phases did not appear large enough to account for the dramatic differences in productivity.

Harvesting plus slashburning appears to have had little effect on the rates of N mineralization in the humus or mineral soil of the HA-phase. However, in the CH-phase harvesting plus slashburning has had a significant influence on the mineralization rates of the humus but not of the mineral soil. Harvesting initially resulted in a significant ($p=.05$) increase in the mineralization rates, however, within five years they returned to levels comparable to that of the control.

Fertilization screening trials were established in five Sitka spruce plantations ranging in age from 8 to 14 years. All plantations were growing on the CH-phase and were exhibiting symptoms of chlorosis and growth check. Changes in the first-year needle dry-weight, needle nutrient composition, and leader growth were monitored. Treatments for these trials consisted of a N, P, K factorial experiment, and one separate treatment of a complete nutrient mixture. Each treatment was replicated seven times in each of the five plantations.

N or N plus K fertilization resulted in a 10%

increase in needle dry-weight and a 25 to 30% increase in first-year leader growth response over that of the control. P fertilization had a strong synergistic effect and when added in combination with N or N plus K resulted in a needle dry-weight increase of 40 to 41% and a leader growth increase of 78 to 83%. A limited sample of naturally occurring hemlock in some of the plots exhibited similar trends, although leader growth increases were somewhat greater.

Fertilization with P and K, alone or together, had no effect on leader growth or needle weight despite the severe deficiencies of these two elements. However, P had a positive influence on the uptake of N, K, Ca and Mg, whereas K positively affected Ca and depressed Mg.

After N fertilization, foliar N concentrations increased dramatically, ranging from a mean of 3.2% for the lowest (200 kg N/ha) application rate to 4.1% for the highest (400 kg N/ha) application rate. The high foliar N concentrations had a significant negative influence on foliar K concentrations. This decline in K concentrations could only partially be attributed to a growth dilution effect and occurred whether or not K was added. A similar effect on P, Ca or Mg was not noted. The high N concentrations also appeared to have had a negative influence on both needle weight and leader growth as there was a tendency for the response of both to decline as N concentrations increased.

There were significant differences in both leader growth and needle weight responses between some of the plantations, but treatments receiving both N and P

fertilizers consistently gave the greatest responses. The individual treatment, however, which gave the greatest and most consistent overall response was that containing all macro- and micro-nutrients.

Results from this study indicate that the poor performance of Sitka spruce plantations established on the CH-phase of the salal-moss ecosystem is partially due to a severe N and P deficiency. These deficiencies are associated with the complete invasion of these cutovers by salal. It has also been shown that the Sitka spruce in these plantations would be highly responsive to N and P fertilization. Although K does not appear to limit growth and no apparent benefits were gained from K fertilization, a severe N induced K deficiency is likely.

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INTRODUCTION

Considerable attention has recently been focused on the poor performance of Sitka spruce (Picea sitchensis (Bong.) Carr.) plantations on the cedar-hemlock phase of the salal-moss ecosystem association described by Lewis¹ (1982). Although these plantations had initially performed well in both height growth and survival, they are now experiencing a severe decline. Presently, the annual height increment of the Sitka spruce in many of these plantations only averages about 10 cm and the trees are now extremely chlorotic.

Over 1900 ha of Sitka spruce plantations have been established on the salal-moss, and the similar but wetter, cedar-skunk cabbage ecosystem association in Block 4 of Tree Farm Licence 25 (T.F.L. 25) (Figure 3). The potential for similar plantation failures throughout coastal British Columbia may be considerably greater, since these ecosystem associations, or very similar ones, presently supporting old-growth cedar-hemlock stands are common. To date, little attention has been paid to the nutritional aspects of these sites and their capability to support second growth plantations after harvesting.

¹ Terry Lewis, 1982. Ecosystems of the Port McNeill block (Block 4) of Tree Farm Licence 25. Unpublished Internal report, Western Forest Products Ltd..

The poor performance of the plantations established on the cedar-hemlock phase becomes even more dramatic when compared to the good growth performances of the spruce plantations established on the highly productive hemlock-amabilis fir phase, also of the salal-moss ecosystem association (See pages 28 to 44 for a complete description and discussion of both phases). Although these two phases often occur contiguous to each other, the plantations of the hemlock-amabilis fir phase have not experienced the decline in growth commonly associated with the plantations of the cedar-hemlock phase.

Lewis (1982) suggested that the differences in productivity between the two phases were related to the differences in their development histories. Lewis hypothesized that the lack of dramatic disturbances to the mature stands of the cedar-hemlock phase, such as the periodic windthrow disturbances which is believed to occur to the mature stands of the hemlock-amabilis fir phase, has led to a gradual decline in organic matter decomposition and nutrient turnover and thus, productivity of this site. He suggested that the key to improved productivity lay in the management of the surface organic layer and believed that this would best be achieved by scarification.

While this approach may be feasible for future cutovers, it is not acceptable for existing plantations, since, despite their growth check, even the youngest plantations are approaching two metres in height. In addition, as Lewis noted, there is some question as to

whether a single disturbance would be sufficient to ensure continued productivity throughout the entire rotation. In fact, there is increasing evidence to suggest that on some sites, growth benefits from scarification are short-lived (Ross and Malcolm, 1982; Tiarks, 1983). Thus if productivity is to be maintained, additional treatments such as fertilization may be required. Therefore, it is important to know what benefits may be derived from fertilization and which nutrients would most likely stimulate growth. This knowledge will provide guidelines for the management of future plantations and may also provide a solution to the present problem of stagnation.

This study will address some of the questions concerning the poor performance of Sitka spruce plantations on the cedar-hemlock phase of the salal-moss ecosystem association. Specifically, the objectives will be to:

1. Determine which nutrient(s) are presently deficient and limiting growth on the cedar-hemlock phase.
2. Identify the potential responsiveness of the Sitka spruce to fertilization.
3. Compare the differences of the two phases of the salal-moss ecosystem association and to provide plausible explanations for the dramatic differences in productivity.

LITERATURE REVIEW

Foliar Analysis

A considerable body of literature presently exists on the uses, merits and problems associated with foliar analysis. Since much of this work has already been summarized in a number of excellent reviews, notably Smith, 1962; Leaf, 1973; Morrison, 1974; van den Driessche, 1974; and Turner et al., 1978, it is felt that a detailed reiteration of this work is not necessary. However, since much of this thesis is based on the interpretation of foliar analysis, a brief review, particularly of the more recent literature is given.

The use of foliar analysis lies in the belief that the plant itself is the best integrator of all factors affecting its mineral nutrient status (Ballard, R., 1979; Maynard, 1982). Changes in the plant environment, external or internal, are usually readily reflected in the concentration of some or all of the fifteen essential elements found in the foliage.

Richards and Bevege (1972) identified two uses of foliar analysis: (i) -- a diagnostic tool for identifying nutrient disorders, and (ii) -- a predictive tool for determining possible growth responses to fertilization. It has been used extensively in agriculture for both purposes,

however in forestry, while foliar analysis is accepted and used routinely as a diagnostic tool, it is generally considered to be too imprecise to quantitatively predict fertilizer responses (van den Driessche, 1974; Ballard, R., 1979). However, foliar analysis has usually been found to be better correlated with fertilizer responses than soil analysis and therefore it tends to be used more often (Ballard, R., 1979).

Many of the factors contributing to the imprecision of foliar analysis in both its diagnostic and predictive applications are well known, but the control of these are difficult and still under investigation. Some of these factors are:

(i) Critical nutrient levels: For many nutrients and species, statistically established critical nutrient levels and growth response curves have not been determined. Even where significant relationships have been developed, they are usually not sensitive enough to identify marginal deficiencies. As a result, the ability of foliar analysis to identify potentially responsive sites tends to be good only in the very deficient range (Ballard, R., 1979).

(ii) Within-tree variability: A considerable amount of inherent variability exists within the tree. While much of this variability may be overcome through standardization of sampling methods, there is still some debate over which methods should be adopted. For example, for many of the coniferous species in the Temperate and Boreal forest regions, it is generally accepted that foliage

sampling for foliar analysis be done in the fall and be restricted to the current year's foliage from the upper portion of the crown (Ballard, T., 1979). Waring and Youngberg (1972) however, argued that sampling during the period of most active growth would provide a more sensitive indicator of possible nutrient deficiencies. This same sentiment has recently been echoed by Morrow and Timmer (1981) and Powers (1983), all of whom also suggested that sampling of current plus one-year-old needles could greatly improve foliar diagnosis. Ballard, R. (1979) noted that many researchers do not fully appreciate an elements' physiological function and behaviour. Thus, many of the sampling and analytical techniques developed in foliar analysis may not provide a good index of the nutrient status of the tree.

(iii) Fertilizer - induced interactions: Past researchers have often failed to recognize some of the fertilizer-induced interactions which regulate potential responses. Examples of these would be the stocking x fertilizer response interaction which has been shown to strongly regulate the response of stands to nitrogen fertilization (Ballard, R., 1979), or the species x nitrogen source interaction which has been suggested as a possible reason for the differential responses of western hemlock (Tsuga heterophylla (Raf.) Sarg.) stands to nitrogenous fertilizers (Webster et al., 1976; Gill and Lavender, 1983a).

(iv) Forest stand variability: Conventional methods of measuring growth responses from fertilizer trials usually consist of comparing differences in growth of the control

plots to that of fertilized plots (Salonius and Mahendrappa, 1983). Numerous empirical trials have shown that research plots are seldom similar, and the natural variation occurring in forest ecosystems can often mask potential fertilizer responses (Shumway and Atkinson, 1977; Olson et al., 1979). Attempts to improve the predictability of growth responses has led researchers to examine alternative methods. Salonius and Mahendrappa (1983) suggested that since the past growth performance of a tree was a good indicator of possible future growth, each tree could be used as its own control. They expressed growth response by establishing a ratio of the 10-year post-fertilization radial growth to the 10-year pre-fertilization radial growth for each treatment. Shumway and Atkinson (1977) suggested using an individual tree approach where tree pairs, one fertilized and one not fertilized, of similar attributes are compared.

(v) Growth parameter selection: Fertilizer responses and degree of correlation with foliar nutrient levels are also affected by the growth parameter being measured. Madgwick (1964) noted that foliar P concentrations correlated well with total height but not with leader length in red pine (Pinus resinosa Ait.). More recently, Comerford et al. (1980) showed that different measures of growth (radial, basal area, height, volume, biomass, and specific volume) gave different results for the longevity and magnitude of response of red pine to K fertilization. It is apparent that improved mensuration techniques and a better understanding of the physiological relationships between the

elements and the various growth parameters may eventually lead to better correlations between foliar nutrient levels and fertilizer responses.

The basis for the use of foliar analysis lies in the relationship between foliar nutrient levels and growth. This relationship, illustrated in Figure 1, is often described as one of "diminishing returns" (Macy, 1936; Richards and Bevege, 1972). Various modifications to this curve have been made to better describe the relationship (Richards and Bevege, 1972). The original Mitscherlich equation is frequently altered to include a "depression factor" to account for toxicity at supra-optimum nutrient levels (D to E, Figure 1). Leyton (1958) suggested that a simple parabola could be used as a good approximation of the Mitscherlich equation. Steenbjerg (1952) suggested a sigmoidal relationship may exist at the lower end of the curve which would account for an initial dilution effect due to large growth responses. A much more radical departure from this traditional curve has recently been proposed by Ingestad (1977, 1979). He suggests that the "diminishing return" type curves are an artifact of the experimental design and that the growth curve for nitrogen was best described by an increasing exponential function rather than a decreasing logarithmic function.

Interpretations of foliar analysis however, are usually based on the relationship described by the conventional curves. These curves are typically divided into regions of deficiency, critical, luxury and toxicity. Macy

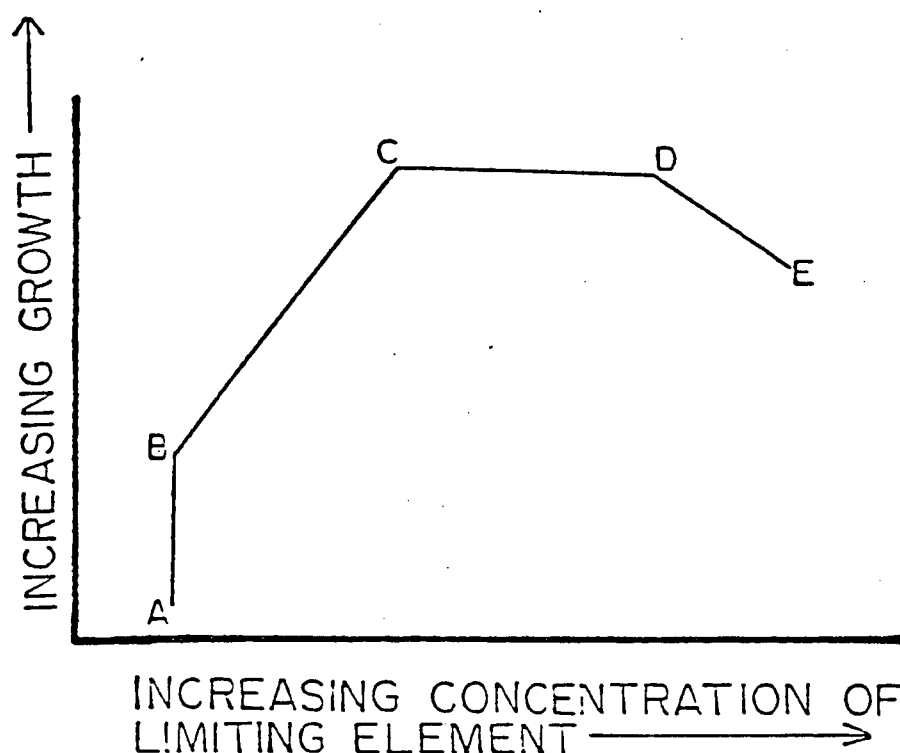


FIGURE 1. Theoretical relationship between growth and foliar nutrient concentration.

(1936) felt that the key to interpreting such a relationship lay in the fact that there was a critical level (Point C, Figure 1) for each nutrient, below which there was "poverty adjustment" (B to C, Figure 1) and above, "luxury consumption" (C to D, Figure 1).

Macy's zone of poverty adjustment corresponds to the deficiency region of nutrients in plant species. According to the near linear relationship of the curve within this region, an increase in the foliar concentration of the

limiting nutrient should result in an almost proportional increase in growth or yield until the critical nutrient level is reached. Trees with foliar nutrient concentrations in this range would normally be expected to respond to fertilization (Pritchett, 1979).

Luxury consumption on the other hand is not supposed to result in any increase in yield (Macy, 1936). This belief appears to have largely originated from agricultural research and greenhouse and pot trials on seedlings. In forest ecosystems, however, luxury consumption, through internal retranslocation of nutrients, may be one mechanism by which prolonged growth responses can be obtained from fertilization (Miller, 1981).

The critical percentage identified by Macy (1936) has led to the development of the critical nutrient level concept. This concept is based on the premise that the concentration of a particular nutrient is a unique measure of growth provided that it is the only limiting factor (Leyton, 1958). While Macy believed that the critical percentage of each nutrient could be identified by a definite point, it is now generally accepted that there is no single optimum or critical concentration, but rather, a certain identifiable range (Farr et al., 1977).

The use of the critical nutrient concept assumes that the relationship between foliar nutrient concentrations and growth is relatively consistent for any one species. Recent research indicates however, that this assumption may not be entirely valid. "Optimum" nutrient levels in the

foliage of a species have been shown to change with provenance (van den Driessche, 1973), age (Miller et al., 1981), height (Dighton and Harrison, 1983) and even site (Bonneau, 1973).

Foliar nutrient compositions are typically reported in relative terms such as concentration (i.e. percentage or ppm of oven dry-weight) (Leaf, 1973; van den Driessche, 1974). When expressed in such terms, fertilizer treatment effects, such as dilution and antagonism, often become obscured (Timmer and Stone, 1978). The use of content (i.e. mg per fascicle, per 100 needles or per sq cm of leaf area) as an expression of foliar nutrient levels has been suggested as an alternative (Leaf, 1973). However, Brockley (1981) suggested that from a nutritional viewpoint, absolute uptake is less important than concentration. Ideally, a method which expresses nutrient composition in both concentration and content would be superior to using simply one or the other.

A graphical technique, originally developed by Krauss (1967), which effectively incorporates needle nutrient concentration, content and needle weight has been used by a number of researchers (Heinsdorf, 1967; Czapowskyj et al., 1980; Timmer and Stone, 1978; Weetman and Fournier, 1983). This method enables researchers to effectively distinguish between treatment effects (Timmer and Stone, 1978). This same approach has therefore been used in this study to help interpret foliar analysis and indicate where potential future growth responses may be expected.

In this method the absolute or relative changes in needle nutrient concentrations, needle content, and needle weight, resulting from actual fertilizer trials, are graphically compared to a control (Weetman and Fournier, 1983) (Figure 2). The interpretations as to whether a nutrient is deficient and whether a response to fertilization can be expected are based on the direction and magnitude of the shifts from the control (Figure 2).

Use of this technique is based on two assumptions: (i) -- dry-weight of needles is closely correlated with fertilizer growth responses, and (ii) -- needle number is fixed in the first season following fertilization (Timmer and Stone, 1978).

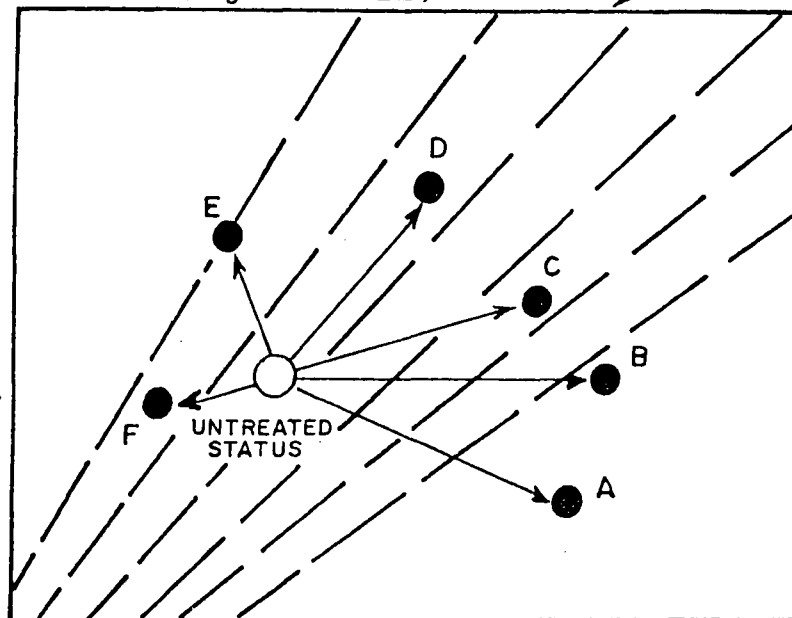
For most conifers, this latter assumption is met since the leaf primordia are initiated and set in the previous year. This has been shown to be true for Sitka spruce (Cannel and Willett, 1975), but species such as hemlock and cedar do not have this characteristic and therefore the technique may not be as applicable to them.

Good correlation has either been found or has been suggested to exist between the weight of needles one year after fertilization and subsequent growth responses (Leyton, 1956; Keay et al., 1968; Weetman and Algar, 1974; Timmer and Stone, 1978; Morrow, 1979). Numerous other studies, while not directly investigating the relationships of needle weight, have noted a connection between changes in needle weight and subsequent growth responses following fertilization (Maki, 1960; Ferda, 1975; Haines et al., 1975;

UNIT NEEDLE WEIGHT
(mg/NEEDLE) →

-13-

ELEMENT CONCENTRATION
% DRY WEIGHT ↑



ELEMENT CONTENT ($\mu\text{g}/\text{NEEDLE}$)

DIRECTION OF SHIFT	RESPONSE IN			CHANGE IN	
	NEEDLE WEIGHT	NUTRIENT CONC.	NUTRIENT CONTENT	NUTRIENT STATUS	POSSIBLE DIAGNOSIS
A	+	-	+	DILUTION	NON-LIMITING
B	+	0	+	UNCHANGED	NON-LIMITING
C	+	+	+	DEFICIENCY	LIMITING
D	0	+	+	LUXURY CONSUMPTION	NON-TOXIC
E	-	++	+	EXCESS	TOXIC
F	-	-	-	EXCESS	ANTAGONISTIC

Possible Diagnosis:

1. A shift towards A implies nutrient supply diluted by additional growth, suggesting nutrient may not be limiting.
2. A shift towards B implies nutrient transport into foliage just sufficient to keep pace with shoot or leaf expansion, indicating nutrient may not be limiting.
3. A shift towards C implies the nutrient was limiting.
4. A shift towards D implies luxury consumption by the foliage.
5. A shift towards E implies a toxic effect of the nutrient unless associated with other growth constraints.
6. A shift towards F implies a deficiency induced by the treatment, true antagonism.

FIGURE 2. Schematic relationships between needle nutrient concentration, content and needle dry-weight following fertilization (Morrow, 1979).

McIntosh, 1982). Still other fertilization studies have used alternative needle parameters such as, needle area, length, and total biomass to characterize treatment responses (Brix, 1971; Tamm, 1974; Miller and Miller, 1976; Turner and Olson, 1976). Individual needle weight has been shown to be highly correlated with needle length (Timmer and Stone, 1978) and surface area (Gordon and Gatherum, 1967; Mellor and Tregunna, 1972; van den Driessche, 1974) and, since needle weight is easier to determine, it tends to be used more often (Morrow, 1979).

Timmer and Stone (1978) argued that since shoot growth is determinate, differences in total weight of first year foliage/tree must closely reflect differences in weight of individual needles in the first season after fertilization. They further suggested that this should then be related to future growth performance since it has been shown that the dominant mechanism underlying growth responses is increased photosynthetic area (Tamm, 1974; Fagerstrom and Lohm, 1977). A similar assumption was first alluded to by Leyton (1956). He noted that when a treatment had an effect on tree growth, the response was first reflected in an increase in needle weight. Keay et al. (1968) suggested that changes in needle weight following fertilization may provide a rapid method of identifying potentially responsive stands.

The use of needle weight as a predictor of growth responses is not without problems however. Mahendrappa and Salonius (1982) found little change in black spruce (Picea mariana (Mill.) BSP) needle weight after urea fertilization

despite a significant growth response. Everard (1973), while acknowledging that needle weight is a good indication of the health and vigour of a tree, suggested that it may not be as well correlated to growth as needle nutrient concentrations.

Part of the problem associated with correlating growth responses with needle weight increases lies in the fact that needle weight, like nutrient concentrations, is highly variable and strongly influenced by environmental factors (Turner and Olson, 1976). Garrett and Zahmer (1973) noted that moisture stress during the growing season could significantly influence the number, size, and presumably weight, of needles in the following growing season by influencing the number of needle primordia initiated. Similarly, Pollard and Logan (1977) found that photoperiod and temperature had a significant influence on the needle primordia initiated in Picea species. Connell and Willett (1975) noted that shoot extension in determinate species such as Sitka spruce was largely controlled by the number of needle primordia initiated in the current year rather than the elongation of internodes between primordia. Trees with fewer needles may therefore grow less than trees with more needles despite a greater needle weight. Moreover, a tree with fewer needles in the year of fertilization may have a relatively larger increase in needle weight than a tree with more needles since growth would be concentrated on fewer needles. Thus it is apparent that some care must be exercised in interpreting changes in needle weight. This will be particularly true when comparing needle weight

responses of trees from stands of widely differing geographic and/or site characteristics.

Despite some of the problems associated with using needle weight as a growth predictor, the graphical technique used in this study has some advantages over the critical nutrient level concept since it allows for the identification of the different treatment effects. Moreover, needle weight appears to be a sensitive indicator of the general health of a tree (Everard, 1973) and therefore should be related to growth. Trees growing on nutrient deficient sites typically show a gradual shortening of needles and a decrease in needle weight. These same trees once fertilized usually show an increase in needle weight followed by a subsequent increase in height growth (Ferda, 1975). It should therefore be possible, based on changes in needle weight and nutrient composition, to identify potentially responsive stands.

Sitka spruce Nutrition and Fertilizer Response

Although Sitka spruce is recognized as an important timber and pulp species in the Pacific Northwest, little attention has been given to its nutritional requirements (Farr et al., 1977). This is probably due to the fact that Sitka spruce was of relatively minor importance for reforestation (Roche and Fowler, 1975), particularly when compared with other coastal species such as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). This has not been the case in Europe, especially in Britain where Sitka spruce was originally introduced as an exotic species in 1831 (Roche

and Fowler, 1975). Its potential for rapid growth and high volume production was recognized quickly and small scale plantations of Sitka spruce were established as early as 1866, with larger commercial plantations being established by 1913 (Davies, 1982). Since then Sitka spruce plantations have been established on a large scale in Britain (Roche and Fowler, 1975) and it is now the predominant species planted (Davies, 1982). In 1970, the national requirement for Sitka spruce seed in Britain totalled over 1300 kg (Buszewicz, 1970), whereas in British Columbia, in 1969, the total seed requirement was only 39 kg (B.C. For. Serv., 1969). Much of our knowledge of this species' nutritional requirements has therefore originated from research in British forests.

Nutritionally, Sitka spruce is considered to be a relatively demanding species (Krajina et al., 1982), however, its geographic distribution is thought to be restricted more by climate and physiography rather than edaphic factors (Roche and Fowler, 1975). In its natural habitat, the species is restricted to low elevations of the Pacific coastal fog belt. This area is characterized by having a perhumid climate of moderate temperature and high precipitation.

Sitka spruce has been shown to be as tolerant to high water tables as western red cedar (Minore, 1970; Krajina et al., 1982). However, on sites subjected to flooding, root development is restricted to the upper horizons (Cordes, 1972). Although capable of producing both deep and shallow root systems (Blyth and Macleod, 1981; Cordes, 1972), best

growth occurs on deep, acidic to mildly acidic soils which allow free rooting to a depth of at least 1 m (Roche and Fowler, 1975). Lack of adequate rooting volume is considered to be one of the main factors limiting productivity on many sites in both the Pacific Northwest and Britain (Day, 1957; Ross and Malcolm, 1982).

Although Sitka spruce seedlings can tolerate high levels of ammonium compounds, best growth is believed to occur when nitrates predominate (Krajina et al., 1982). Taylor (1935) also noted that Sitka spruce regeneration in Alaska was most abundant and vigorous on soils with high nitrifying capabilities. These findings however, are in contrast with those of van den Driessche (1971) who found that ammonium tended to produce better growth than nitrate. Similarly, extensive nursery research in Britain has found that ammonium sulphate consistently gave better growth than calcium nitrate (Benzian, 1965). However, Leyton (1952) found little difference in growth between ammonium- and nitrate- fed seedlings. There is still no consensus on the species' preference of N form (van den Driessche and Dangerfield, 1975; Adams and Atwill, 1982). The ability of a tree to utilize any one form of N depends on factors such as pH, light, moisture, age, carbohydrate supply, and nitrate reductase activity (Michael et al., 1970; Beevers and Hageman, 1969; Bigg and Daniel, 1978). Although it has been shown that plants vary in their capabilities to grow on ammonium and nitrate (Beevers and Hageman, 1983), it seems unlikely that a tree, in its natural environment, would

actively prefer one form of N over the other. In fact, numerous fertilizer trials have shown that significantly greater responses can often be obtained when both forms of N are added simultaneously (Binns, 1975; Beevers and Hageman, 1983).

There have been numerous attempts to quantify foliar nutrient levels associated with good and poor growth of Sitka spruce (Table 1). In general, it can be said that poor growth of Sitka spruce occurs when foliar nutrient levels are less than 1.2%, 0.14%, and 0.5% for N, P and K respectively, whereas good growth is associated with levels greater than 1.5% N, 0.18% P, and 0.8% K. Values in between these limits are described as being marginal, and although growth responses to fertilization can be expected in this range, the responses are often small (Everard, 1973).

Nutrient deficiencies severe enough to significantly influence growth of Sitka spruce plantations in Britain have commonly been recorded for N, P, K, and occasionally Cu (Binns et al., 1980). Countless numbers of fertilizer trials have shown the species to be highly responsive to remedial fertilization when these deficiencies exist (Dickson, 1973; Charlisle and Brown, 1973; Dickson and Savill, 1974; McIntosh, 1978, 1981, 1983). Similarly, in the Pacific Northwest, Sitka spruce plantations and second growth stands have been shown to be highly responsive to nitrogenous fertilizers, often more so than other species such as hemlock or Douglas-fir (Austin and Strand, 1960; Webster et al., 1976; Farr et al., 1977).

TABLE 1. Foliar nutrient concentrations associated with good and poor growth of Sitka spruce, western hemlock and western red cedar.

SPECIES	PERCENT OVEN-DRY WEIGHT				
	N	P	K	Ca	Mg
Sitka spruce					
Good growth - mean ¹	1.47	0.24	1.15	0.24	0.12
- range	(1.07-1.76)	(0.18-0.33)	(0.68-1.58)	(0.15-0.40)	(0.09-0.16)
- mean ²	1.38	0.22	0.80	0.31	0.09
- range	(1.05-1.66)	(0.13-0.32)	(0.55-1.35)	(0.13-0.56)	(0.06-0.15)
Optimum ³	>1.50	>0.18	>0.70	-	>0.07
Poor growth - mean ¹	0.95	0.16	0.69	0.28	0.10
- range	(0.72-1.27)	(0.08-0.19)	(0.30-0.89)	(0.21-0.37)	(0.08-0.12)
- mean ²	0.88	0.15	0.65	0.31	0.07
- range	(0.69-1.12)	(0.10-0.21)	(0.42-0.92)	(0.14-0.50)	(0.03-0.10)
Deficient ³	<1.20	<0.14	<0.50	-	<0.07
Western hemlock					
Good growth - mean ²	1.28	0.28	0.68	0.20	0.13
- range	(1.00-1.48)	(0.18-0.34)	(0.26-0.94)	(0.09-0.34)	(0.09-0.17)
Optimum ³	>1.50	>0.30	>0.80	-	-
Poor growth - mean ²	0.83	0.18	0.62	0.17	0.09
- range	(0.60-1.02)	(0.09-0.40)	(0.40-0.82)	(0.08-0.28)	(0.07-0.14)
Deficient ³	<1.20	<0.25	<0.60	-	-
Western red cedar					
Deficient ⁴	1.50	0.13	0.40-0.80	0.10-0.20	0.06-0.12

Sources: 1. Binns and Atterson, 1967.
2. Farr et al., 1977.
3. Binns et al., 1980.
4. Ballard, 1982.

Webster et al. (1976) noted that hemlock-spruce stands in Oregon fertilized with 168 and 336 kg N/ha had average diameter responses 4 to 6 years after fertilization of 27% and 49%, respectively for spruce, but only 3% and 18%, respectively for hemlock. Farr et al. (1977) found that the addition of 448 kg/ha of urea to Sitka spruce plantations in Alaska resulted in an average 20 to 25% increase in height growth over a 3 to 4 year period.

Fertilizer trials from Britain have shown that Sitka spruce is particularly responsive to phosphorus fertilization. While the most responsive sites have been from sites with deep organic soils, particularly the oligotrophic peats, P deficiencies in spruce or responses to P fertilization have been known to occur on a range of different sites (McIntosh, 1981). It is now recognized that satisfactory growth of Sitka spruce on organic soils is virtually impossible unless a top dressing of P or P plus K is applied at the time of planting (McIntosh, 1983).

In the Pacific Northwest, little attention has been given to P fertilization as it is generally believed that nitrogen is the most limiting element in soils of this region (Atkinson, 1975). However, a number of greenhouse and pot trials using soils from a variety of coastal sites have shown significant growth responses of Sitka spruce, hemlock, and Douglas-fir seedlings to P and N plus P fertilization (Meurisse, 1976; Heilman and Ekuan, 1980; Anderson et al., 1982). Gessel et al. (1979) also noted that in many fertilizer trials within the Pacific Northwest where other

nutrients besides N have been tested, N plus P often gave better responses than simply N alone.

In general, benefits from P or P plus K fertilization on organic soils in Britain have been found to last 7 to 10 years (McIntosh, 1981). Considerably longer benefits from P fertilization, often exceeding 20 years, have occurred on some sites in New Zealand (Ballard, R., 1978) and on a variety of sites in the southeastern States (Pritchett and Comerford, 1982).

The need for K fertilization has been shown to vary by site, but it is generally believed that widespread K deficiencies will occur on most deep organic soils and that many plantations established on these sites will require K fertilization at some time in their development (Atterson and Binns, 1975). McIntosh (1981) noted that the probability of a K deficiency occurring increased with increasing peat depth. He suggested that there seemed to be a threshold value of about 30 cm, above which a K deficiency is unlikely, and below which a K deficiency is highly likely.

Responses to K appear less consistent and dramatic than responses to P. However, a number of fertilizer trials have shown that it is possible to gain significant additional benefits by adding both P and K at the time of planting rather than simply adding P alone (McIntosh, 1981). The inclusion of N at this time has not been effective (Dickson and Savill, 1974). Actual growth responses to P plus K fertilization in Britain have been very dramatic. Dickson

and Savill (1974) found that seven years after P plus K fertilization, increases in total height growth of Sitka spruce ranged from 128% to 265% for P applications ranging from 36 to 216 kg P/ha. Leader growth at the end of this time was still 100 to 250% greater than the controls. Based on a survey of the British literature, these values appear to be the norm rather than the exception.

In many of the spruce plantations established in Britain, signs of N deficiency often begin to appear 6 to 8 years after planting (Dickson and Savill, 1974). These plantations have been shown to be highly responsive to N fertilization. As mentioned previously, Sitka spruce has also been shown to be highly responsive to nitrogenous fertilizers in the Pacific Northwest. Unlike the case for P, responses to N are typically of short duration, often lasting only 3 to 4 years (McIntosh, 1981; Farr et al., 1977). However, there are numerous examples where considerably longer responses to N fertilization have been obtained (Atkinson, 1975). Miller (1981) showed that the longevity of response to N fertilization was related to luxury consumption; i.e. the greater the N uptake over and above the trees immediate requirements, the longer the response.

The short-term nature of N fertilizer responses has led investigators to look for alternative methods of improving the N nutrition of Sitka spruce. In Britain this has primarily been achieved through weed control and/or cultivation. Both methods have been shown to be effective in

improving the N nutrition of Sitka spruce plantations (Dickson and Savill, 1974; Ross and Malcolm, 1982). Dickson and Savill (1974) noted however, that regardless of type and time of treatment, on the poorest sites, growth of Sitka spruce will become limited by a N deficiency. Ross and Malcolm (1982) noted that the benefits of intensive site preparation may only last for 10 to 15 years. Moreover, weed control or cultivation appear to mainly benefit the N nutrition of the tree and not so much the P and K nutrition. Thus, fertilization with P plus K is still required if satisfactory growth is to be achieved.

Although Sitka spruce has been planted in Britain in pure stands following fertilization on Calluna moorland soils, recent analysis of mixed stands have shown improved growth rates and P nutrition of Sitka spruce when associated with lodgepole pine. The reasons for this improved P nutrition are believed to be due to changes in the mycorrhizal infection of the spruce. Similarly, Calluna roots are suspected of upsetting Sitka spruce P nutrition via some unknown mycorrhizal process. Calluna eradication results in improved P nutrition. A parallel between this effect of Calluna and the reduced growth of Sitka spruce on sites dominated by salal (Gautheria shallon Pursh.) in B.C. is suspected (Weetman, Faculty of Forestry, University of British Columbia, personal communications).

STUDY AREA AND SITE DESCRIPTION

Location

Five Sitka spruce plantations, located near Port McNeill on northern Vancouver Island (Figure 3), and ranging in age from 8 to 14 years, were selected for the fertilizer trials. All plantations are located in Block 4 of Tree Farm Licence 25 which is presently under the management of Western Forest Products Ltd. All plantations are established on the Cedar-Hemlock phase of the salal-moss ecosystem association and are exhibiting severe chlorosis and growth check.

Climate

The region has a Cfb climate (after Koppen's classification: Lewis, 1982). Thus it is characterized by having mild winters, cool moist summers and a relatively long spring and autumn. Table 2 gives the 30-year normal values of temperature and precipitation as summarized by Lewis (1982), as well as the climatic means for the 1983 growing season. All data were obtained from the Port Hardy Airport weather station, located about 15 km northwest of the plantations (Figure 3).

The mean daily maximum temperature during the warmest months of the year (July and August) only averages slightly above 17°C and the mean daily minimum temperature

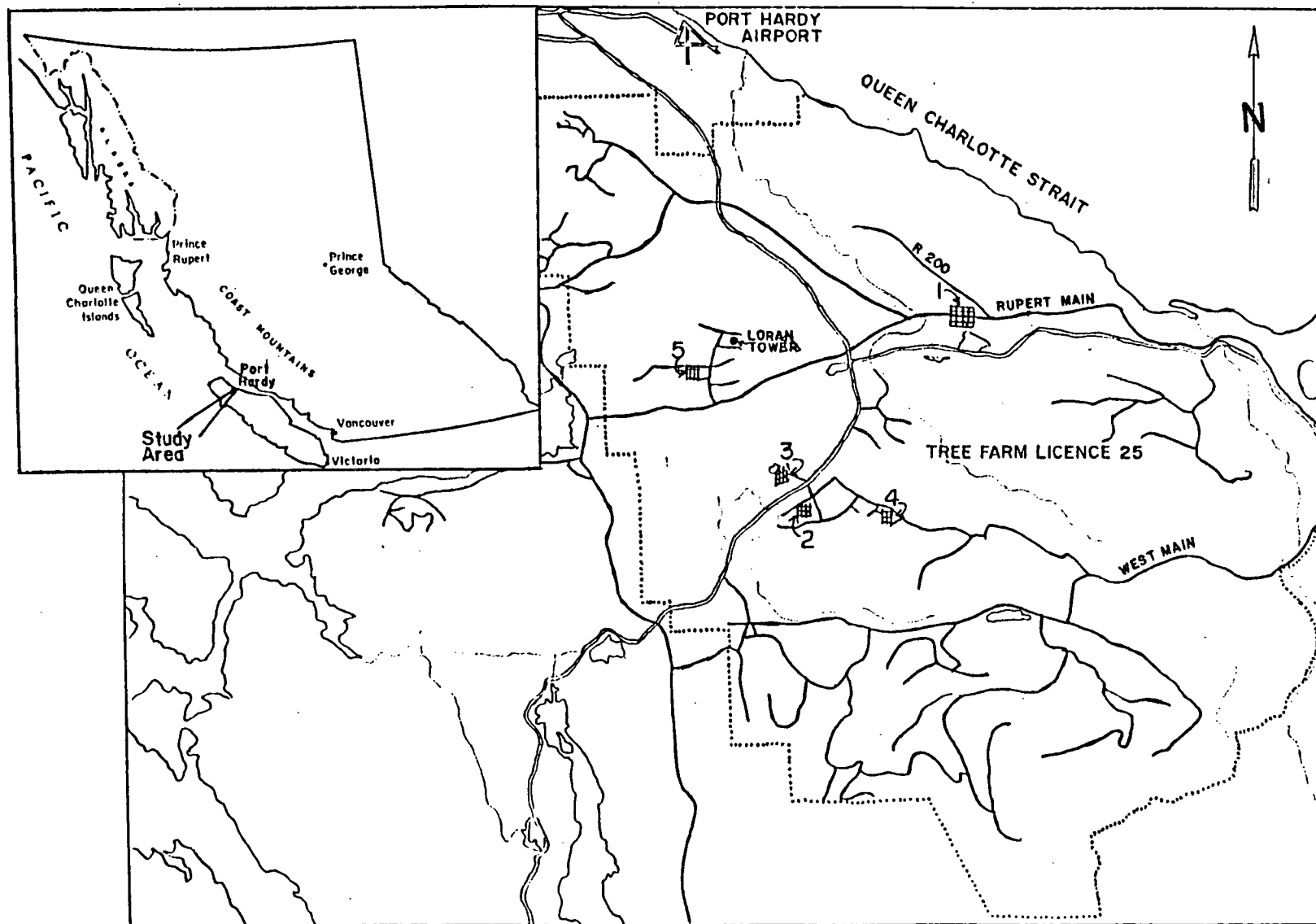


FIGURE 3. Location of study area.

TABLE 2. Temperature and precipitation values for Port Hardy.

MONTHS	MEAN DAILY TEMP. (°C)		MEAN DAILY MAX. TEMP. (°C)		MEAN DAILY MIN. TEMP. (°C)		MEAN RAINFALL (mm)		MEAN SNOWFALL (mm)		MEAN PRECIPITATION (mm)	
	30 YEAR NORM	1983	30 YEAR NORM	1983	30 YEAR NORM	1983	30 YEAR NORM	1983	30 YEAR NORM	1983	30 YEAR NORM	1983
January	2.4	5.6	4.7	7.9	0.0	3.2	181	273	284	Trace	209	273
February	3.4	6.0	6.6	8.9	1.1	3.0	144	216	132	-	157	216
March	4.4	6.5	7.7	10.7	1.1	2.3	123	153	91	-	133	153
April	6.5	7.8	10.3	12.4	2.7	3.2	108	68	13	Trace	109	68
May	9.5	11.2	13.7	15.6	5.4	6.7	63	35	Trace	-	63	35
June	11.0	12.4	15.8	15.3	8.3	9.4	59	163	0	-	59	163
July	13.6	14.0	17.3	17.5	9.9	10.4	54	151	0	-	54	151
August	13.8	14.0	17.3	18.1	10.2	10.4	68	56	0	-	68	56
Septembe	11.9	11.3	15.4	15.1	8.4	7.5	132	119	0	-	132	119
October	8.7	8.0	11.3	11.4	5.6	4.6	253	170	0	Trace	253	170
November	5.3	6.3	7.8	8.7	2.8	3.9	231	288	33	33	234	291
December	4.5	1.1	5.7	4.0	1.2	-1.9	242	120	152	6	258	123
ANNUAL	8.0	8.7	11.2	12.1	4.7	5.2	1649	1812	706	6	1730	1818

*Note - Normal, mean values of temperature and precipitation for Port Hardy are projected from 25 - 29 years of record during the period 1941 - 1970 (Lewis, 1982).
1983 - Data from Environment Canada's Weather Record for Port Hardy.

during the coldest month (January) only drops to 0°C. The mean annual precipitation is about 1700 mm and occurs mostly as rain. Although May through August tends to be the driest period of the year, mean monthly precipitation rarely drops below 50 mm and thus soil moisture deficits are rare. However, due to heavy rainfall, many sites may suffer from excessive moisture levels either year-round or during part of the year. For 1983, precipitation in April and May was considerably lower than the 30-year average. This was important since the fertilizer was applied in the last 2 to 3 weeks of April, and thus the chance of leaching, particularly of the nitrate ion, would probably be less than in a "normal year".

Site and Ecosystem Description

Block 4 of T.F.L. 25 encompasses parts of two major physiographic subdivisions--the Vancouver Island ranges and the Nawahitti Lowlands, with the latter being further subdivided to account for a low-lying area known as the Suquash Basin (Holland, 1976). All five plantations in this study are located within this basin. It is characterized by having a gently undulating topography which seldom exceeds 300 m in elevation. The surface material of the Suquash Basin mainly consists of very deep, unconsolidated, morainal glacial and glacial fluvial outwash material.

Lewis (1982) recently completed the ecosystematic classification of Block 4 of T.F.L. 25. His classification approach closely follows the biogeoclimatic ecosystem

classification presently used by the British Columbia Ministry of Forests. Within Block 4, the most prominent subzone is the Wetter Northern Maritime Coastal Western Hemlock Subzone (CWHe) occupying approximately 98 percent of the productive land base (30,529 ha). This subzone is further subdivided into two variants, a lower elevation submontane variant and a higher elevation montane variant. The submontane variant encompasses about 91 percent of the land area in the CWHe subzone. Lewis identified eleven ecosystem associations in this variant of which the zonal or "climatic" ecosystem is the Thuja plicata - Tsuga heterophylla - Abies amabilis - Gautheria shallon - Rhytidiadelphus loreus (referred to hereinafter as the S1 or salal-moss ecosystem association). The S1 ecosystem association is the dominant ecosystem association within Block 4 and occupies some 60 percent of the productive land base in the CWHe subzone (Lewis, 1982). It is also thought to occupy a significant portion of the remaining area of the productive land base of northern Vancouver Island and may even extend as far south along the west coast of Vancouver Island as Tofino (Dumont, Western Forest Products Ltd., personal communication).

According to Lewis (1982), the salal-moss ecosystem association is comprised of two distinct phases--the hemlock-amabilis fir (HA-) phase and the cedar-hemlock (CH-) phase. These phases have apparently developed due to differences in stand histories.

The CH-phase is the climatic climax community of the salal-moss ecosystem association. The mature stands on these sites can be described as being relatively open, containing large decadent old-growth western red cedar (Thuja plicata Donn) and hemlock with a minor component of amabilis fir (Abies amabilis (Dougl.) Forbes) (Figure 4).

The understory usually consists of a very dense, tall shrub layer, invariably dominated by salal. The herb layer tends to be sparse with the dominant herb being Blechnum spicant (L.) Roth. The dominant mosses found in this phase are Hylocomium splendens (Hedw.) B.S.G. and Rhytidiadelphus loreus (Hedw.) Warnst. These stands have developed over a number of centuries with little or no disturbance. Despite their appearance, they are considered to be highly valuable and average yields, predominantly due to western red cedar, typically exceed 700 cu m/ha.

The HA-phase is characterized by dense, even-aged stands of hemlock and amabilis (Figure 4). The forest floor is dominated by a continuous cover of mosses, mainly Stokesiella oregana (Sull.) Robins. and Hylocomium splendens. Although the herb layer is not well-developed, it tends to be more varied than in the CH-phase, and includes such species as Blechnum spicant, Polystichum munitum (Kaulf.) Presl. and Tiarella trifoliata L. The shrub layer, unlike that in the CH-phase, tends to be sparse with only a sporadic cover of salal and Vaccinium species.

According to Lewis these stands are seral, and if allowed to develop without disturbance, will eventually



FIGURE 4.
Mature stands of the
HA- and CH-phases.

a)
HA-phase -- this stand is
approximately 70 years old
and originated from a 1906
blowdown.



b)
CH-phase -- this stand is
unevenaged (140-300+ years)
and has developed with
little or no disturbance.

revert to the CH-phase. Apparently, the HA-phase develops as a result of extensive windthrow disturbances, the latest of which resulted from a severe storm in 1906. Similar dense stands of Sitka spruce and hemlock and of hemlock and amabilis have developed due to extensive windthrow in the Estevan and West Vancouver Island Wetter Maritime Biogeoclimatic subzones (Klinka et al., 1979). Since remains of the original old-growth stands, particularly the red cedar component, are not readily evident in many of the stands of the HA-phase, it is unlikely that these stands developed from a single windthrow disturbance, but rather, were probably subjected to a series of periodic disturbances. This was highlighted recently in 1982, when more than 400 ha of these stands had to be salvaged due to severe blowdown (Coastal Silvicultural Committee² (CSC) Workshop, 1983).

Such dramatic disturbances would provide large areas of mixed mineral soil/organic matter seedbeds. After disturbance, extremely dense and vigorous hemlock and amabilis natural regeneration develops on these sites. Density estimates of 10,000 to 20,000 stems/ha or more appear typical for this phase. These sites have proven to be extremely productive. Unmanaged mature 70-year-old stands have estimated yields of 12 to 15 cu m/ha/yr (CSC Workshop, 1983). However, comparison of height growth in young 10 to 15 year old plantations with those of British yield curves

²Coastal Silvicultural Committee. 1983. Unpublished proceedings of the northern Vancouver Island 1983 CSC Workshop on the Coastal Western Hemlock Zone.

(see Bradly, 1971) suggest that potential yields of newly established plantations could be significantly increased if intensive management, particularly in the form of stocking control, were practised.

Traditional management of both phases has consisted mainly of clearcutting and then broadcast burning followed by planting, primarily with Sitka spruce. It has recently become evident however, that there is a substantial difference in the performance and productivity of the plantations between the two phases. Plantations established on the CH-phase, while initially performing well in both survival and height growth for a period of 3 to 5 years after planting, are now experiencing a severe decline in growth (Figures 5 to 7). The mean annual height growth in 1982 and 1983 for the five plantations in this study was only 10.5 and 9.6 cm, respectively. The decline these plantations are experiencing becomes even more dramatic when compared to the excellent performance of the regeneration on the HA-phase and the fact that these two phases often occur adjacent to each other (Figure 5).

Unlike the plantations established on the CH-phase, the plantations established on the HA-phase have continued to perform well (Figures 5 to 7). As mentioned earlier, extremely dense and vigorous natural hemlock and amabilis regeneration typically develop on these sites after logging. Hemlock growth in these stands was equivalent or better to that of spruce. For example, the 1982 and 1983 mean annual height increment for 10 co-dominant spruce and hemlock

FIGURE 5.
Development of plantations
on the HA- and CH-phases
after logging. Rick
Fournier is seen here
standing in two plantations
which were both established
in 1973. These photos were
taken approximately 40 m
apart.



a) HA-phase.

b) CH-phase.



a)

Onset of
decline. →



b)

1983 - 1 cm —
1982 - 3 cm —
1981 - 5 cm —
1980 - 9 cm —



FIGURE 6. Illustrations of growth patterns for Sitka spruce growing on the CH-phases. Note the naturally occurring cedar in center of photo a), current height growth is about 25 cm compared to 8 cm for the spruce.

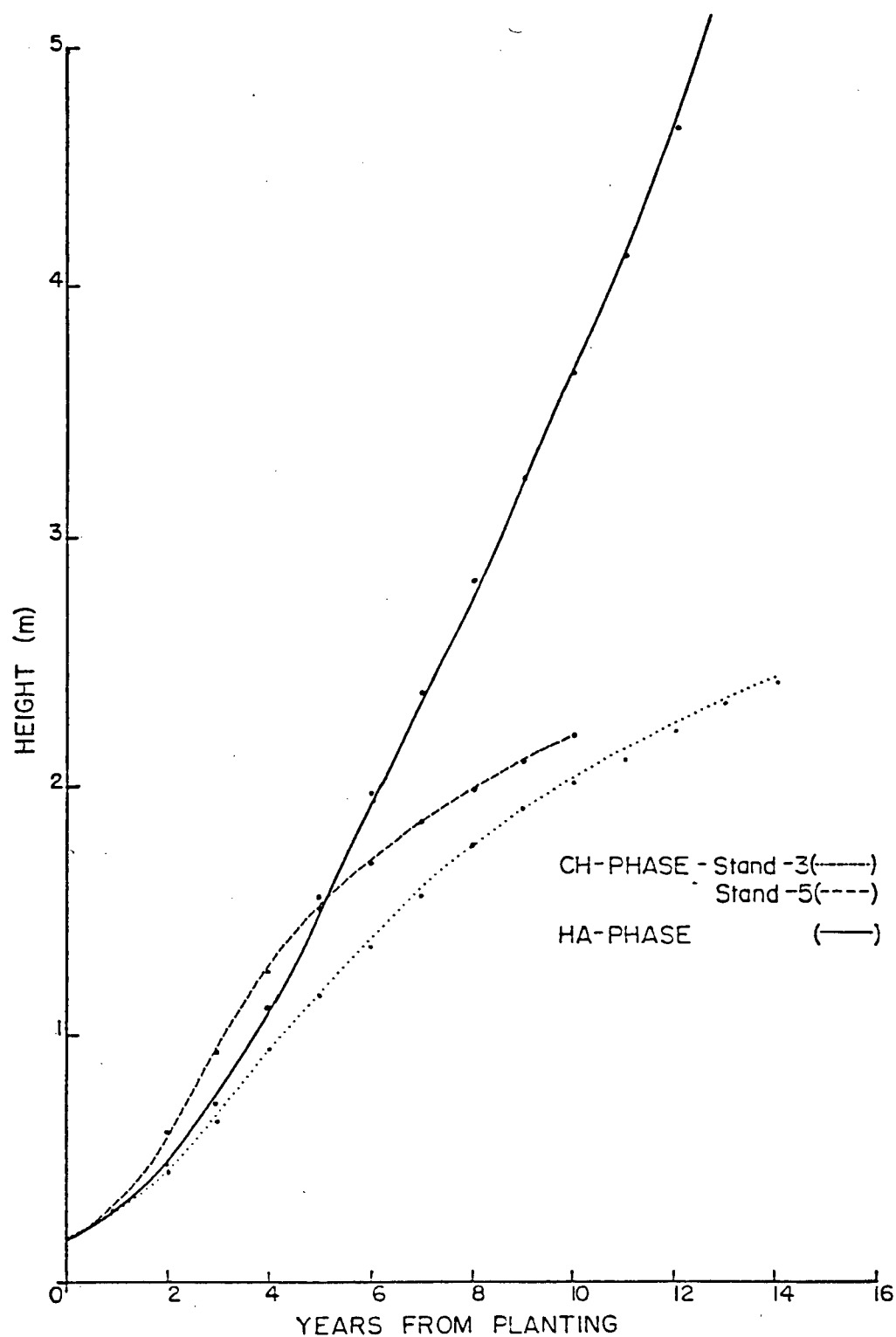


FIGURE 7. Mean cumulative height growth of Sitka spruce on the CH- and HA-phases. Means are based on 14 and 10 sample trees for the CH- and HA-phases, respectively.

selected from a 16-year-old plantation was 63.2 and 72.2 cm for spruce and 56.9 and 87.3 cm for hemlock, respectively.

Similar hemlock ingress does not occur to the same extent on the CH-phase and estimates of densities usually average less than 400 stems/ha. While the height growth of these hemlock appears to be better than that of the spruce (16.9 and 17.1 cm in 1982 and 1983 respectively) it is still poor and well below that of the HA-phase. Considerably more cedar ingress occurs in this phase than in the HA-phase, and while no growth estimates have been obtained for this species, it is the preferred species for the site and is capable of producing acceptable growth (Dumont, personal communication).

Lewis (1982) hypothesized that the main reason underlying the differences in productivity between the two phases was related to the differences in stand development and its effect on nutrient turnover. He suggests that the periodic windthrow disturbances of the HA-phase has had a "cultivating effect" on the soils, creating a much more favourable physical and chemical environment for root development and tree growth. Descriptions of a typical soil profile for both phases are given in Tables 3 to 5 and Figure 8. Although the soils in both phases can be predominantly classified as a Duric Ferro-Humic Podzol (Can. Dept. Agr., 1978), their physical properties are quite dissimilar.

The HA-phase is characterized by having deep (1+ m), well drained soils of loose consistency. Organic accumulations tend to be less in this phase, although it



FIGURE 8.

Typical soil profiles of the HA- and CH-phases. Profiles shown were dug on the same day and occupy the same relative topographic location.

a)

HA-phase--note the lack of vegetation on the forest floor. Also note the lack of water accumulation despite the fact that the pit is 1+ m deep.



b)

CH-phase -- note the dense salal growth in this phase. Water accumulation began at a depth of 60 cm from the top of the forest floor.

TABLE 3. Soil profile description of the CH-phase.

HORIZON	DEPTH (cm)	DESCRIPTION
LF	27 - 26	Mixture of coniferous and salal litter and mosses; loose consistency; no roots; abrupt wavy boundary to,
H	26 - 0	Reddish black (5R 2.5/1 m), dark reddish brown (5YR 3/2 d); massive; abundant roots all sizes; abrupt wavy boundary to,
Ae	0 - 4	Grey (5YR 6/1 m) to brown (7.5YR 4/2 m); medium subangular blocky, friable; few fine and medium roots; clear, broken boundary to,
Bhf	4 - 19	Red (2YR 4/6 m), dark brown to brown (7.5YR 4/4 to 5/4 d); sandy loam; weak medium subangular blocky; firm when moist; non-sticky and slightly plastic, wet; plentiful fine roots, few medium and coarse roots; abrupt wavy boundary to,
Bf	19 - 34	Yellowish red (5YR 5/6 m), yellowish brown (10YR 5/8 d); sandy loam; medium subangular blocky; firm when moist; non-sticky and non-plastic, wet; few fine roots; abrupt wavy boundary to,
Bfgj	34 - 48	Yellowish brown (10YR 5/8 m), yellowish brown (10YR 5/8 d); gravelly sandy loam; weak, medium and coarse subangular blocky, extremely firm when moist, non-sticky and non-plastic; no roots; common faint mottles, seepage water present; abrupt wavy boundary to,
BCc	48+	Strongly cemented to indurated gravelly sandy loam.

TABLE 4. Soil profile description of the HA-phase.

HORIZON	DEPTH (cm)	DESCRIPTION
LF	15 - 12	Variegated mixture of coniferous litter and mosses; loose consistency; not roots abrupt wavy boundary to,
H	12 - 0	Black (2.5YR 2.5/0 m), dark reddish brown (5YR 3/2 d); highly decomposed organic matter; granular, slightly greasy in lower horizon; abundant roots of all sizes; abrupt, wavy boundary to,
Ae	0 - 3	Grey (5YR 6/1 m) to brown (7.5YR 4/2 m); medium subangular blocky; friable; few fine roots; clear, broken boundary to,
Bhfu	3 - 18	Reddish brown (2.5YR 4/4 m), strong brown (7.5YR 5/8 d); sandy loam; weak medium subangular blocky; friable when moist; non-sticky and slightly plastic, wet; abundant fine and few medium roots; abrupt wavy boundary to,
Bf1	18 - 33	Strong brown (7.5YR 5/6 m), yellowish brown (10YR 5/8 - 5/6 d); gravelly sandy loam; weak medium subangular blocky; friable when moist; non-sticky and non-plastic, wet; few fine roots; clear wavy boundary to,
Bf2	33 - 48	
Bf3	48 - 63	
Bfgj1	63 - 78	Yellowish brown (10YR 5/8 m), brownish yellow (10YR 6/8 d); gravelly sandy loam, weak, medium and coarse subangular blocky, firm when moist; non-sticky and non-plastic, wet; very few roots; few faint mottles; abrupt wavy boundary to,
Bfgj2	78 - 88	
BC	88+	Olive grey (5Y 5/2 d), extremely firm when moist; no roots.

TABLE 5. Physical and chemical description of soil profiles from the CH- and HA- phases.

[illegible]

appears to vary with logging. Lewis (1982) found that organic accumulations in the HA-phase averaged between 5 to 10 cm. Similar accumulations were found in this study in the mature unlogged stands. Areas which had been disturbed by logging however, had much more variable depths with accumulations often exceeding 20 cm. The CH-phase is characterized by having a thicker (15 to 30 cm), somewhat compacted organic layer. The Bf horizon is of firm consistency and only moderately deep due to a highly cemented till layer which occurs at a depth of 40 to 50 cm. The compacted nature of this soil strongly influences water movement and thus they tend to be only imperfectly to moderately well drained (Figure 8).

A distinguishing feature of the CH- and HA-phase, aside from the difference in productivity, is the presence or absence of salal. The CH-phase is characterized by having an extremely dense salal cover, whereas in the HA-phase it is virtually absent. There has been some suggestion that salal may in part contribute to the low productivity of the CH-phase. Strong similarities have been noted between the performance of these plantations and of the Sitka spruce plantations in Britain suffering from "heather" (Calluna vulgaris) (L.) Hull. check (Weetman, personal communication). Some possible reasons for a "salal" effect might be attributed to:

- (1) Excessive competition for a limited supply of available nutrients. On these sites salal forms a very dense root mat which exploits the entire organic layer and the upper portions of the mineral soil and is thus in direct competition with the spruce.

- (2) Presence of high concentrations of organic compounds such as polyphenols and simple fatty acids in the salal litter. These substances are resistant to microbial attack (Minderman, 1966) and possess fungal- and phytotoxic properties capable of suppressing the decomposing micro-organisms (Berg et al., 1980) and inhibiting root growth (Jalal and Read, 1983 a, b). While it is not known if salal has high concentrations of these compounds, they are apparently readily produced in many evergreen sclerophyllous heath-forming species of the Ericaceae family (Specht, 1979). Moreover, leaf polyphenol production tends to increase in plants exposed to nutrient stress (Davies et al., 1964; Gosz, 1981). Recently, Jalal and Read (1983 a, b) have extracted and identified a number of these compounds from Calluna heath soils in concentrations significantly higher than levels which have been previously shown to totally inhibit root growth in agricultural crops and severely inhibit fungal mycelial growth in forest soils.
- (3) A possibility of an allelopathic influence being exerted by the salal. Allelopathy is a commonly known phenomenon amongst many plant species (for example see Rice, 1979). In particular however, allelopathic properties have been commonly associated with Ericaceae species in different parts of the world (Handley, 1963; Peterson, 1965; Jalal and Read, 1983 a, b). In the case of Calluna heaths, it has been suggested that metabolites produced by the mycorrhizal fungi of Calluna roots may be toxic to the mycorrhizal fungi of tree species (Handley, 1963; Robinson, 1972). Jalal and Read (1983 a, b) suggested that the mycorrhizae of Calluna may be better able to utilize lipids as a carbon source and would thus be able to tolerate the high concentrations of fatty acid residues produced. As mentioned above, these residues are highly toxic to many other fungal species. Most Ericaceous species have been shown to form a distinct mycorrhizal association known as "ericoid" mycorrhizae rather than the ecto- or vesicular-arbuscular (VA-) mycorrhizae typically found on other vascular plants (Pearson and Read, 1973; Largent et al., 1979; Molina and Trappe, 1982). Pearson and Read (1973) have shown that the endophytes which readily form mycorrhizal association with Calluna also readily infect other Ericaceae species. Salal has also been

shown to form the typical "ericoid" type mycorrhizal association (Largent et al., 1979). McNabb (1961) noted that the ericoid mycorrhizae on Gaultheria species in New Zealand were anatomically similar to that found on Calluna vulgaris in Britain.

- (4) The type, quality and quantity of litter input. In addition to the possible input of toxic organic compounds, the high rooting densities of salal may result in a substantial amount of woody root litter leading to the development of a thick "root" mor humus with a high C/N ratio.

Recently, Youngberg (1978) showed that nitrogen mobilization and subsequent uptake by Douglas-fir seedlings grown in different forest floor materials was significantly less when the humus material had a salal component despite a higher N concentration. These findings led Youngberg to suggest that something other than total N was playing an important role in influencing growth and N uptake.

Although not investigated in this thesis, the possibility of some sort of "salal effect" cannot be discounted. This should be kept in mind throughout this thesis.

COMPARISONS OF SOIL NUTRIENT STATUS AND NITROGEN MINERALIZATION POTENTIAL OF THE CH- AND HA-PHASES

INTRODUCTION

The general appearance of the plantations in the CH-phase, i.e., severe chlorosis and growth check, strongly suggests the possibility of a nutrient disorder, and in particular, a nitrogen deficiency. Preliminary foliar and soil analysis (Lewis, 1982) supports this suggestion. As mentioned earlier, Lewis hypothesized that organic decomposition and nutrient turnover were much slower in the CH-phase as compared to the HA-phase. If such is the case, differences in the soil nutrient status, and in particular, N mineralization rates, should be expected between the two phases. Therefore, soil samples were collected from both phases and analyzed in order to identify possible differences.

It is not the intent of this study to quantify the absolute amounts of nutrients on these sites, but rather, to obtain an indication of relative differences between the two phases. Thus, although the sample size per cutover is small (see Methods), it should be large enough to adequately distinguish differences between the two phases.

MATERIALS AND METHODS

Field Procedure

Many of the Sitka spruce plantations established on the CH-phase experienced an initial period of good growth before the onset of the decline. The Assart effect has been suggested as a possible explanation for this initial growth (Weetman, personal communications). Therefore, in order to investigate this possibility, an age sequence of cutovers were selected for sampling. Five plantations, which were initially logged and then burned 3, 5, 9, 14 and 24 years ago, plus a mature unlogged stand, were selected from each phase. The 9 and 14 year old cutovers were subsequently used for the fertilizer trials.

In each of the unfertilized plantations, samples were taken along five, 100 m transects using a soil core sampler. Along each transect, five samples of the top 15 cm of the FH layer and three samples of the top 15 cm of mineral soil were collected at 20 m intervals and placed in individual plastic bags. In the fertilized plantations, sampling was restricted to the perimeter of five of the control plots. Large roots and poorly decomposed woody material were avoided in all phases of sampling. The cores were later bulked by transect or plot to give a total of ten (five FH and five mineral soil) samples per plantation. At

the time of sampling, total depth of organic accumulation to mineral soil was measured at each sampling spot.

Laboratory Analysis

All samples, organic and mineral, were initially air dried for one week, and then sift through a 2-mm sieve. A subsample of 50 g from each sample was then taken and composited by transect or plot and soil fraction. A further subsample was taken and finely ground for the determination of total N, P and C.

Mineralizable-N was determined on duplicate samples using the anaerobic incubation method of Waring and Bremner (1964). Two grams of forest floor and five grams of mineral soil were incubated in 23 ml of water for two weeks at 30°C. Mineralizable-N was then extracted by shaking the solution for one hour in 1 N KCl. The extract was analyzed colorimetrically with a Technicon autoanalyzer for ammonium. Nitrate concentrations were not determined. Due to the logistics of sample storage and transportation in the field, samples were exposed to room temperature conditions for a period of one to two weeks prior to the commencement of air drying. Thus, the data in this study will mainly be expressed as gross N mineralization (Jones and Parsons, 1970; Powers, 1980) rather than net mineralization. However, for purposes of comparison with other studies, net mineralization was also determined. Thus, prior to incubation, available N was extracted from duplicate samples using the same methods as above. Net mineralizable-N was then determined by

subtracting the amount released during the incubation from the amount of available N initially present in the soil. Total N and P were determined by a semimicro Kjeldahl digestion, then analyzed colorimetrically with a Technicon autoanalyzer. Total C was analyzed using a Leco Induction Furnace. Available P was determined using the Bray P extraction procedure (dilute acid-fluoride extraction) (Olsen and Sommers, 1982). Exchangeable cations (K, Ca, Mg and Na) were determined by displacement of cations by neutral normal NH_4OAc (Chapman, 1965). Displaced cations were analyzed by atomic absorption. CEC was determined by steam distillation of NH_3 (Chapman, 1965). Values for pH were determined in both a 1:2 soil: 0.01 M CaCl_2 and 1:2 soil: water suspension for mineral soil and an 1:5 0.01 M CaCl_2 and 1:5 water suspension for organic material. Particle size was determined by the Bouyoucos hydrometer method (Day, 1965).

Statistical Analysis

Mineralizable-N was subjected to a 6 x 2 (years since harvest x phase) factorial analysis, followed by a Student-Newman Keuls' multiple range test. Comparisons of the other soil parameters were based on simple Student-t tests. For these tests, the data from all cutovers were combined by phase. All statistical analyses were performed with the aid of U.B.C.'s computer using either the program GENLIN, for the factorial analysis, or MIDAS for the Student-t tests.

RESULTS AND DISCUSSION

Table 6 summarizes the estimates of the soil nutrients investigated. Soils in both phases are acidic. There was no significance difference in pH when measured in a CaCl_2 solution. However, when measured in a water solution, the pH of the mineral soil in the HA-phase was significantly greater ($p=.05$) (Table 6). The actual differences however, are slight, and would not account for differences in the availability of nutrients between the two phases.

With the exception of Ca, there is relatively little difference in the exchangeable bases between the two phases. Significantly greater ($p=.01$) amounts of Ca found in the humus of the CH-phase may be a reflection of the higher cedar content of this phase. However, other studies in this area have found comparable concentrations in the HA-phase (Table 7). Both K and Mg concentrations were significantly greater ($p=.05$) in the mineral soil of the HA-phase, although the actual differences between phases are slight.

When compared with a variety of other sites throughout the Pacific Northwest (see Heilman, 1979), the values for Ca and Mg appear to be normal, but K values appear to be well below the average for both organic and mineral soils. There are indications that the low K levels experienced in this study are deficient, particularly in the

CH-phase. Mean K concentrations of the humus are comparable to, or only slightly higher than concentrations found in oligotrophic peats known to be K deficient (Gore and Allen, 1956; Williams et al., 1978). In addition, mean foliar K concentration of spruce trees from both phases are low and in the critical range (Table 1). In fact, visual symptoms characteristic of K deficiency were observed on the occasional spruce in the plantations selected for fertilization (see Figure 20 and corresponding discussions). Similar symptoms were not noted on spruce in the HA-phase. This may be due to a greater portion of the roots reaching and exploiting the mineral soil in this phase.

Both available and total P were significantly greater ($p=.01$) in the organic and mineral soils of the HA-phase as compared to the CH-phase. Absolute differences between the phases were again small, and in both cases the soils appear to be extremely P deficient. Klinka et al., (1979) noted, however, that care must be exercised when interpreting available P data since different extraction methods yield different results and the best method for coastal B.C. is still unknown. Compared to other soils throughout the Pacific Northwest (see Heilman, 1979) the estimates obtained in this study are well below average, but agree with estimates from other sites of western Vancouver Island (Table 7). Similarly, total P concentrations are within the ranges found on mesotrophic and oligotrophic peats, known to be P deficient (Toleman, 1973). In addition, mean foliar P concentrations of spruce and hemlock sample

TABLE 6. Comparison of nutrient contents in the CH- and HA-phases averaged over all cutovers.
Values in parenthesis are + SD.

	HUMUS		MINERAL SOIL	
	CH-PHASE	HA-PHASE	CH-PHASE	HA-PHASE
pH H ₂ O	3.4 (0.109)	3.4 (0.116)	4.2 (0.224)	4.4 (0.210) *
CaCl ₂	2.8 (0.157)	2.8 (0.134)	3.9 (0.231)	4.0 (0.196)
Total N (%) [†]	0.90 (0.085)	1.17 (0.136) **	0.18 (0.049)	0.26 (0.086) **
C/N [†]	59 (5.940) **	45 (6.960)	45 (5.480) **	32 (4.990)
KCL Extractable N (ppm) [†]	83 (18.980)	129 (25.921) **	4.8 (3.253)	8.7 (5.313) **
Mineralizable-N (ppm) [†]	133 (28.820)	191 (29.205) **	18 (4.476)	36 (11.817) **
Total P (%) [†]	0.06 (0.007)	0.08 (0.011)	0.03 (0.008)	0.04 (0.013) **
Available P (ppm)	7.9 (3.966)	13.8 (3.964) **	0.8 (0.517)	2.0 (1.126) **
Exchangable Bases				
Ca (meq/100g)	14.30 (4.620) **	10.80 (3.359)	0.27 (0.297)	0.41 (0.251)
K (meq/100g)	0.80 (0.156)	0.76 (0.186)	0.06 (0.023)	0.08 (0.028) *
Mg (meq/100g)	6.10 (1.129)	5.70 (1.020)	0.25 (0.097)	0.36 (0.164) *
Na (meq/100g)	0.50 (0.061)	0.51 (0.072)	0.05 (0.017)	0.06 (0.020)

* Denotes significance at p = .05.

** Denotes significance at p = .01.

† Based on 30 composited samples, all remaining analysis were based on 20 composited samples.

TABLE 7. Estimates of soil nutrient contents found in other studies on the CH-phase and the HA-phase and in other soils of Vancouver Island. Values in parenthesis are ranges.

LOCATION	NUMBER OF SOILS	PHASE OR FOREST TYPE	HORIZON (cm)	TOTAL		C/N	AVAILABLE P (ppm)	EXCHANGEABLE			pH (H ₂ O)
				N	P			Ca	K	Mg	
				— % —				— meq/100 g —			
Jeune Landing ¹	-	HA	L - H	1.16	-	-	66.6*	26	0.4	2.5	4.6
	-	HA	5-15	0.29	-	-	3.0*	2	0.1	0.6	4.2
Woss Camp ¹	-	hemlock	L - H	1.21	-	-	46.5*	18	1.2	4.5	5.3
	-	hemlock	5-15	0.28	-	-	8.1*	1	0.1	0.3	4.8
T.F.L. #25 ²	6	HA	H	1.13	0.10	39	-	14	0.7	4.6	-
				0.74	0.09	59	-	(8-21)	(0.5-1.1)	(4.9-4.5)	-
	4	CH	H	(0.89-1.69)	(0.08-0.15)	(47-72)	-	11	0.71	5.6	-
							-	(5-14)	(0.65-0.78)	(3.7-7.8)	-
Port Hardy ²	-	HA	H	1.30	-	36	10.4	-	-	-	3.2
	-	HA	0-15	0.14	-	30	1.6	0.01	0.07	0.16	5.4
Port Hardy ³	-	hemlock	FH	1.00	0.06	49	-	16	1.3	12.2	3.6
				(0.80-0.13)	(0.04-0.09)	(37-62)	-	(5-25)	(0.8-2.0)	(8.5-22.0)	(3.3-3.8)
	-	hemlock	6-11	0.32	-	42	-	0.22	0.14	0.37	4.1
N. Van. Is. ⁴	2	CH	LFH	1.03	0.06	44	-	25	1.58	9.16	3.2
	2	CH	Bf	0.18	-	47	0.1	0.01	0.18	0.14	4.9
Tofino ⁵	2	Plantation	L - H	0.89	-	38	42.1	13.3	1.2	8.3	-
	2	Plantation	0-14	0.14	-	28	1.3	0.37	0.31	0.11	-
W. Van. Is. ⁶	4 - 7	hemlock	L - H	1.09	-	40	2.4	15.8	0.5	5.6	-
				(0.80-1.57)	-	(24-63)	(0.7-3.5)	(4.9-26.0)	(0.2-1.2)	(1.0-14.1)	-
	4 - 7	hemlock	Bh-Bhf	0.26	-	32	1.3	2	0.1	0.5	-
				(0.08-0.70)	-	(26-41)	(0.6-2.0)	(0.2-3.3)	-	(0.1-1.1)	-

* Based on a Sodium Bicarbonate extraction. Remaining are based on Bray's Dilute acid-Fluoride extraction.

Sources: 1. Baker, 1970. 2. Lewis, 1982. 3. Quesnel, 1981. 4. M.O.F., 1983.³ 5. BCFP, 1981.
6. Heilman, 1979.

³Unpublished data supplied by Fred Nuszdorfer of the the British Columbia Ministry of Forests.

trees taken from both phases were low and well below known critical values (see discussion of foliar P).

Total and KCl extractable N in both the organic and mineral soils were also significantly greater ($p=.01$) in the HA-phase. Mean KCl extractable N in the humus of the HA-phase was considerably higher than values reported by Vogt and Edmonds (1984) for high site Douglas-fir or by Sidle and Shaw (1983) for a number of spruce-hemlock micro-sites in Alaska. Extractable N estimates from the mineral soils and the humus of the CH-phase were comparable to those reported by the above authors.

Compared to other sites throughout the Pacific Northwest (see Heilman, 1979), total N in the HA-phase appears to be above average, but lower than a number of sites known to be highly productive (see Klinka et al., 1979). Total N in the CH-phase on the other hand is much lower, but still appears to be average or only slightly below average. Total N in both phases is considerably lower than the estimates of total N in oligotrophic peats in Britain where N deficiencies are common (Toleman, 1973; Williams et al., 1978).

The higher total N of the HA-phase has resulted in a significantly lower C/N ratio compared to the CH-phase. These factors have led Lewis (1982) to suggest that decomposition and nutrient turnover are much greater in the HA-phase. Total N however, is not necessarily correlated with tree productivity (Klinka et al., 1979). Similarly, Berg and Ekbohm (1983) have shown that N release varies with

site and concluded that there is no fixed C/N ratio which dictates whether N is immobilized or released. In fact, there is increasing evidence which suggests that other factors, such as initial lignin content of litter, are more important in regulating N release than C/N ratios (Berg et al., 1982). Attempts to improve estimates of N availability has led researchers to move from these static measurements to more dynamic and biological measures such as incubation studies (Keeney, 1980). Such methods are believed to provide a good relative assessment of the potential of different soils to supply N (Williams et al., 1979).

Figure 9 illustrates the patterns of gross N mineralization found over an age sequence of cutovers on each phase for both the FH-layer and the top 15 cm of mineral soil. In general, significantly more N was mineralized in the humus and mineral soils of the HA-phase as compared to the CH-phase (Figure 9). Patterns of mineralization over time in the humus were considerably different between the two phases. Although the fluctuations between successive cutovers of the HA-phase are large, harvesting appears to have had little influence on N mineralization. Mineralization on the CH-phase however, appears to follow a steady decline over time. The high mineralization rate in the 3-year-old cutover of the CH-phase is unlikely due to chance since the samples from the control were selected from an unlogged portion of the same stand immediately adjacent to the cutover.

It should be remembered, that in addition to logging, all these sites were also burnt. The higher rates of mineralization on the more recent clearcuts may therefore be a reflection of an increase in nutrient availability resulting from the burn rather than the so-called "Assart effect".

Similar patterns were not evident in the mineral soil and thus harvesting or burning appears to have had little effect on N mineralization in these horizons.

Anaerobic N-mineralization is well correlated with site index, tree growth and growth responses to N fertilization for some soils (Powers, 1980). Powers (1984) suggests that in California only those soils with less than 50 ppm mineralizable N should be considered for fertilization. Similarly, Shumway and Atkinson (1978) outlined general guidelines for N fertilization when using net N mineralization (see Materials and Methods for definition of "net") for soils in the Pacific Northwest. They suggested that soils with <25 ppm N would indicate a high response potential, soils testing 26 - 50 ppm N a moderate response potential, and >51 ppm a low response potential. In the present study, gross N mineralization of the mineral soil was 35.7 ± 11.817 ppm and 17.6 ± 4.476 ppm for the HA-phase and CH-phase, respectively, and net mineralization was 27.1 ± 9.780 ppm and 12.8 ± 5.991 ppm respectively. Thus, based on the above criteria, the CH-phase would be considered to have a high response potential, whereas, the HA-phase would be considered to have, at best,

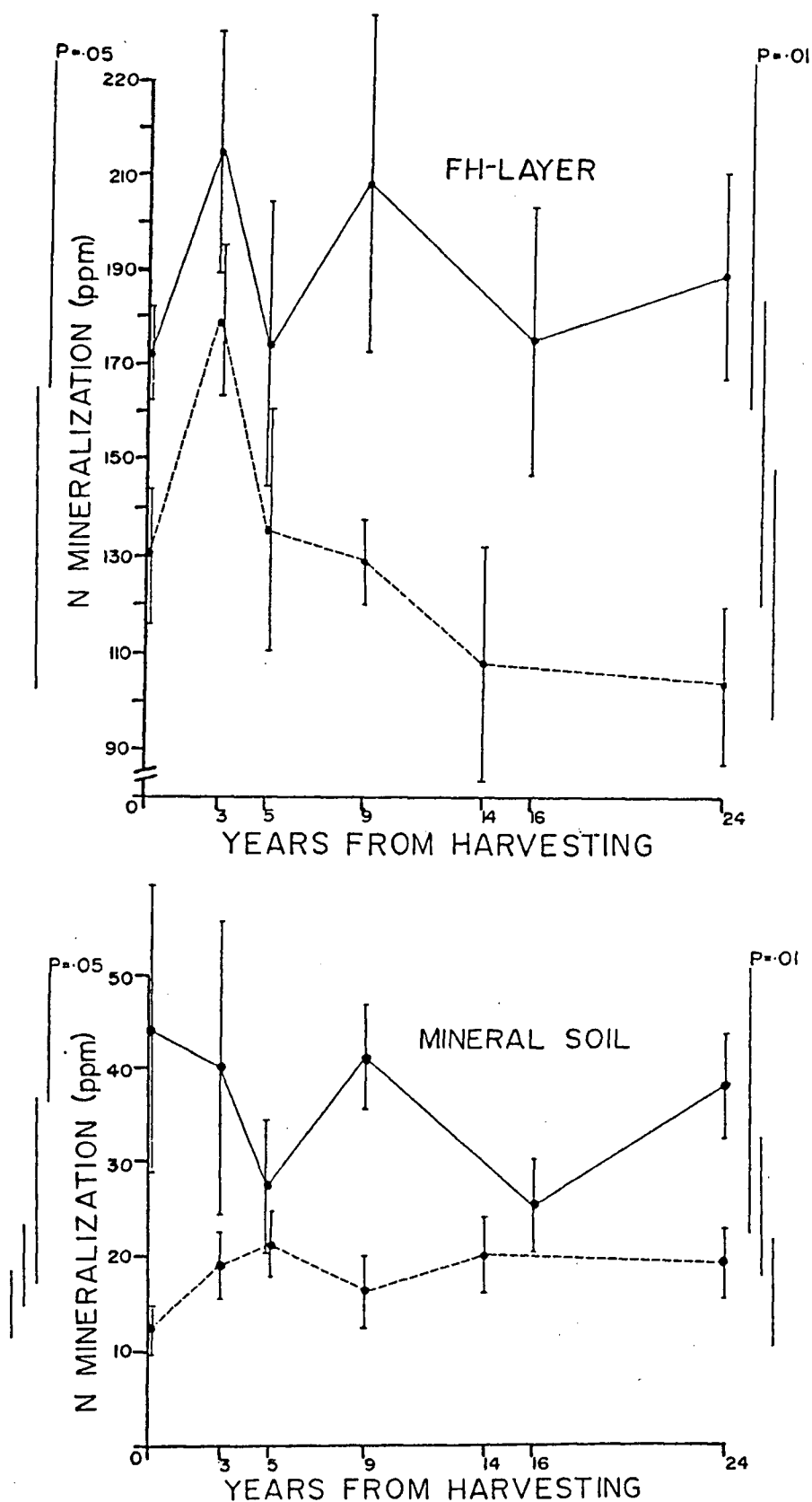


FIGURE 9. N mineralization rates of the FH layer and the mineral soil of the HA-phase (—) and the CH-phase (---). Lines connecting the same points are not significantly different. Vertical bars \pm 1 SD.

TABLE 8. Estimates of mineralizable N for a variety of sites throughout the Pacific Northwest and in Britain.

LOCATION	NUMBER OF SITES	FOREST TYPE	HORIZON (cm)	MINERALIZABLE N (ppm)
Oregon, Wash. ¹	16	Douglas-fir	0 - 15	46.6
Vancouver Is. ²	10	High site Douglas-fir	Ah	19.7
Cowichan Lake ³	17	High site Douglas-fir	0 - 30	58.4*
Cowichan Lake ³	17	High site Douglas-fir	0 - 30	45.4
Cowichan Lake ³	11	Low site douglas-fir	0 - 30	24.3*
Cowichan Lake ³	11	Low site Douglas-fir	0 - 30	11.9
Tofino ⁴	1	Douglas-fir plantation	LFH	20.0
Tofino ⁴	1	Douglas-fir plantation	0 - 14	3.0
Tofino ⁴	1	w. hemlock plantation	FH	13.8
Tofino ⁴	1	w. hemlock plantation	0 - 11	2.8
Britain ⁵	3	Eutrophic peat	0 - 15	133
Britain ⁵	2	Oligotrophic peat	0 - 15	117
Britain ⁵	1	Oligotrophic peat	0 - 15	67

* Values represent gross N mineralization, all others are net mineralization.

Sources: 1. Shumway and Atkinson, 1977.
 2. Klinka et al., 1979.
 3. Roy, 1983.⁴
 4. BCFP, 1983.⁵
 5. Williams et al., 1979.

⁴R. Roy. 1983. Relationships between N availability, site productivity, and several indices of soil N status. Unpub. Forestry 504 Term Paper. UBC, Vancouver, B.C.

⁵British Columbia Forest Products Co. Ltd. 1983. Personal correspondence with D. McMullan, Silviculturalist.

only a moderate response potential. However, both these criteria apply only to mineral soil; it is difficult to say if Shumway and Atkinson's criterion could be applied to the sites of this study since the relative contribution of the humus layer to site index or tree growth compared to that of mineral soil is not known.

Given the thick organic accumulations found on these sites however (15 to 30 cm in the CH-phase and 5 to 15 cm in the HA-phase), the humus fraction may be more important than the mineral soil in regulating N availability. This may be particularly true for the CH-phase since the majority of feeding roots would probably be restricted to the thicker organic layer. Moreover, this is supported by the patterns of N mineralization of the humus, which closely follow the growth patterns of plantations established on each phase (Figures 7 and 9).

There are very few studies on N mineralization available for comparison, but some of the estimates obtained for different sites throughout the Pacific Northwest and Britain are given in Table 8. Since N mineralization has been shown to vary with site index as well as actual methods used (Powers, 1980; Shumway and Atkinson, 1978), direct comparisons are difficult. In general however, N mineralization estimates in the mineral soil for the HA-phase are within the ranges found for high site Douglas-fir, whereas, those for the CH-phase are more comparable to N mineralization rates of low site Douglas-fir (Table 8).

SUMMARY AND CONCLUSIONS

The greater N mineralization rates of the HA-phase lend support to Lewis's hypothesis that decomposition and nutrient turnover are much slower in the CH-phase, and thus may account for some of the differences in productivity between the two phases. However, while significant differences in mineralizable N, total N, and total and available P have been noted between the phases, the actual differences do not appear to be large enough to account for such dramatic differences in productivities. This is particularly true for total and available P, and net N mineralization of the humus. In fact, considering the relatively high mineralization rates found in the humus of both phases, there would appear to be sufficient quantities of available N in either to sustain growth. Moreover, this is supported by the relatively good growth of cedar in the CH-phase. Also, with respect to P, foliage concentrations of vigorous hemlock and spruce selected from the HA-phase are only marginally greater than the foliage concentrations found in the CH-phase, and on both sites foliar P concentrations are in the deficiency range (see discussion on foliar P). Cedar on the other hand, has considerably higher foliage P concentrations which appear to be adequate. These findings suggest the possibility that some factor(s), other than the

lack of available nutrients, may be contributing to the differences in productivity.

While it is beyond the scope of this thesis to fully explore these factors a brief discussion is provided. Differences in productivity between the phases may be related to a possible salal effect discussed earlier and/or differences in the soil physical properties. Lewis (1982) also suggested that differences in the soil physical properties between the two phases may play a significant role in contributing to the higher productivity of the HA-phase. The cultivation effect of the periodic windthrow disturbances would favour root development and penetration into the mineral soil of this phase. If in fact root development is predominantly restricted to the organic layer of the CH-phase, then the combined contribution of nutrients in the humus and mineral soil fractions of the HA-phase would provide a distinct advantage in terms of this site's potential capability to supply nutrients.

EFFECTS OF FERTILIZATION ON 1983 LEADER GROWTH, CURRENT YEARS NEEDLE WEIGHT, AND NEEDLE NUTRIENT COMPOSITION

INTRODUCTION

Efficient operational forest fertilization depends on identifying the nutrients that limit growth and the potential responsiveness of the stands to be fertilized. Evidence presented thus far in this and other studies suggest the possibility of multiple nutrient deficiencies existing in the spruce plantations of the CH-phase. Much of this evidence however, is based on preliminary data. Therefore, a much more detailed foliar analysis is required in order to accurately identify deficient nutrients, and fertilizer trials must be established to determine potential responses.

Conventional fertilizer trials typically require 3 to 5 years to obtain reliable response information. Moreover, they often require a large homogeneous area, which severely restricts the number of plots and treatments (see Literature Review). Weetman and Fournier (1983) suggest that the use of mini-plots combined with a graphical approach for interpreting foliar analysis can provide a rapid method of testing a large number of different treatments and provide a qualitative estimate of potential growth responses. This

method is described in detail in the Literature Review. It was adopted here because its advantages in meeting the objectives of this thesis.

MATERIALS AND METHODS

Field Procedures

Five plantations, ranging in age from 8 to 14 years were selected for study. Table 9 gives the stand characteristics for each plantation. For convenience, they are referred to as stands 1 to 5; Figure 3 gives the corresponding location of each stand.

TABLE 9. Stand characteristics of five Sitka spruce plantations selected for fertilization.

STAND NUMBER	YEAR LOGGED	YEAR PLANTED	MEAN* HEIGHT (m)	ANNUAL HEIGHT INCREMENT**		
				1983 (cm)	1982 (cm)	1981 (cm)
1	1971	1972	2.70 (2.31-3.28)	9.8 (5-16)	12.0 (6-23)	9.7 (5-23)
2	-	1969	2.44 (2.13-2.71)	9.5 (3-18)	7.9 (2-19)	10.2 (4-24)
3	-	1969	2.61 (2.26-2.97)	9.2 (2-12)	10.1 (3-16)	11.7 (4-22)
4	1972-1973	1975	1.96 (1.76-2.33)	10.9 (5-23)	11.1 (2-28)	15.7 (4-38)
5	1971	1973	2.17 (1.90-2.46)	9.2 (2-20)	10.6 (2-20)	11.9 (3-24)

* Includes sample trees from all treatments -- range of treatment means in parenthesis.

** Only includes sample trees from control plots -- ranges in parenthesis.

The experimental design and methods used in this study are based on the single tree, mini-fertilizer plots after Weetman and Fournier (1983). A completely randomized 4 x 2 x 2 factorial design ((N0, N1, N2, N3) x (P0 + K0, P, K, PK)) with seven replications per treatment was established in each of the plantations. The treatments and type of fertilizer applied was as follows:

Ammonium Nitrate (NH_4NO_3) at 0-(N0), 200-(N1), 300-(N2), 400-(N3) kg N/ha

Treble Superphosphate ($\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot 2\text{H}_2\text{O}$) at 0-(P0) and 50-(P) kg P/ha

Muriate of potash (K_2O) at 0 - (K0) and 50-(K) kg K/ha

In addition, a mixture of all essential macro- and micro-nutrients was applied to each stand as a separate treatment in combination with 300 kg N/ha. (Table 10). These plots were replicated seven times giving a total of 119 plots per plantation.

Preliminary fertilizer trials established by Western Forest Products Ltd. indicate a possible synergistic effect of P when applied together with N. Therefore, an additional small screening trial was established where the amounts of P were increased to 100 and 150 kg P/ha. This trial was located in stand #2 along with one of the larger screening trials. The design was a completely randomized 4 x 2 ((P0, P1, P2, P3) x (N0, N)) factorial experiment with five replications per treatment. The treatment combinations for this trial were: P0 - 0 kg P/ha, P1 - 50 kg P/ha, P2 - 100

kg P/ha, P3 - 150 kg P/ha, N0 - 0 kg N/ha and N - 300 kg N/ha. The plots for treatments P1, P1N and PON were taken from the main fertilizer trial of this stand and used to complete the design of the smaller trial.

TABLE 10. Rates of application in kg/ha for macro- and micro-nutrient mixture.

NUTRIENT	AMOUNT APPLIED	NUTRIENT	AMOUNT APPLIED
N	300	Fe	1.80
P	38	B	0.30
K	98	Zn	0.70
Ca	56	Cu	0.30
Mg	48	Mn	0.75
S	31	Mo	0.20

Each treatment consisted of a manual application of fertilizer to circular 0.008 ha (5 m radius) plots. In each plot, two trees, a centre (plot centre) and an off-centre tree, were selected as sample trees. Each plot was identified by fastening an aluminum tag with the treatment code for that plot on the centre tree. The fertilizer was applied in the last two to three weeks of April, 1983. In the last week of October and the first week of November, 1983, all plots were revisited and each tree measured for first-year growth responses. Growth parameters measured

include total height, 1983 leader length, 1981 and 1982 height growths, and current year needle weight. Foliage samples were also collected at this time. Sampling was restricted to current years foliage from the upper third and fourth whorls of the crown. Samples were placed in paper bags (plastic bags were used to store samples which were analyzed for micro-nutrients) and bulked by plot.

It is realized that one growing season (the time available for this study) may not be sufficient for height growth responses to become apparent. However, these stands are tentatively scheduled for remeasurement at the end of the third growing season.

Although this thesis was mainly designed to study the effects of fertilization on spruce, many plots had naturally occurring cedar and hemlock. Since these sites are now considered to be better suited to these species than spruce, whenever a suitable specimen between 1.5 m and 2.5 m in height occurred within a plot, foliage samples were collected for analysis. On these species, sampling was restricted to the terminal shoots of the top four lateral branches.

Laboratory Analysis

All samples were dried for 24 hours at 70°C in forced-draft ovens. After drying, all needles were removed from the twigs. The mean oven-dry weight of 100 needles was then determined on three lots of 100 whole needles for each sample. The remaining needles were ground in a small

electric coffee grinder and stored in snap-cap plastic vials for subsequent chemical analysis. All samples were analyzed for N, P, K, Ca and Mg. In addition, treatments NO (control), N1 (200 kg N/ha), N2 (300 kg N/ha), N3 (400 kg N/ha) and NPKT (macro-plus micro-nutrient mixture) were also analyzed for total S, B, Cu, Zn, Mn and active Fe. The micro-nutrient analysis was done by Norwest-Priva Plant Laboratories Inc. All other chemical analysis was done at UBC. Nitrogen and phosphorus concentrations were determined by a standard semimicro-Kjeldahl digestion, then analyzed colorimetrically with a Technicon autoanalyzer. Base elements (K, Ca and Mg) were determined by atomic absorption spectrophotometry after initially dry ashing 1 g of sample and dissolving it in 20% HCl solution. Total S was determined using a Leco Sulfur analyzer.

Interpretations of the foliar analysis with respect to changes in needle nutrient concentrations and content, and needle weight were based on the graphical approach described in the Literature Review.

Statistical Analysis

For the purpose of this study, all five stands have been combined for analysis with each stand being treated as a separate block. Individual analysis of each stand is given in Appendix I. All analyses of variance were performed using U.B.C.'s computer program GENLIN. A two-way analysis of variance followed by a Student-Newmans-Keuls' multiple range test was performed on all treatments. All treatments, except

NPKT, were also subjected to a $4 \times 2 \times 2$ factorial analyses of variance. Covariant analysis, using the 1982 height increment as the covariate, was used in all analysis concerning the 1983 leader growth. Because of the limited sample sizes, Student-t tests were used for the comparison and analyses of hemlock and cedar data.

There was considerable heterogeneity amongst the various treatment cell variances and therefore it was necessary to apply a series of transformations to the data before analysis. Since each of the variables under study reacted differently to the various treatments, different transformations were used for certain variables. In all cases, except for spruce K content, which was transformed by a square root transformation, logarithmic transformations were used. Spruce N content, 1983 leader growth, and cedar N and P concentrations were transformed by $\log(x)$, spruce nutrient concentrations by $\log(x+1)$, and spruce P, Ca and Mg content and hemlock N and P concentration by $\log[\log(x+1)]$. Even after the transformations of the spruce needle nutrient concentrations to $\log(x+1)$ some heterogeneity between variances still existed. These differences appear to be minimal and it is doubtful that they will have any influence on the statistical outcome. Comparisons of the analysis of variance of transformed and untransformed data indicated that the transformations resulted in only a few minor changes in the significance of treatment mean differences. All data throughout the thesis are presented in their original values.

RESULTS & DISCUSSION

The analysis of variance indicated that fertilization had a highly significant ($p=.01$) effect on first year height growth, needle weight, and needle nutrient concentration and content. Not only were the main effects of N, P and K highly significant, but there were also a number of highly significant interactions (Table 11).

For the purpose of presentation, all five stands were combined for the analysis of variance and graphical interpretations of foliar analysis. The analysis of individual stands are given in Appendix I.

Effects on Needle Weight and Leader Growth

Fertilization significantly increased both the current year's needle dry-weight and the 1983 leader growth (Table 11). Although N alone had a significant influence ($p=.05$) on both needle weight and leader growth, there was a highly significant ($p=.01$) N x P interaction (Figure 12). P had a strong synergistic effect on both needle weight and leader growth when added together with N (Figures 10 and 11).

N alone or in combination with K resulted in only a 10% increase in needle weight and a 25 to 30% increase in the 1983 leader growth over that of the control. However, when

TABLE 11. Analysis of variance of first year leader growth, needle dry-weight, and needle nutrient concentration and content.

SOURCE OF VARIATION:	TREATMENT EFFECTS							BLOCK
	N	P	K	NP	NK	PK	NPK	
DEGREES OF FREEDOM:	3	1	1	3	3	1	3	4
Needle weight	(+)**	(+)**	-	**	-	-	-	**
1983 Leader growth	(+)**	(+)**	-	**	-	-	-	-
Nutrient concentration								
N	(+)**	(+)*	-	-	**	-	-	**
P	-	(+)**	-	**	*	-	-	**
K	(-)**	-	(+)**	**	**	-	-	**
Ca	(+)*	-	(+)**	-	-	-	-	**
Mg	-	-	(-)**	*	-	-	-	**
Nutrient content								
N	(+)**	(+)**	-	**	-	-	-	**
P	(+)**	(+)**	-	-	-	-	-	**
K	(-)**	(+)**	(+)**	**	**	-	-	**
Ca	(+)**	(+)**	(+)**	**	-	-	-	**
Mg	(+)**	(+)**	(-)**	**	-	-	-	**

* Significant at 0.05 level.

** Significant at 0.01 level.

- Signifies non-significant.

added together with P or P plus K, needle dry-weight increased by 40 to 41% and leader growth by 78 to 83% (Table 12).

While a relative increase in growth of 83% seems impressive, it should be kept in mind that the 1983 annual height increment of these plantations only averaged 10.0 cm, thus, in absolute terms, an 83% increase corresponds to an annual increment of only 18.3 cm. This however, was only the first-year response. Many researchers have shown that growth responses in the year of fertilization are often minimal and that significant gains from fertilization typically only become apparent after the first growing season (Atkinson, 1975; Dickson and Savill, 1974; Fagerstrom and Lohm, 1977). Preliminary fertilizer trials established by Western Forest Products Ltd. in similar Sitka spruce plantations have also shown greater responses in the second and third year from fertilization as compared to the first year growth responses.

Increasing the rates of N application from 200 to 400 kg N/ha tended to result in a progressive decline in both needle weight and leader growth responses. While the effects of increasing N varied between stands (Table 12), particularly for leader growth, the decline is readily evident in Figure 12 which illustrates the effect of the N x P interaction on growth. This decline was significant for needle weight only when N and P were added together and it was not significant for leader growth.

The depression of growth at the 300 and 400 kg N/ha rates appears to be largely due to the resulting high foliar

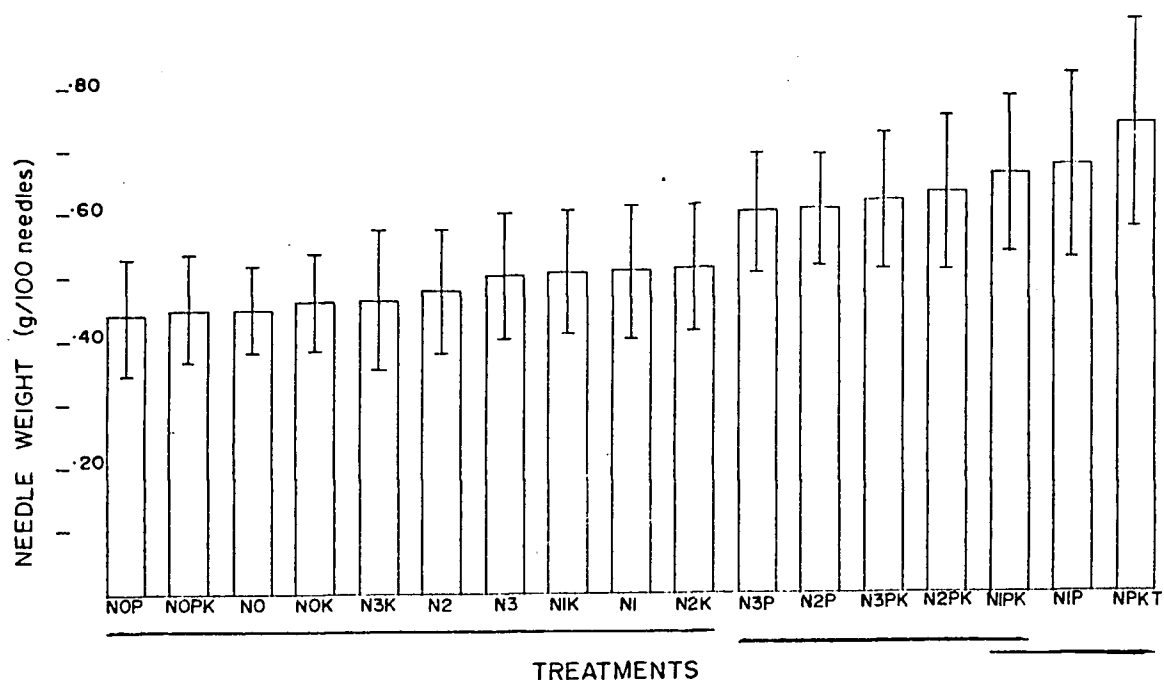


FIGURE 10. Needle weight response. Treatments connected by the same line are not significantly different at $p=.01$. Vertical bars ± 1 SD.

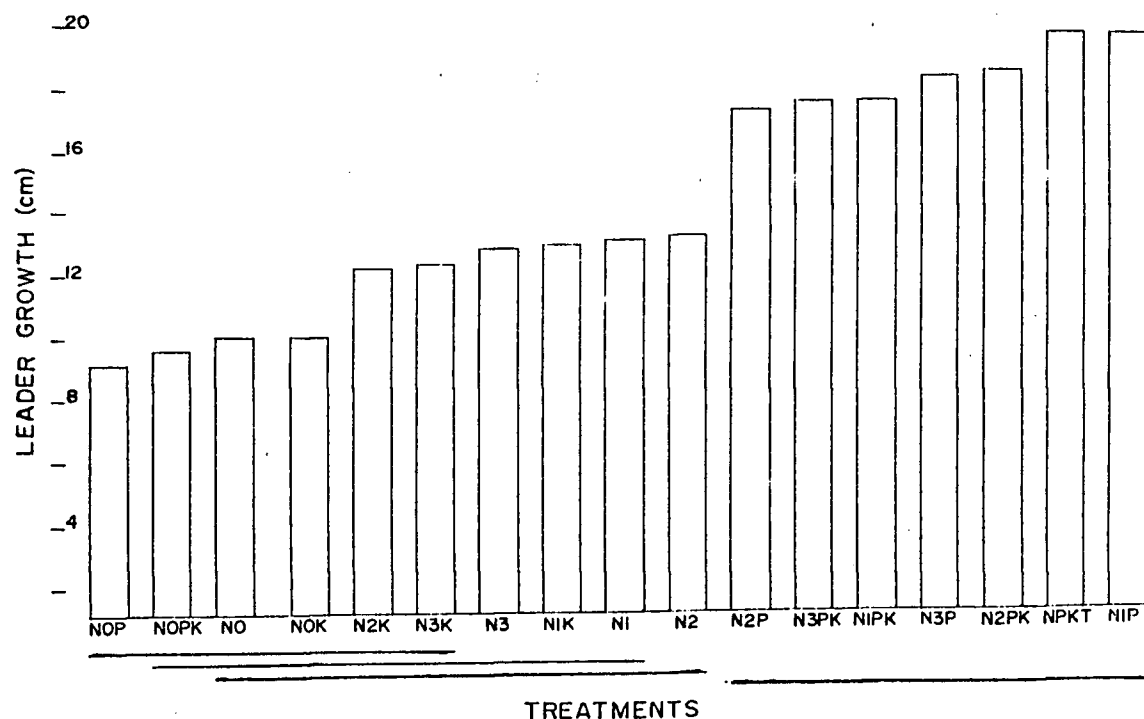


FIGURE 11. Leader growth response. Treatments connected by the same line are not significantly different at $p=.01$.

TABLE 12: Percent change from control in needle dry-weight and 1983 leader growth for each stand.

TREATMENT	OVEN-DRY NEEDLE WEIGHT						1983 LEADER GROWTH					
	STAND					ALL STANDS COMBINED	STAND					ALL STANDS COMBINED
	1	2	3	4	5		1	2	3	4	5	
NOK	13	0	4	-15	18	4	16	-13	9	-36	35	4
NOP	-2	1	-6	2	-17	-4	7	-38	-4	-16	3	-16
NOPK	10	2	-8	1	-6	-1	3	-2	-14	-8	5	-5
Average	7	1	-3	-4	-2	0	9	-18	-3	-20	14	-5
N1	28	12	6	-3	24	13	46	14	45	5	45	31
N2	18	-6	-1	14	10	6	46	-5	22	44	43	31
N3	8	-5	9	27	21	11	40	-5	18	31	61	28
Average	18	0	5	13	18	10	44	1	29	27	50	30
N1K	20	5	2	21	17	12	79	-4	30	16	35	30
N2K	15	9	11	26	11	14	47	-7	29	9	35	22
N3K	24	-7	-5	16	0	5	56	-6	23	7	44	23
Average	20	2	3	21	9	10	61	-6	27	11	38	25
N1P	84	46	28	54	39	49	116	85	68	82	138	96
N2P	43	37	29	37	38	36	72	49	68	74	99	72
N3P	46	25	39	40	21	34	121	40	102	65	77	81
Average	58	36	32	44	33	40	103	58	79	74	105	83
N1PK	56	43	43	56	41	47	102	30	96	68	79	75
N2PK	62	33	29	40	38	39	122	40	104	73	82	84
N3PK	46	24	31	24	59	37	110	43	67	42	124	75
Average	55	33	34	40	46	41	111	38	89	61	95	78
NPKT	70	66	73	66	51	65	88	87	93	81	145	95

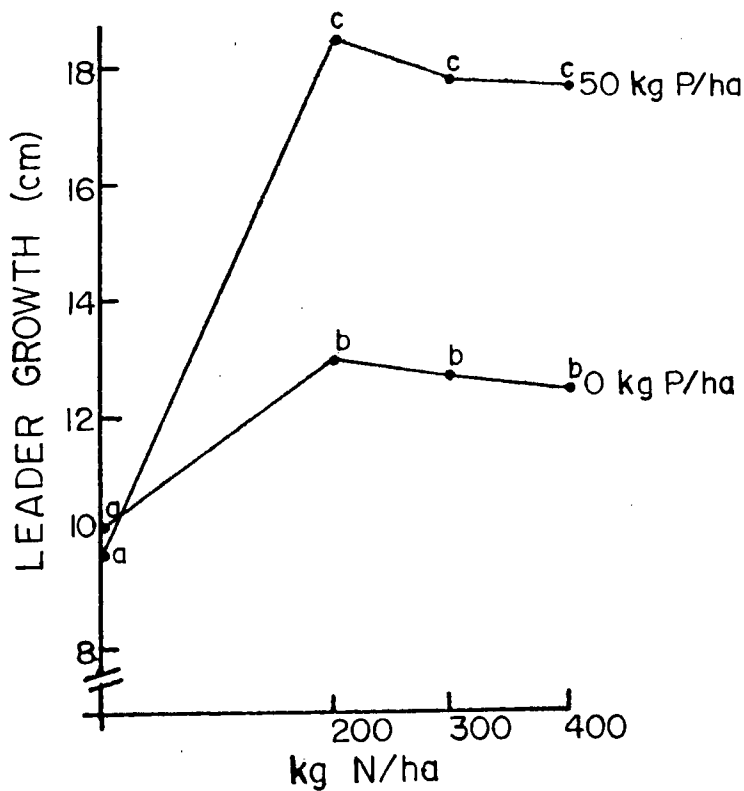
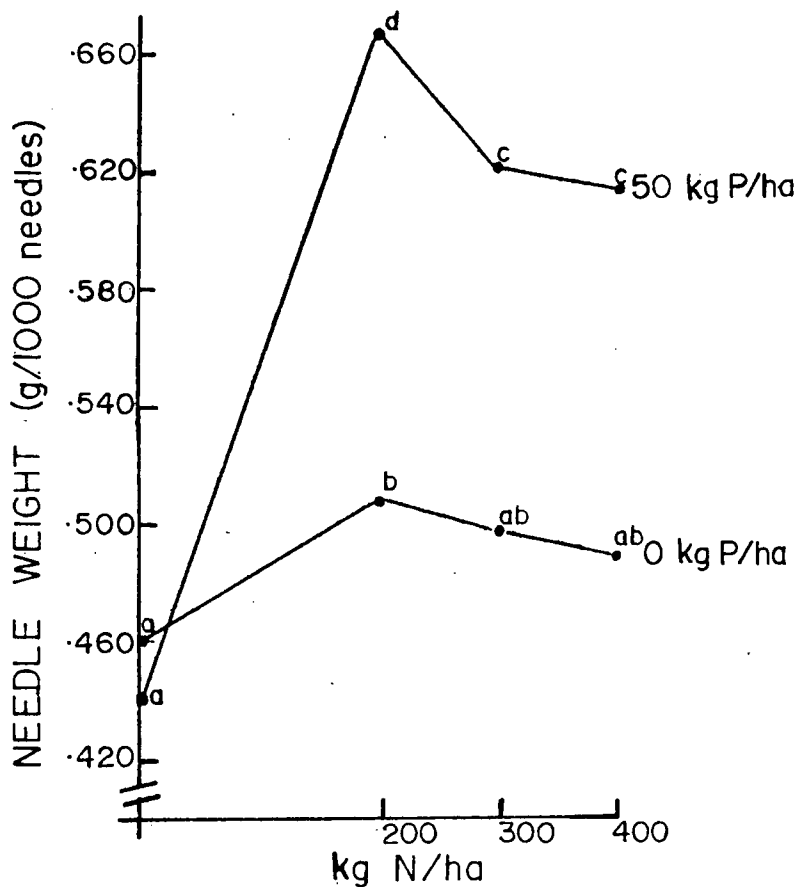


FIGURE 12. N x P interaction effects on 1983 leader growth and needle weight. Points followed by the same letter are not significantly different at $p=.05$.

N concentrations. The mean foliar N concentration at these rates was 3.9% and 4.1%, respectively, as compared to 3.2% for the 200 kg N/ha treatments. Ebell (1972) found that stem growth of a 22 year old Douglas-fir stand benefited from increasing foliar N levels up to about 2% but was adversely affected by foliar N levels above 3%. Similarly, Brockley (1981) noted adverse effects on the growth of Douglas-fir seedlings when foliar nutrient levels increased to 4 and 5%. A value of about 2.0 to 2.5% foliar N also seems to be the upper tolerance limit for other species such as Picea abies and Pinus nigra (Tamm, 1968, 1974; Miller et al., 1981). These findings of Ebell (1972) and others suggest that even at the lowest application rate of 200 kg N/ha, foliar N concentrations may have been high enough to adversely influence both needle and leader growth.

After adjusting for differences in initial growth, the 1983 leader growth of the sampled hemlock was significantly greater than the spruce only in those N treatments where the mean foliar N concentration was less than 3.0% (Tables 12 and 14). There was also a weak, but highly significant negative correlation between N and hemlock leader growth ($r = -.5247$), but not between N and spruce leader growth. The fact that N was not correlated to spruce leader growth may be due to its determinate growth nature. Although the high N concentrations may have had an initial detrimental effect on growth, it is possible that these losses may largely be compensated by prolonged growth responses from internal retranslocation of N (Miller, 1981).

Increasing the amounts of P to 100 and 150 kg/ha had no effect in counteracting the adverse effects of the high foliar N concentrations on needle weight or leader growth. The addition of the complete nutrient mixture (NPKT) however, resulted in a significant ($p=.01$) increase in needle weight over all other treatments, except N1P and N1PK (Figure 10) and appears to have had somewhat of a positive effect on leader growth. Unfortunately, because of the nature of this treatment, it is not possible to say which nutrient or nutrients are causing the additional effect. Presumably much of the beneficial effect can be attributed simply to a more balanced supply of nutrients. Growth response of Scots pine growing on deep peats are frequently improved when micro-nutrients were added to heavily NPK fertilized trees (Veijalainen, 1981).

Of note in the NPKT treatments in the present study, is the possible beneficial effects of the additional K. The K content of this treatment was equivalent to 98 kg K/ha (Table 10) as compared to 50 kg K/ha for all other treatments where K was added. As a result, both the K content and concentration were significantly higher ($p=.05$) than in other responsive treatments (Table 16). Besides K, additional benefits from the NPKT treatment may have also been derived from the addition of Mg and/or S (see subsequent discussions).

Although P and K appear to be deficient on these sites, the addition of either nutrient alone or in combination without N had no significant influence on growth.

In fact, there was a tendency for these treatments to depress growth (Table 12). Presumably the lack of response is due to the limiting effect of N. Carey (1977) noted that checked Sitka spruce in Britain did not respond to P or P plus K fertilization when N was also limiting. This however is in contrast to Dickson and Savill (1974) who noted Sitka spruce would often respond favourably to P fertilization when both P and N were limiting. They attributed the response to the fact that P fertilization often increases the availability of N to the trees.

Although needle weight and leader growth were found to be significantly correlated, the relationship was weak (r values ranged from .4472 to .5292). This weak relationship may have resulted because only first-year growth responses were being considered. As mentioned previously, the determinate growth nature of spruce can significantly influence growth in any one year, obscuring any relationship which may exist. This contrasted with Timmer and Stone (1978) who found that changes in needle weight of Abies balsamea accounted for 65 to 73% of the total variation in the first seasons shoot growth. Despite the weak relationships found in the Port McNeill study, there appeared to be a general trend of increasing leader growth with increasing needle weight. This becomes evident if only plot means were considered as the overall r value increased to .7529 with a range of .8673 to .9182 for the individual stands.

Patterns of shoot response for hemlock were very similar to that of spruce, although somewhat greater (Table 13). The addition of N or N plus K alone had a highly significant, positive effect on growth. As in spruce however, the addition of P with N or N plus K resulted in a highly significant synergistic response over N alone, whereas, the addition of P or P plus K without N had no significant influence on growth. Increasing the rates of N application from 200 to 400 kg/ha also resulted in a progressive decline in the response of this species.

Initial results from recent fertilizer trials established on similar sites by British Columbia Forest Products Ltd. (BCFP), have also found hemlock to be highly responsive to fertilization with ammonium nitrate (BCFP, personal correspondence). The fact that hemlock appears to be responsive on these sites is encouraging since numerous other fertilizer trials have shown the species to be highly erratic in its ability to respond to fertilization (DeBell et al., 1975; Webster et al., 1976). Gill and Lavender (1983a) have recently shown that urea can negatively influence mycorrhizal development and thus may limit the trees ability to respond to this form of nitrogen. Since ammonium nitrate was used in the present study, such adverse effects would not be expected, although, fertilizer trials elsewhere using ammonium nitrate have largely proven to be inconclusive (Webster et al., 1976; Radwan and DeBell, 1980).

The strong synergistic effect of P on these sites suggest that P is limiting. There is increasing evidence

TABLE 13. 1983 Leader growth responses of sampled hemlock. Treatments connected by the same line are not significantly different at $p=.01$.

TREATMENT	LEADER GROWTH (cm)	% CHANGE FROM CONTROL	STANDARD DEVIATION	NUMBER OF SAMPLES
NOK	15.6	-11	6.499	17
NO	17.5	-	7.138	18
NOPK	19.4	11	9.735	12
NOP	20.1	15	6.379	15
N3	25.3	45	12.572	13
N3K	26.5	51	13.428	16
N2K	28.0	60	10.116	12
N2	29.3	67	12.172	11
N3PK*	32.1	83	12.365	11
N1K*	35.0	100	12.125	13
N1*	35.1	101	10.673	9
N3P*	38.9	122	10.847	11
N2PK*	40.0	129	12.552	11
N1PK*	42.5	143	11.649	19
N2P*	46.7	167	13.269	15
NPKT*	53.4	205	12.104	17
N1P*	53.7	207	10.863	16

* Treatments in which hemlock had a significantly greater response ($p=.01$) than spruce.

indicating that many coastal sites are P deficient. It has been suggested that such deficiencies may account for some of the erratic fertilizer responses exhibited by hemlock (Radwan and Shumway, 1983; Gill and Lavender, 1983b).

Effects on Foliar Nitrogen

Mean foliar N concentrations of the Sitka spruce in the control plots was only 0.79% (Table 14) which suggests that the spruce in these stands are suffering from a severe N deficiency. In contrast, more vigorous spruce from the HA-phase had a mean foliar N concentration of 1.29% which, although considerably higher than that of the CH-phase, is also well below what is considered to be optimum for the species (Table 1).

Fertilization with N resulted in a highly significant increase in foliar N concentration (Table 14). There was also a highly significant N x K interaction. The effects of this interaction on N concentrations however, was relatively minor compared to the main effect of N and does not influence the interpretations. Increasing rates of N application resulted in a corresponding significant increase in mean foliar N concentrations to 3.19%, 3.94% and 4.09% for the 200, 300 and 400 kg/ha application rates, respectively.

The high N concentrations experienced in this study are unusual and there are few published examples from other fertilizer trials where similar high concentrations were experienced, in fact, foliar concentrations exceeding 2.5% appear to be rare. Some notable exceptions however, are the

TABLE 14. Within and between species comparisons of mean foliar N concentrations (% oven-dry weight) for spruce, hemlock and cedar. Treatments connected by the same line or followed by the same letter are not significantly different at $p=.01$.

WITHIN SPECIES COMPARISON			*BETWEEN SPECIES COMPARISON					
SPRUCE	HEMLOCK	CEDAR		SPRUCE	HEMLOCK	CEDAR		
TREATMENT			TREATMENT	%				
NO	NOP	NOP	NO	0.79 a	(.122)	0.96 a	(.245)	1.27 b (.211)
NOK	NOK	NOK	N1	3.12 a	(.545)	2.70 a	(.803)	1.89 b (.335)
NOP	NOPK	NOPK	N2	3.96 a	(.572)	3.12 b	(.835)	2.11 c (.338)
NOPK	NO	NO	N3	4.20 a	(.603)	3.52 b	(.856)	2.60 c (.516)
N1P	N1P	N1	NOP	0.89 a	(.166)	0.87 a	(.123)	1.06 b (.119)
N1	NPKT	N1PK	N1P	3.04 a	(.568)	1.84 b	(.497)	2.05 b (.318)
N1K	N1PK	NPKT	N2P	4.08 a	(.529)	2.34 b	(.595)	2.31 b (.465)
N1PK	N2P	N1P	N3P	4.06 a	(.471)	2.88 b	(.664)	2.47 b (.278)
NPKT	N1K	N2	NOK	0.82 a	(.132)	0.87 a	(.186)	1.15 b (.199)
N2K	N2PK	N1K	N1K	3.30 a	(.650)	2.40 b	(.619)	2.15 b (.407)
N3K	N1	N2PK	N2K	3.75 a	(.560)	3.05 b	(.925)	2.33 b (.466)
N2	N3P	N2P	N3K	3.92 a	(.642)	3.44 a	(.704)	2.39 b (.569)
N2PK	N3PK	N2K	NOPK	0.91 a	(.185)	0.90 a	(.144)	1.19 b (.165)
N3P	N2K	N3K	N1PK	3.31 a	(.613)	2.09 b	(.478)	1.91 b (.386)
N2P	N2	N3P	N2PK	3.97 a	(.513)	2.69 b	(.898)	2.27 b (.459)
N3PK	N3K	N3PK	N3PK	4.17 a	(.460)	2.92 b	(.819)	2.50 b (.415)
N3	N3	N3	NPKT	3.41 a	(.606)	2.04 b	(.347)	2.03 b (.332)

* Values in parenthesis \pm SD.

study by Dangerfield and Brix (1979) who found mean foliar N concentrations in a 24 year old Douglas-fir stand increased to 3.5% in the first year after fertilization with 448 kg N/ha. Similarly, Ebell (1972) attained mean foliar N concentrations in excess of 3% after fertilization with 400 kg N/ha and over 4% after fertilization with 800 kg N/ha. Brockley (1981) noted a strong moisture x N interaction on N uptake in Douglas-fir seedlings and found mean foliar N concentrations at the highest moisture level ranged from 4.0 to 5.2% .

As in the present study, the above fertilizer experiments, with the exception of Brockley, who applied ammonium sulphate, used ammonium nitrate as the N source as opposed to the more commonly used urea. An increasing number of studies are showing a superiority of growth responses from ammonium nitrate over urea (Weetman and Algar, 1974; Nommick and Moller, 1981; Dangerfield and Brix, 1979; Miller and Tarrent, 1983). This superiority has been attributed to the greater initial uptake of N from ammonium nitrate than from urea (Dangerfield and Brix, 1979). This appears to be true even in those cases where foliar N concentration only increased to 2.0 to 2.5%. In the above-mentioned study, Dangerfield and Brix (1979) added an equivalent amount of urea and found mean foliar N concentrations did not increase above 2.0%. Recently, Melin et al. (1983) have shown a greater uptake of NO_3^- than NH_4^+ when ammonium nitrate is used as an N source. Many studies have shown that N from urea is more prone to losses by volatilization or

immobilization in the humus layer and soil microbial population, and thus may not reach the rooting zone (Overrein, 1969; Nommik and Popovic, 1971). The nitrate ion however, is highly mobile and therefore more readily distributed throughout the rooting zone (Dangerfield and Brix, 1979). In addition, since ammonium nitrate does not have a positive influence on the pH like urea does, losses due to volatilization or microbial immobilization will likely be less. Increased uptake and superiority of ammonium nitrate over urea has also been shown to occur quite readily in many agricultural crops (Mengel and Kirkby, 1979). In these cases however, superiority is thought to be related not only to improved uptake, but also to differences in the complex physiological and metabolic processes that occur in the assimilation of the two ions (NH_4^+ and NO_3^-) (Kirkby and Hughes, 1970).

At first glance, the large increases in N concentration appear to be largely due to luxury consumption. However, examination of Figure 13 reveals two distinct clustering of points. As mentioned before, the addition of N or N plus K alone resulted in a large increase in needle N concentration, but only a modest, although significant, increase in needle weight. This is indicative of luxury consumption (Figure 2) and suggest that although N appears to be highly deficient, its addition will result in only a modest increase in growth (it should be remembered that the high N concentrations experienced may have had a negative effect and that lower application rates may have resulted in

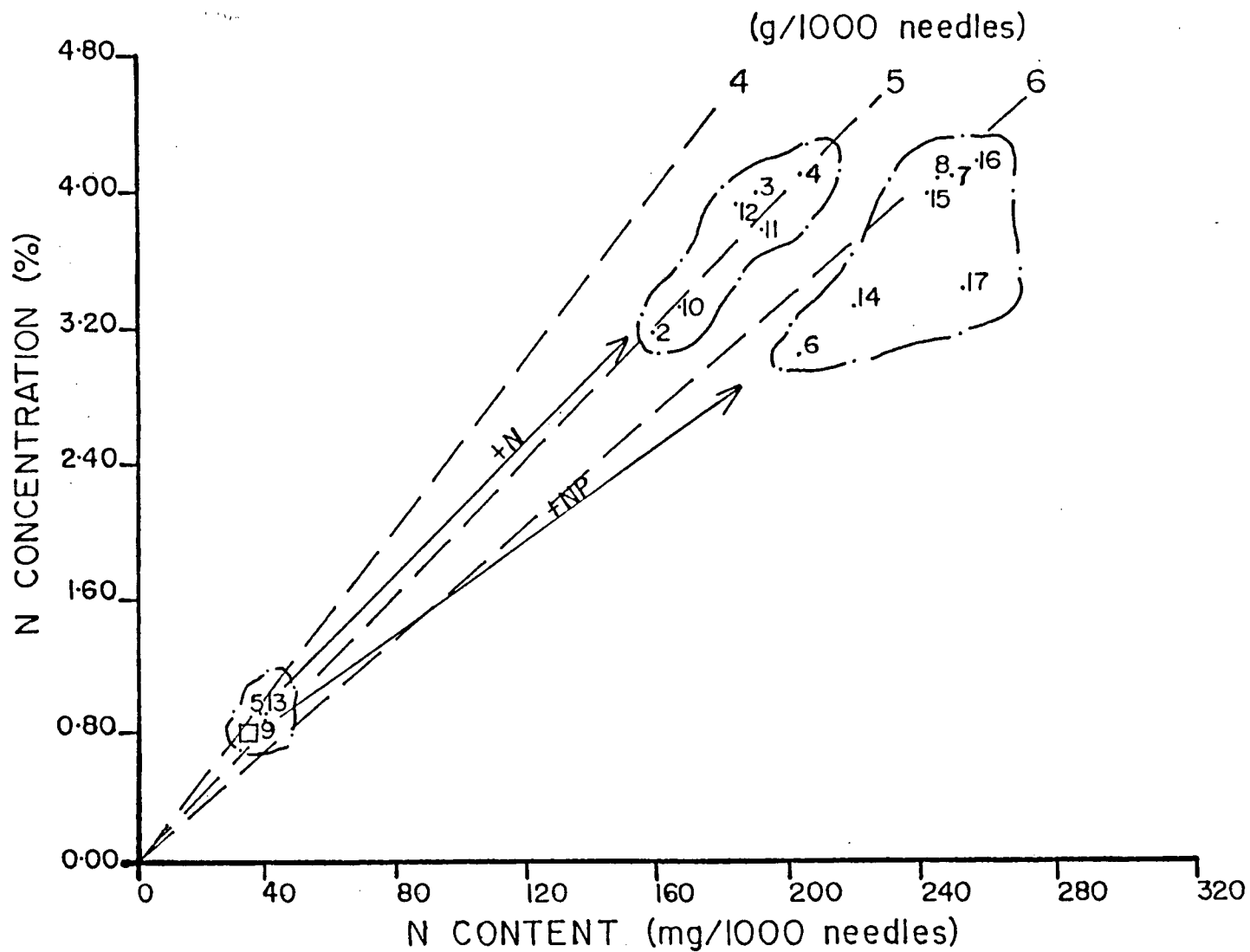


FIGURE 13. Relationship between foliar N concentration, content and dry weight.

a larger needle weight response). The addition of P together with N or N plus K however, resulted in a significantly greater response in needle weight. This is clearly evident in Figure 13 as a shift in the clustering of points into Macy's (1936) "poverty adjustment" range (Figure 2). These findings suggest that although the trees are deficient in N, their ability to respond to N fertilization is limited by a P deficiency. This same pattern of response was evident in all five stands of this study (see Appendix II).

The addition of P had a positive influence on the N nutrition of the trees and resulted in a significant increase in both N concentration and content (Table 11). In addition, there was a highly significant N x P interaction which affected N uptake (Figure 14). Numerous other studies have noted increased foliar N concentrations following P fertilization (Tamm, 1968, 1982; Dickson and Savill, 1974; Fiedler et al., 1983). Others have noted a significant increase in the release of available N after the addition of inorganic P (Carey et al., 1981). Tamm (1982) suggests that the increase in N is largely due to a stimulation of N mineralization. Carey et al. (1981) however, noted that most studies have found that P fertilization has either had no effect or a negative effect on N mineralization and suggested that the exact mechanism is not entirely understood. In the present study, P only increased N uptake when N was also added (Figure 14). The addition of P alone resulted in only a slight and non-significant increase in foliar N content and concentration. Increasing the amount of P to 100 and 150

kg/ha had no apparent additional effect and resulted in a slight reduction in N content. These findings contrasted with Dickson and Savill (1974) who found that the addition of P alone to highly deficient N and P Sitka spruce plantations in Britain resulted in a significant increase in both foliar N and P concentrations which in turn led to highly significant growth responses.

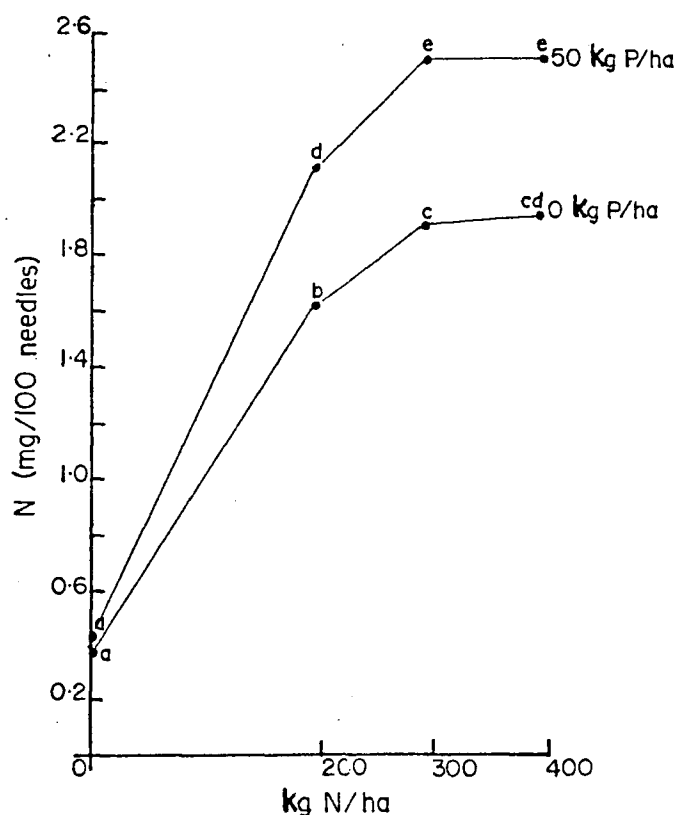


FIGURE 14. Effects of N x P interaction on N uptake. Points followed by the same letter are not significantly different at $p=.05$.

N fertilization also had a significant influence on the foliar N concentrations of both hemlock and cedar (Table 14). However, the effects tended to be less than in spruce. Moreover, increases in the N concentrations of cedar foliage tended to be less than that of hemlock (Table 14).

Mean foliar N concentrations of hemlock from the control plots was 0.96% indicating that a severe deficiency may also exist in this species (Table 1). In contrast, foliar N levels of well growing hemlock from the HA-phase were considerably higher (1.52%).

Mean foliar N levels of unfertilized hemlock were not significantly different from that of spruce. However cedar, with a mean concentration of 1.27%, was significantly greater ($p=.01$) than both hemlock and spruce. This finding was consistent with the preliminary results of Lewis (1982) who also noted that the foliar nitrogen concentration of cedar in the CH-phase was considerably higher than either spruce or hemlock. No explanation can be offered for the higher N concentrations found in the cedar. However, it suggests that factors other than the lack of available N were causing the severe N deficiencies in the spruce and hemlock. Moreover, these findings were consistent with the improved relative growth of cedar and also with that of the N mineralization study which indicated, that although N mineralization was significantly less in the CH-phase than in the HA-phase, the amounts being released appeared to be relatively high. Despite the higher N concentrations in the cedar however, they were still low and possibly deficient

(Table 1). This suggests that even the growth of cedar may be significantly improved by N fertilization.

Effects on Foliar Phosphorus

Phosphorus fertilization not only increased foliar P concentration and content, but also had a significant influence on needle weight, leader growth, foliar N concentration and foliar N, K, Ca and Mg content (Table 11). Similar increases in foliar nutrient composition have been noted following P fertilization in other species such as Picea abies (Fiedler et al., 1983). In addition, there was a highly significant N x P interaction and a significant N x K interaction which affected the P concentration but not content. Figure 15 illustrates the effect of the N x P interaction. Foliar P concentrations decreased with increasing rates of N when N and P were added together, but increased when N was added alone (Figure 15). The decrease in concentration from N plus P fertilization is due to a dilution effect from the enhanced growth. Note that despite the decrease in concentration, foliar P content was significantly increased (Table 11).

These findings are consistent with other studies. Sheppard and Racz (1980) cited numerous examples where a positive ammonium ion effect was noted on the uptake of P. They suggested that the main mechanisms responsible for this effect was increased root growth, increased ability to absorb and translocate P, and a pH effect at the soil-root interface increasing P solubility.

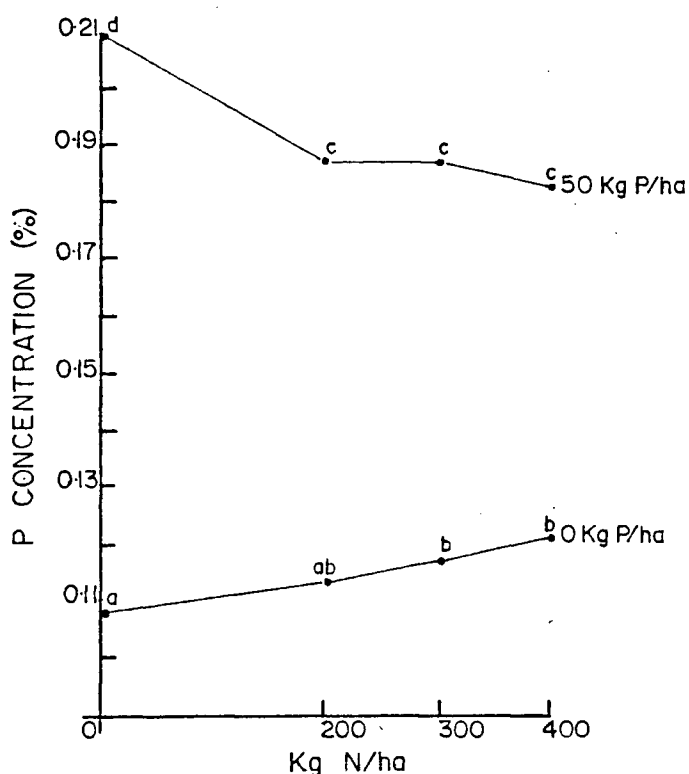


FIGURE 15. Effect of N x P interaction on P concentration. Points followed by the same letter are not significantly different at $p=.05$.

Mean foliar P concentrations of the Sitka spruce in the control plots was 0.11% (Table 15). As with N, this was again well below the critical value of 0.14% (Table 1). Even in the HA-phase where growth was very good, P concentrations were still low, averaging only 0.13%. This estimate however, was considerably lower than that of 0.16% obtained by Lewis (1982) from Sitka spruce on similar sites and indicated that a fair amount of variability exists between plantations.

None-the-less, all the trees from the HA-phase sampled in the present study exhibited excellent growth, with height increments ranging from 47 to 85 cm. This would seem to indicate that substantial gains in growth of Sitka spruce on the CH-phase may be achieved through a modest increase in foliar P concentrations provided the N nutrition were improved. Unfortunately, this did not occur in the present study. Although the addition of N or N plus K alone did result in a slight increase in foliar P to about 0.12%, there was only a minimal effect on growth compared to the N plus P treatments (Figure 10 and 11). The lack of response in these cases however, may be due to the high foliar N concentrations discussed previously which would probably compound the effects of the low P concentrations. Van den Driessche (1974) noted that the optimum N/P ratio for many species is between 6 to 16 and Leyton (1958) suggested a value of 10 for Sitka spruce. N/P ratios in the present study ranged between 28 and 35 for N and N plus K treatments as compared to a range of 17 to 23 for the N plus P treatments and a mean of 10 for the spruce from the HA-phase.

Despite the apparent lack of P on these sites, the addition of P or P plus K alone had no effect on growth or needle weight, although foliar concentrations were significantly increased (Table 15). However, the addition of P and N together resulted in a large increase in needle weight and is clearly evident in Figure 16 as a "C" shift (Figure 2), suggesting that both N and P are deficient. The fact that N alone resulted in some increase in growth,

whereas P alone did not, suggested that N was more limiting. However, given the large additional gains derived from applying both N and P together, it seems likely that for any remedial fertilization program to be effective, both N and P will have to be applied. Moreover, if any other treatment, such as scarification, is undertaken on these sites to improve the N status, a top dressing of P may still be required if maximum benefits are to be achieved.

As in spruce, P fertilization tended to result in a highly significant increase in foliar P concentrations in both cedar and hemlock (Table 15). After fertilization, foliar P levels tended to be highest in hemlock and lowest in spruce. Unlike spruce however, N fertilization tended to result in a reduction in foliar P concentrations, and was particularly noticeable with cedar. Moreover, increasing rates of N tended to result in a corresponding decline of foliar P whether P was added or not (Table 15).

Mean foliar P concentrations of hemlock in the control plots was 0.13%. While this value is considered to be severely deficient (Table 1), it was not only significantly greater than the concentration found in spruce (Table 15), but, it was also slightly higher than the estimate of 0.12% obtained for well growing hemlock from the HA-phase. The estimates obtained in this study were not consistent with those of Lewis (1982) who found mean foliar P concentration to be 0.16% and 0.25% for hemlock growing on the CH- and HA-phases, respectively. Baker (1970) however, found foliar P concentrations in similar high site hemlock

TABLE 15. Within and between species comparisons of mean foliar P concentrations (% oven-dry weight) for spruce, hemlock and cedar. Treatments connected by the same line or followed by the same letter are not significantly different at $p=.01$.

WITHIN SPECIES COMPARISON			*BETWEEN SPECIES COMPARISON						
SPRUCE	HEMLOCK	CEDAR		SPRUCE	HEMLOCK	CEDAR			
TREATMENT			TREATMENT	%					
NO	N2K	N3K	NO	0.11 a	(.021)	0.13 b	(.032)	0.18 c	(.031)
NOK	N1K	N2K	N1	0.11 a	(.022)	0.10 a	(.035)	0.18 b	(.035)
N1	N1	N1K	N2	0.12 a	(.023)	0.11 a	(.029)	0.17 b	(.024)
N2K	N3K	N2	N3	0.12 a	(.024)	0.10 a	(.024)	0.17 b	(.042)
N1K	N3	N3	NOP	0.20 a	(.040)	0.44 b	(.070)	0.19 a	(.030)
N3K	N2	NOK	N1P	0.18 a	(.021)	0.28 b	(.067)	0.28 b	(.060)
N3	NOK	N1	N2P	0.19 a	(.025)	0.27 b	(.092)	0.25 b	(.037)
N2	NO	NO	N3P	0.18 a	(.022)	0.27 n	(.050)	0.24 b	(.051)
NPKT	NPKT	NOP	NOK	0.11 a	(.022)	0.12 a	(.040)	0.17 b	(.028)
N3P	N3PK	NOPK	N1K	0.12 a	(.024)	0.09 b	(.028)	0.17 c	(.026)
N3PK	N2PK	N3PK	N2K	0.11 a	(.023)	0.08 b	(.010)	0.16 c	(.033)
N1P	N2P	N3P	N3K	0.12 a	(.022)	0.11 a	(.041)	0.16 c	(.026)
N2PK	N3P	N2PK	NOPK	0.22 a	(.040)	0.38 b	(.095)	0.22 a	(.031)
N2P	N1PK	N1PK	N1PK	0.19 a	(.023)	0.28 b	(.094)	0.24 b	(.059)
N1PK	N1P	N2P	N2PK	0.19 a	(.022)	0.26 b	(.080)	0.24 b	(.053)
NOP	NOPK	NPKT	N3PK	0.18 a	(.018)	0.23 a	(.064)	0.23 a	(.055)
NOPK	NOP	N1P	NPKT	0.18 a	(.017)	0.22 b	(.044)	0.26 b	(.045)

* Values in parenthesis \pm SD.

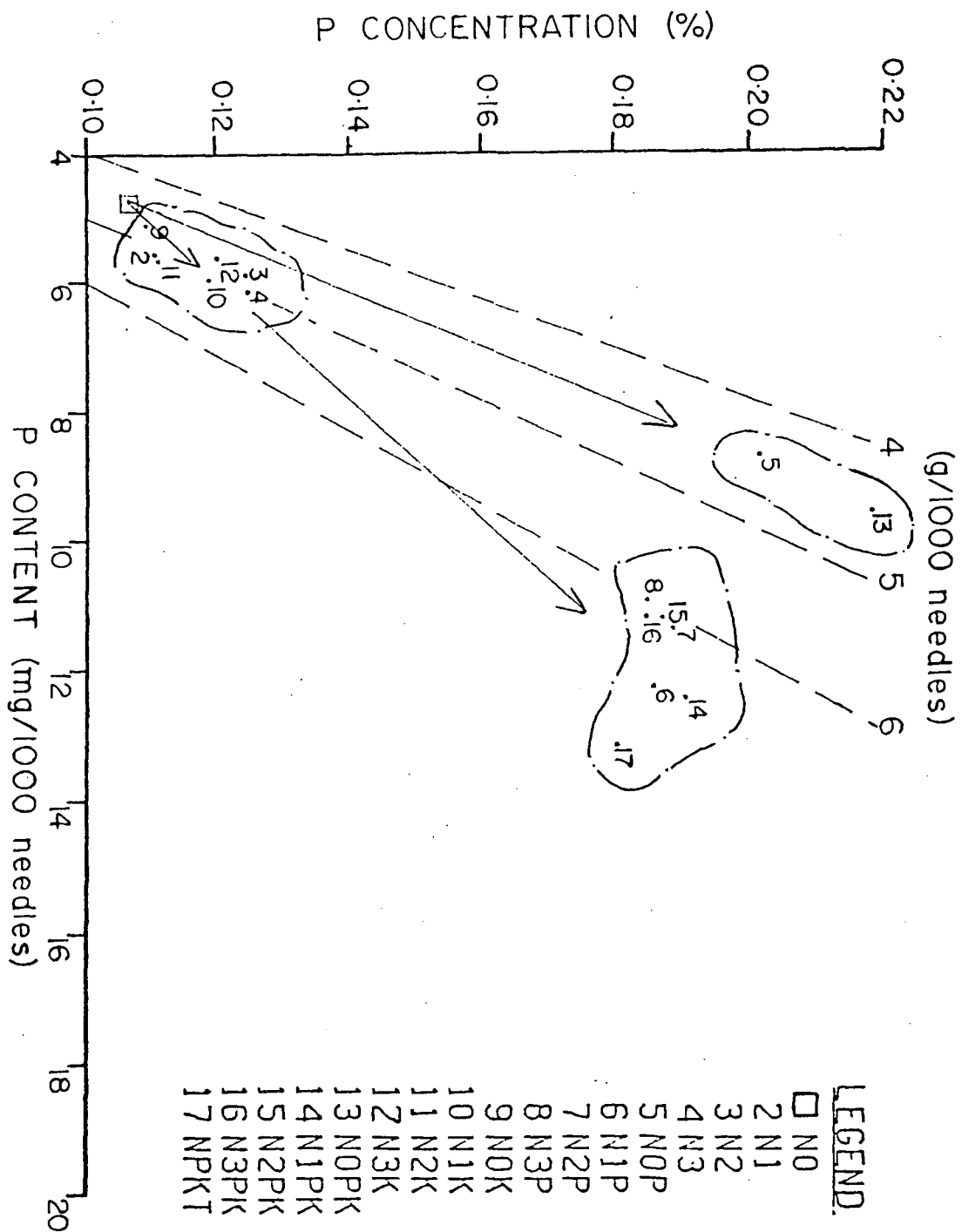


FIGURE 16. Relationship between foliar P concentration, content and dry-weight.

stands to range from 0.14% to 0.21%. Because this study was not designed to study hemlock and the sample size was relatively small (23 control trees from the CH-phase and 10 trees from the HA-phase) these estimates should be viewed with caution. The somewhat better growth of hemlock as compared to spruce after N or N plus K fertilization suggested a better P status in hemlock. However, given the highly significant synergistic effect of P when added with N on hemlock growth, it appeared that P was deficient.

Mean foliar P concentrations of cedar in the control plots is 0.18%, which was extremely high compared to that of spruce or hemlock (Table 15). Because of the lack of information on cedar however, it is difficult to say how this value compares with the general nutritional requirements of the species. However, given the relatively good growth experienced on these sites, it would appear that the P status was adequate or, at most, only marginally deficient. Graham (1982) noted that cedar often responded favourably to release even though foliar P and N concentrations were only 0.13% and 0.90% to 0.95%, respectively, which suggested that the species is capable of exhibiting good growth on low P levels.

Why can cedar perform better on these sites than either spruce or hemlock? It is obvious that the species is more efficient in extracting or competing for available nutrients than either of its counterparts. It is conceivable that this may be related to differences in mycorrhizal associations between the species. Numerous studies have shown that plants infected with mycorrhizae exhibit better

growth than non-infected plants. Invariably, this improved growth has been attributed to an improvement in the plants' nutrition, and in particular P, but also to some extent N (Tinker, 1979; Rovira et al., 1983). The mycorrhizal fungi associated with cedar are different from those of spruce and hemlock. Cedar forms associations with vesicular-arbuscular (VA) fungi, whereas, both spruce and hemlock form associations with ectomycorrhizal fungi (Parke et al., 1983). It is possible that the VA-mycorrhizae of cedar are more tolerant of the conditions found on these sites. Parke et al. (1983) noted that the dominant species infecting cedar was Glomus tenue, a species which is known to tolerate low P levels. Moreover, there may be some relationship between the ability of the mycorrhizae to thrive on these sites and the "salal effect" discussed previously, although it should be noted that cedar, like spruce and hemlock, is considered to be "heather sensitive" (Everard, 1974). In any event, further discussion of such possibilities are beyond the scope of this thesis, and can only be speculated upon until further investigations are undertaken.

Effects on Foliar Potassium

Although K fertilization resulted in a highly significant increase in both foliar K concentration and content, a strong antagonistic effect of N on K resulted in a dramatic decrease in the foliar K levels below that of the controls. In addition, there were a number of highly significant N x P and N x K interactions which influenced

both K concentration and content (Figures 17 and 18).

The addition of P alone resulted in a significant increase in foliar K concentration and content, however, when added together with N, K content increased (Figure 18), whereas, concentration decreased (Figure 17). The reduction in concentration was due to a growth dilution phenomenon rather than antagonism between the P and K ions (Figure 19).

On the other hand, N fertilization resulted in a highly significant and dramatic reduction in both foliar K concentration and content (Figures 17 and 18). This effect was evident whether or not K was added. However, on those plots where K was added, foliar K levels tended to be higher (Table 16) except at the highest N rates where this trend was reversed (Figures 17 and 18).

Mean foliar K levels of trees in the control plots was 0.57% as compared to 0.52% for well growing spruce of the HA-phase. These values suggest the possibility of a moderate K deficiency (Table 1). The addition of K or P plus K alone had no effect on needle weight, but did result in a very large increase in foliar K concentration (Figure 19). However, when N was included, foliar K levels dropped to 0.41%, 0.35% and 0.34% for the 200, 300 and 400 kg N/ha application rates, respectively. Although some of the decrease in K concentration can be attributed to a dilution effect, it appeared to be largely due to an antagonistic influence of the high N concentrations. This was evident from the strong "E" shifts in Figure 19 plus the highly significant negative correlation between N and K ($r=-0.7235$;

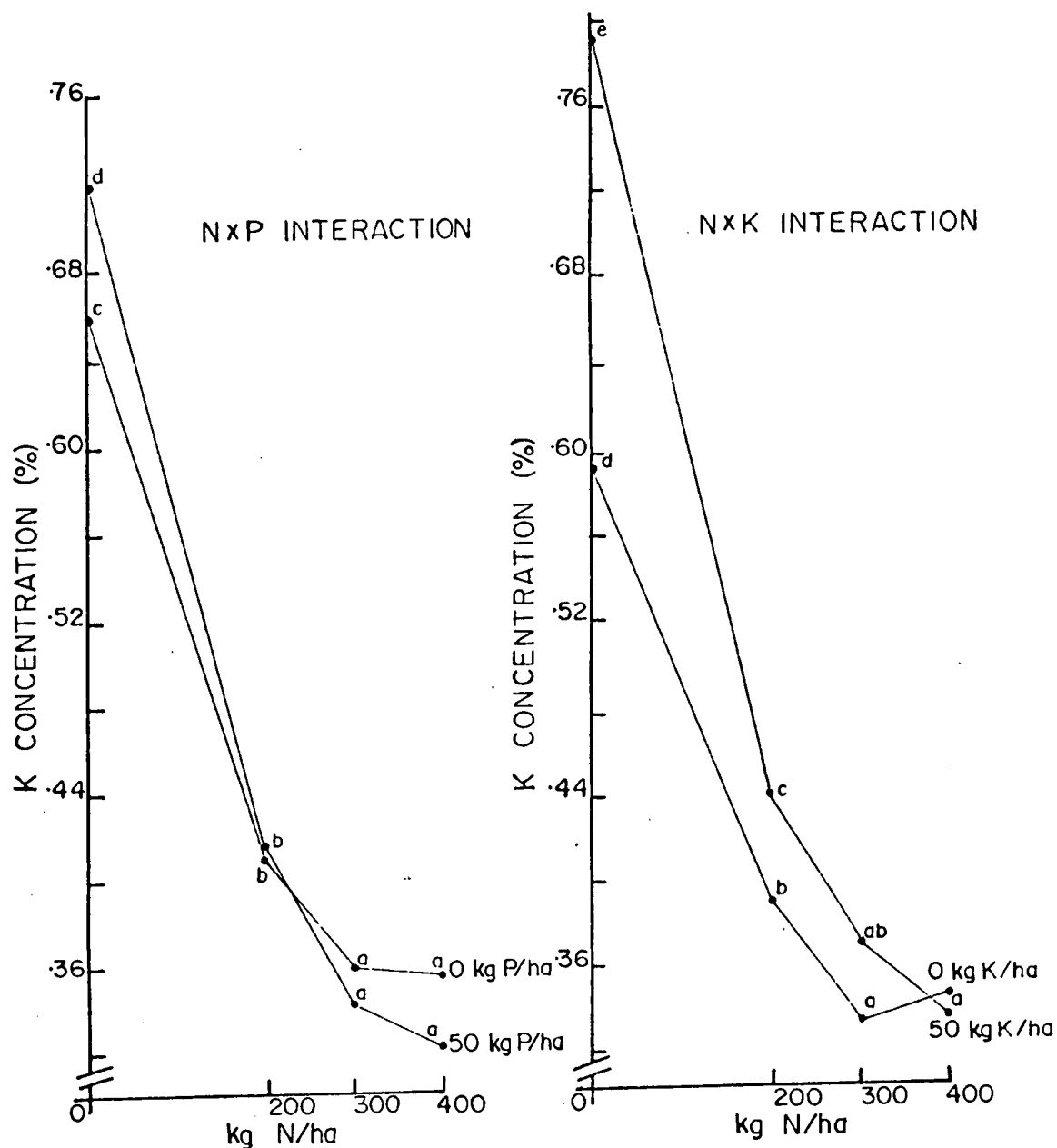


FIGURE 17. Effects of N x P and N x K interactions on potassium concentration. Points followed by the same letter are not significantly different at $p=.05$.

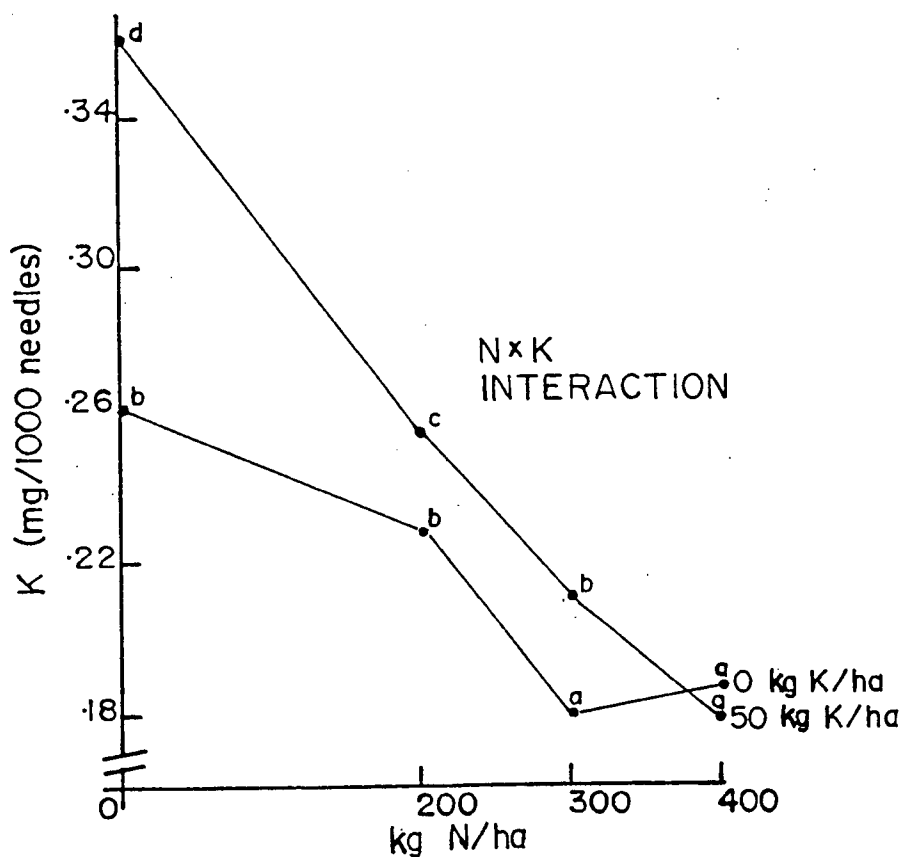
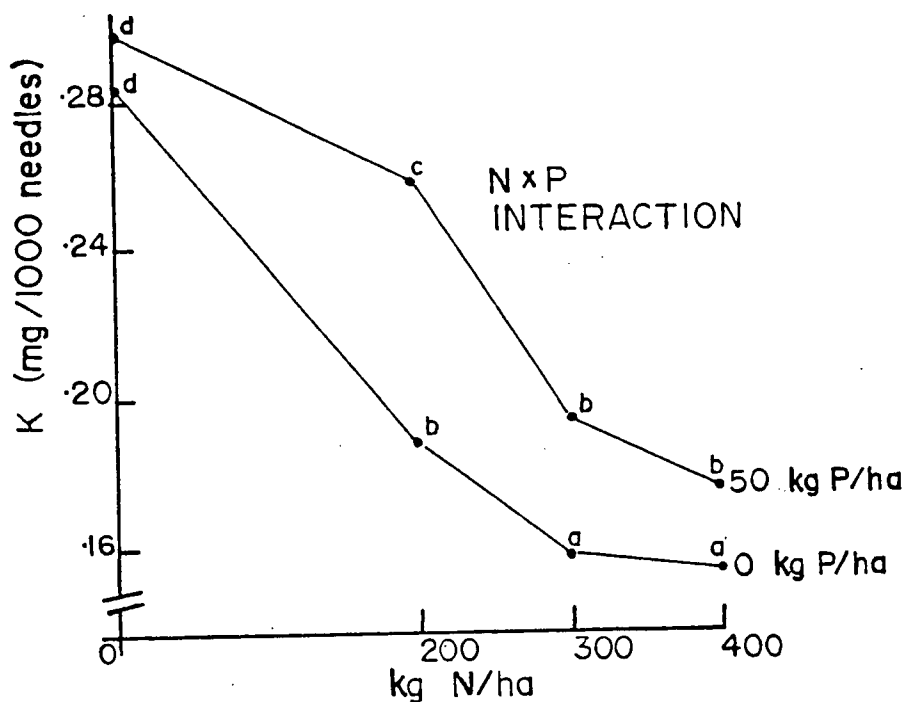


FIGURE 18. Effects of N x P and N x K interactions on potassium content. Points followed by the same letter are not significantly different at $p=.05$.

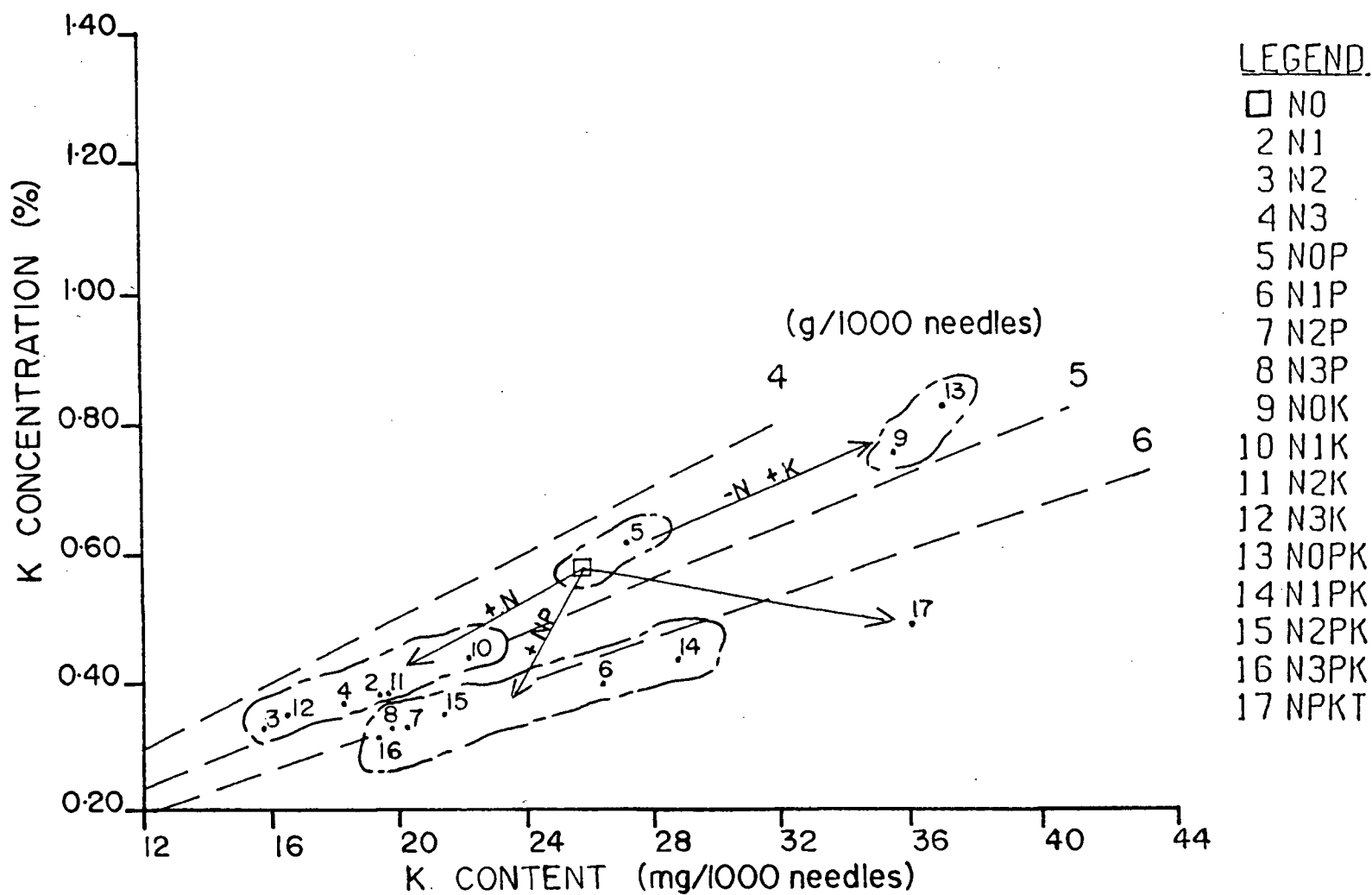


FIGURE 19. Relationship between foliar K concentration, content and dry weight.

note: excludes treatments NOK and NOPK). These patterns were consistent in all five plantations selected for study (see Appendix II).

There are numerous examples, particularly in agriculture, of antagonistic effects of N on K, however, the suppression of K in these cases was related to ammonium ions rather than nitrate ions (Murphy, 1980). In contrast with the present study, the addition of a nitrate source of N, such as ammonium nitrate, or simply the addition of K was sufficient to overcome the antagonistic effect of the ammonium ion (Murphy, 1980). Two main theories were suggested to explain this effect. Woodhouse and Hardwick (1966) suggested that since NH_4^+ and K^+ are similar in size and charge, that NH_4^+ could compete with K^+ ions for root surface absorption sites specific for univalent cations. Dekock (1970) however, noted that in some plants, Ca, a divalent cation, may also be inhibited; therefore root surface competition is not the only factor involved. Barker et al. (1967) proposed that high concentrations of ammonium could not only displace exchangeable K from the soil colloids, but also prevent non-exchangeable K from becoming available. Apparently, a significant amount of the non-exchangeable forms of K can be made available to trees, particularly in K deficient soils (Welch and Scott, 1961; Mengel and Kirkby, 1979).

Because of thick organic accumulations on the CH-phase it is doubtful that non-exchangeable forms of K play a significant role in the K nutrition of the spruce. Organic soils are often low in K (Mengel and Kirkby, 1979).

Shickluna et al. (1972) noted that although organic soils have high CECs, humus colloids have very low fixing powers and thus most K remains in readily available forms which can be easily leached.

Leaching losses of K may be greater due to the application of ammonium nitrate as opposed to urea since the nitrate ion could act as a carrier ion for displaced K^+ ions preventing reabsorption onto the soil colloids. Vimmerstedt and Osmond (1963) attributed a reduction in exchangeable K after the application of ammonium nitrate to competition between K^+ and NH_4^+ ions for exchange sites. Similarly, Cole and Gessel (1968) noted significant losses of K from the forest floor after the addition of urea and ammonium sulphate and that losses were greater when ammonium sulphate was used. Presumably in this case, it is the sulphate ion that acts as a carrier ion for displaced K^+ ions.

Loss of K by leaching may be particularly detrimental on these sites, since prior to fertilization, the occasional tree was exhibiting visual symptoms characteristic of K deficiency. In conifers, such symptoms first appear as a general chlorosis, followed by a foliage discolouration of a purplish-tinge or bronzing, often referred to as "scorching", of the most recently matured, current years foliage (Figure 20a) (Benzian, 1965; Leaf, 1967). During the collection of foliage in the fall, the number of trees exhibiting these symptoms had increased dramatically (Figure 20b). All trees exhibiting K deficiency symptoms occurred on plots receiving 300 and 400 kg N/ha. However, although many



FIGURE 20 a.
Sitka spruce prior to
fertilization exhibiting
bronzing or scorching
of foliage. Note the
relatively good leader
growth despite the
foliage discoloration.



FIGURE 20 b.
Sitka spruce exhibiting
symptoms of K deficiency
after fertilization with
300 kg N, 50 kg P and 50
kg K. Foliar nutrient
concentrations (%) were:
N-3.61, P-0.16, K-0.26,
Ca-0.28, Mg-0.08, B-12
(ppm), Cu-3(ppm), Zn-26
(ppm), Fe-6.0(ppm) and
Mn-715(ppm).

trees had foliar K concentrations less than 3.0%, relatively few actually had purplish foliage.

Despite the induced K deficiency, growth did not appear to be adversely effected. This may be due to the fact that even in those treatments where K was added, its uptake was restricted. Thus foliar K levels for all treatments were relatively similar, and therefore, assuming K was limiting growth, differences between treatments would not have been as apparent. However, there was evidence which suggested that the addition of K was beneficial to growth. Of the highly responsive treatments, (i.e.: NP, NPK, and NPKT), those which maintained the highest foliar K concentrations and content tended to exhibit the best growth responses. Lack of real differences in growth may also be related to the mobility of the ion. K is known to be a highly mobile nutrient (Mengel and Kirkby, 1979), thus internal redistribution may have been sufficient, at least in the first growing season after fertilization, to overcome any apparent K deficiency. Should this deficiency persist into subsequent growing seasons, it would seem unlikely that acceptable growth rates could be maintained even with N and P fertilization although there have been cases in Britain where extremely low K levels (3%) have had no apparent effect on growth (Dickson and Savill, 1974).

A statistical analysis of hemlock foliar K levels was not done because all samples were bulked by treatment to give one estimate per stand (Table 16). Similarly, no analysis was done on cedar, but preliminary estimates by

TABLE 16. Mean foliar K concentrations of Sitka spruce and hemlock. Treatments connected by the same line are not significantly different at $p=.01$ -- applicable to spruce only.

TREATMENT	*SPRUCE		HEMLOCK
	% OVEN-DRY WEIGHT		
N3PK	0.31	(.054)	0.62
N3P	0.33	(.056)	0.60
N2P	0.33	(.065)	0.58
N2	0.33	(.070)	0.61
N3K	0.35	(.091)	0.77
N2PK	0.35	(.074)	0.66
N3	0.36	(.088)	0.68
N1	0.38	(.086)	0.60
N2K	0.38	(.109)	0.90
N1P	0.39	(.086)	0.58
N1PK	0.43	(.098)	0.59
N1K	0.44	(.106)	0.83
NPKT	0.48	(.067)	0.65
NO	0.57	(.129)	0.81
NOP	0.62	(.114)	0.72
NOK	0.75	(.108)	0.91
NOPK	0.83	(.095)	0.87

* Values in parenthesis \pm SD.

Lewis (1982) suggested that the K levels of cedar were adequate.

In general, foliar K levels of hemlock were considerably higher than those of spruce and no visible signs of K deficiency were noted. Nitrogen fertilization appeared to decrease K, which was more noticeable in N plus P fertilized plots than in N alone; presumably due to a combined growth dilution and N-antagonism. The addition of K improved foliar concentrations, but levels still remained below those of the controls when N was applied.

Effects on Foliar Calcium and Magnesium

N, P and K fertilization significantly influenced foliar Ca and Mg composition (Table 11). In general, content was influenced more than concentration. N and P significantly ($p=.01$) increased Ca and Mg content. K however, while having a positive effect on Ca concentration and content (Figure 21), appeared to have had a highly significant antagonistic effect on Mg (Table 17). While the negative effects of high K concentrations on Mg uptake are well known (Mengel and Kirkby, 1979), it seemed unusual that Mg was depressed on plots where both N and K were added simultaneously since K was also severely depressed. Although significant differences were observed, the actual differences between treatments were small due to the low Mg value (Table 17).

In addition to the main effects, there were also significant N x P interactions affecting the Ca and Mg

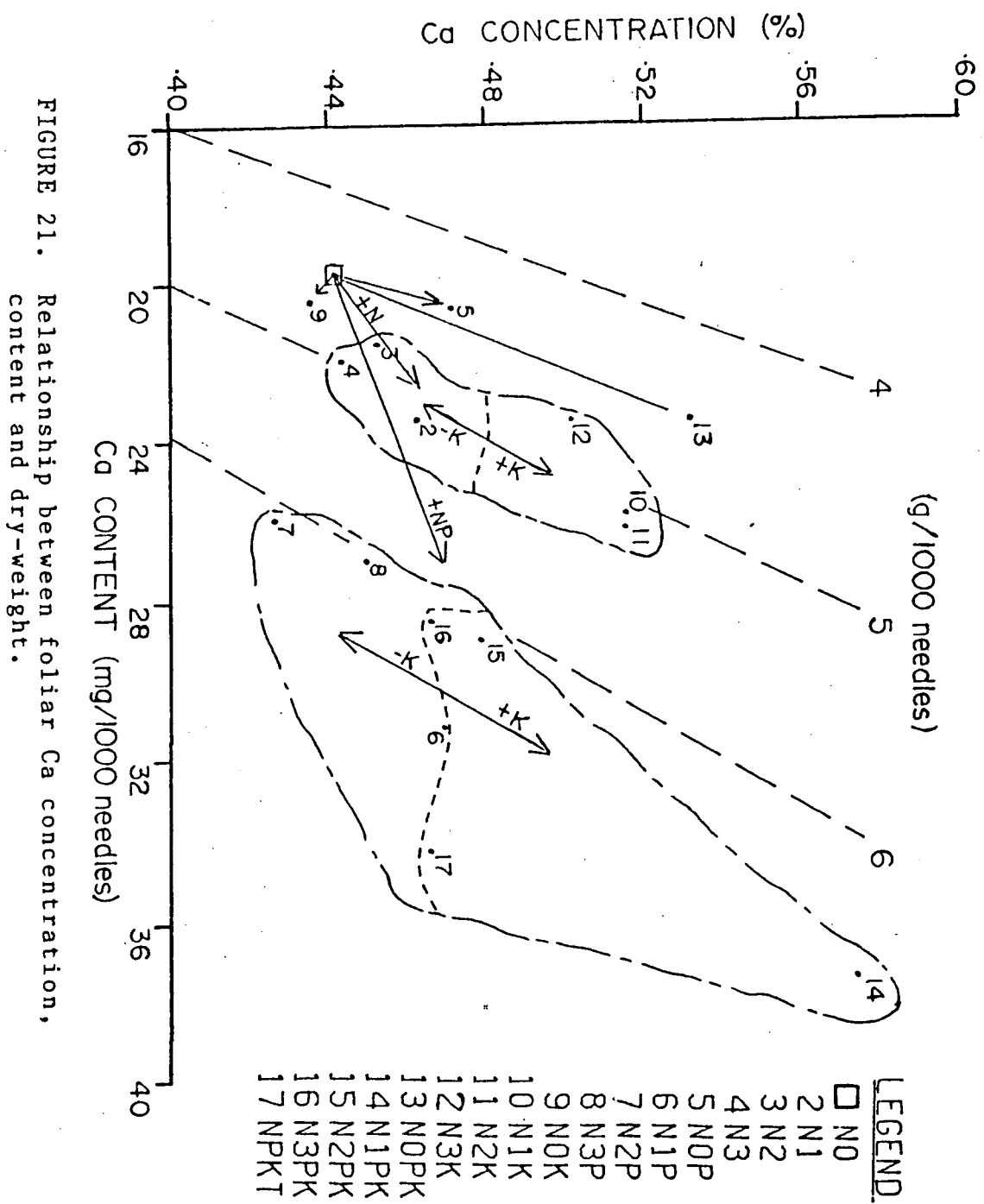


FIGURE 21. Relationship between foliar Ca concentration, content and dry-weight.

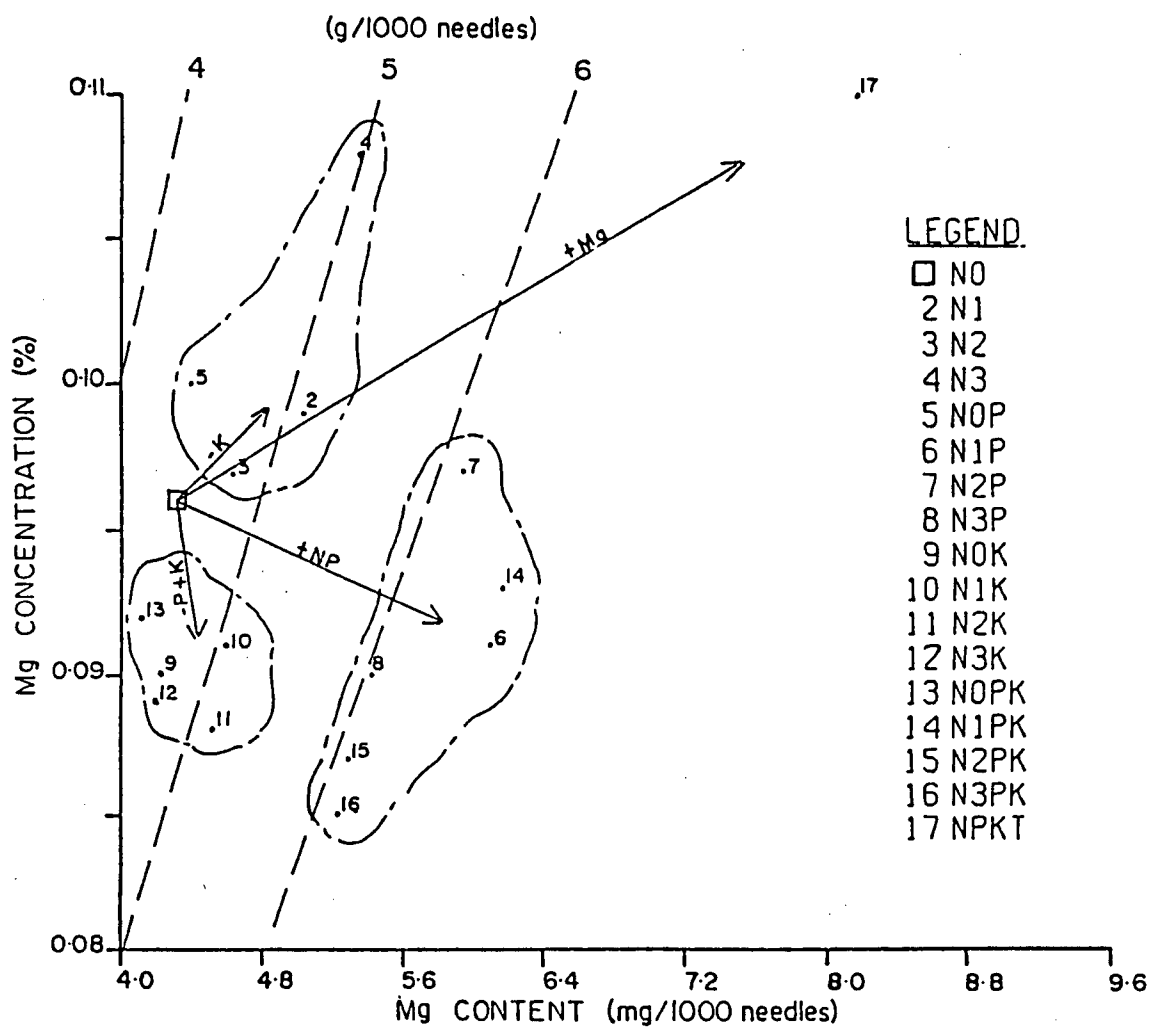


FIGURE 22. Relationship between foliar Mg concentration, content and dry-weight.

content and Mg concentration (Table 11). The N x P interaction on needle nutrient content was due to a greatly enhanced uptake of Mg and Ca when N and P were added together as compared to N alone (Figure 23). Uptake was greatest at the lowest rate of N and tended to decline as the rates increased. The N x P interaction on Mg concentration was largely due to a growth dilution, this is clearly evident in Figure 22 as an "A" shift for those treatments where N and P were added simultaneously.

Mean foliar Mg and Ca concentrations of the Sitka spruce controls were 0.10% and 0.47%, respectively (Table 17). Critical values for these two nutrients have not yet been identified for Sitka spruce, however, when compared with nutrient levels found in good and poor growing Sitka spruce (Table 1) or critical levels of other species (see Morrison, 1974), the values for Ca seemed adequate, whereas the values for Mg were low and possibly slightly deficient.

Fertilizer trials were not established to study the effects of Mg so it is difficult to say if Mg would have any additional benefits on growth. Mg was only added in the NPKT treatment and although it did result in a clear "C" shift (Figure 22), meaningful interpretations cannot be drawn because of the confounding effects of the other nutrients. Examination of the clustering of points in Figure 22 however, indicates that Mg is not limiting growth. This can be concluded because, aside from the apparent antagonistic effect of K, Mg uptake was increased significantly. In the highly responsive N plus P treatments, where concentration

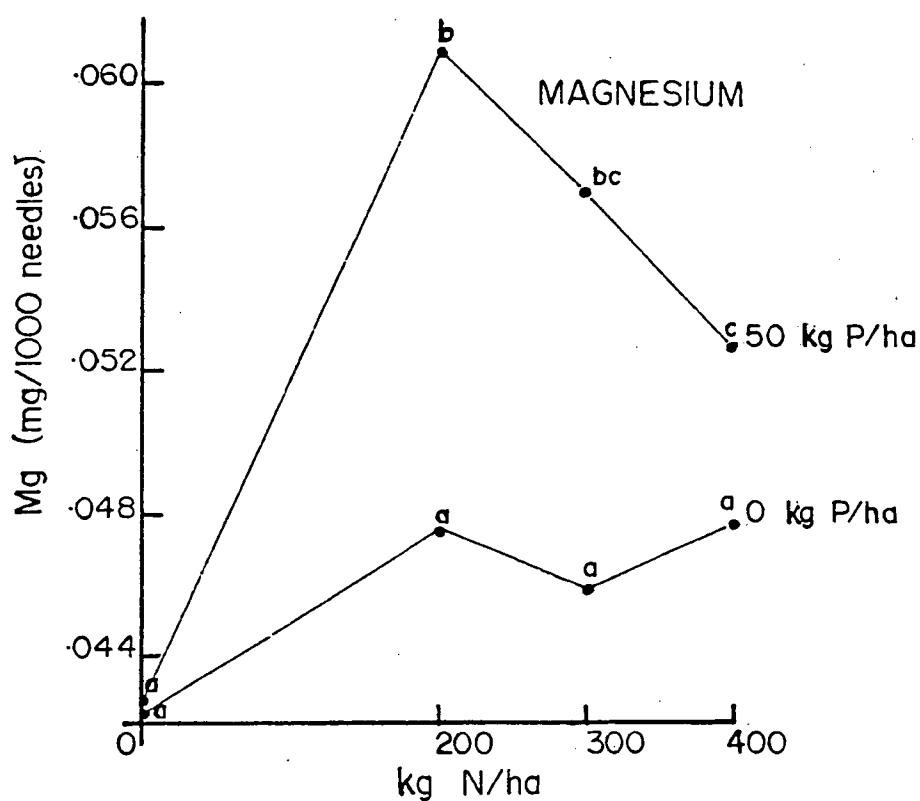
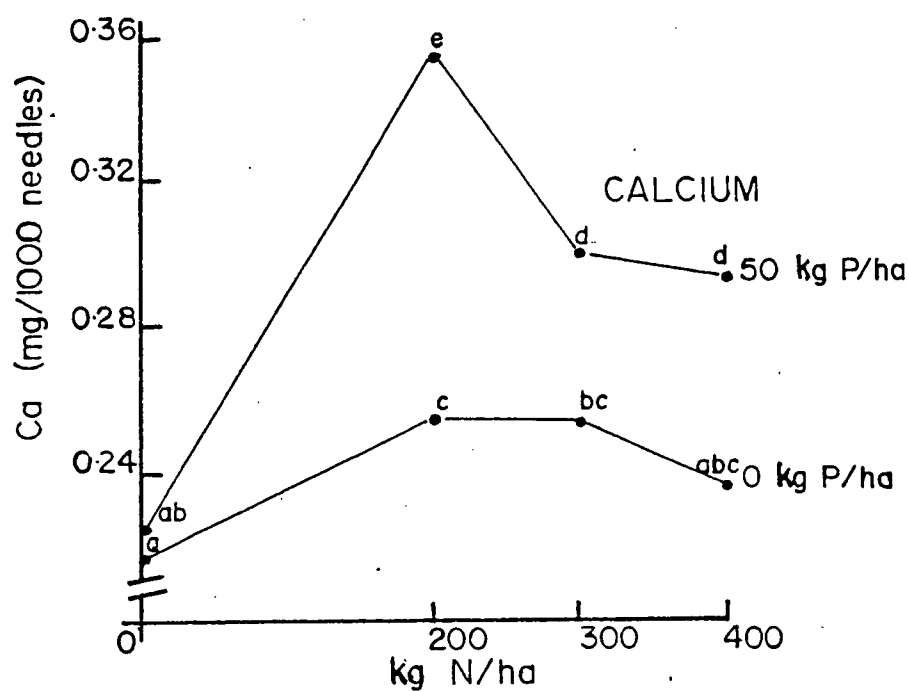


FIGURE 23. Effects of N x P interaction on Ca and Mg content. Points followed by the same letter are not significantly different at $p=.05$.

TABLE 17. Mean foliar Ca and Mg concentrations of Sitka spruce and hemlock. Treatments connected by the same line are not significantly different at $p=.01$ -- applicable to spruce only.

CALCIUM			MAGNESIUM		
TREATMENT	*SPRUCE	HEMLOCK	TREATMENT	*SPRUCE	HEMLOCK
% OVEN-DRY WEIGHT					
N2P	0.46 (.100)	0.36	N3PK	0.08 (.015)	0.09
NOK	0.47 (.119)	0.32	N2PK	0.09 (.022)	0.12
NO	0.47 (0.83)	0.37	NOK	0.09 (.018)	0.10
N3	0.47 (.095)	0.33	N2K	0.09 (.024)	0.10
N2	0.47 (.082)	0.31	N3K	0.09 (.020)	0.11
NOP	0.48 (.102)	0.35	N3P	0.09 (.018)	0.11
N3P	0.49 (.091)	0.30	N1K	0.09 (.022)	0.11
N1	0.49 (.083)	0.34	N1P	0.09 (.021)	0.10
N3PK	0.49 (.097)	0.29	NOPK	0.09 (.013)	0.12
N1P	0.50 (.101)	0.33	N1PK	0.09 (.025)	0.10
N3K	0.50 (.089)	0.29	NO	0.10 (.016)	0.14
N2PK	0.51 (.116)	0.33	N2P	0.10 (.018)	0.09
N1K	0.51 (.104)	0.32	N2	0.10 (.021)	0.09
N2K	0.52 (.097)	0.31	NOP	0.10 (.014)	0.15
NOPK	0.53 (.088)	0.36	N1	0.10 (.021)	0.11
NPKT	0.55 (.096)	0.33	N3	0.11 (.023)	0.12
N1PK	0.57 (.104)	0.25	NPKT	0.11 (.019)	0.09

* Values in parenthesis \pm SD.

decreased from growth dilution, the decrease was not significant (Table 17) and uptake appeared to be sufficient to keep pace with needle expansion. In fact, on the less responsive N alone treatments Mg concentrations increased. Moreover, foliar Mg concentrations from well growing spruce in the HA-phase were slightly lower with a mean of 0.09%.

Hemlock foliage for Ca and Mg was bulked and only a limited analysis was done (Table 17). In general, fertilization appeared to have little or no effect on Ca concentrations, however, Mg concentrations were depressed. Presumably this depression was due to a combined effect of antagonism from the K ion and growth dilutions. As in spruce, P appeared to have enhanced Mg uptake. Other studies have also noted a similar effect of P on Mg uptake (see Fiedler et al., 1983). Mg concentration of hemlock in the control plots were considerably higher than those of spruce and would not be considered deficient (Ballard and Carter, 1983).

Effects of Foliar Sulfur

Mean foliar S concentrations of the control trees was 0.06%. While deficiency levels for Sitka spruce have not been identified, Leaf (1967) noted that foliar S concentrations less than 0.13% for Picea abies was considered deficient. Ballard and Carter (1982) suggested that when N was deficient, the N/S ratio should not exceed a value determined by the equation, $4.2X + 4.94$, where X is the percent foliar N concentration. Using the data from the

present study, the equation yields a value of 8.49, whereas the N/S ratio was 13.28. These findings suggest a S deficiency or possibly a N-induced S deficiency may exist (Ballard and Carter, 1983) and the stands should respond to both N and S fertilization (Ballard, T.M., 1979).

As with Mg, it is difficult to say if these stands have responded favourably to S fertilization as S was only added in the NPKT treatment. Although there was a clear "C" shift in Figure 24, interpretations are confounded by the other nutrients. Recent fertilizer trials established by BCFP (see page 90) found diameter response of hemlock to be 19%, 39% and 44% for urea, ammonium sulphate and ammonium nitrate, respectively. Again, it is difficult to say if the improved response of ammonium sulphate over urea is due to the sulfur or to the possibility of urea having detrimental effects on hemlock as suggested by Gill and Lavender (1983a). The latter seemed more likely because ammonium nitrate had the greatest response. Recent studies by Turner et al. (1977) however, found that much of the variation in the response of Douglas-fir to N fertilization in the Pacific Northwest could be explained by foliar sulphate levels. Those stands showing the highest responses tended to also have the highest foliar sulphate reserves. The basis for improved response lay in the biochemical relationship between N and S in protein synthesis (Turner et al., 1977) and suggests that S deficiencies may be more prevalent in the Pacific Northwest than originally anticipated.

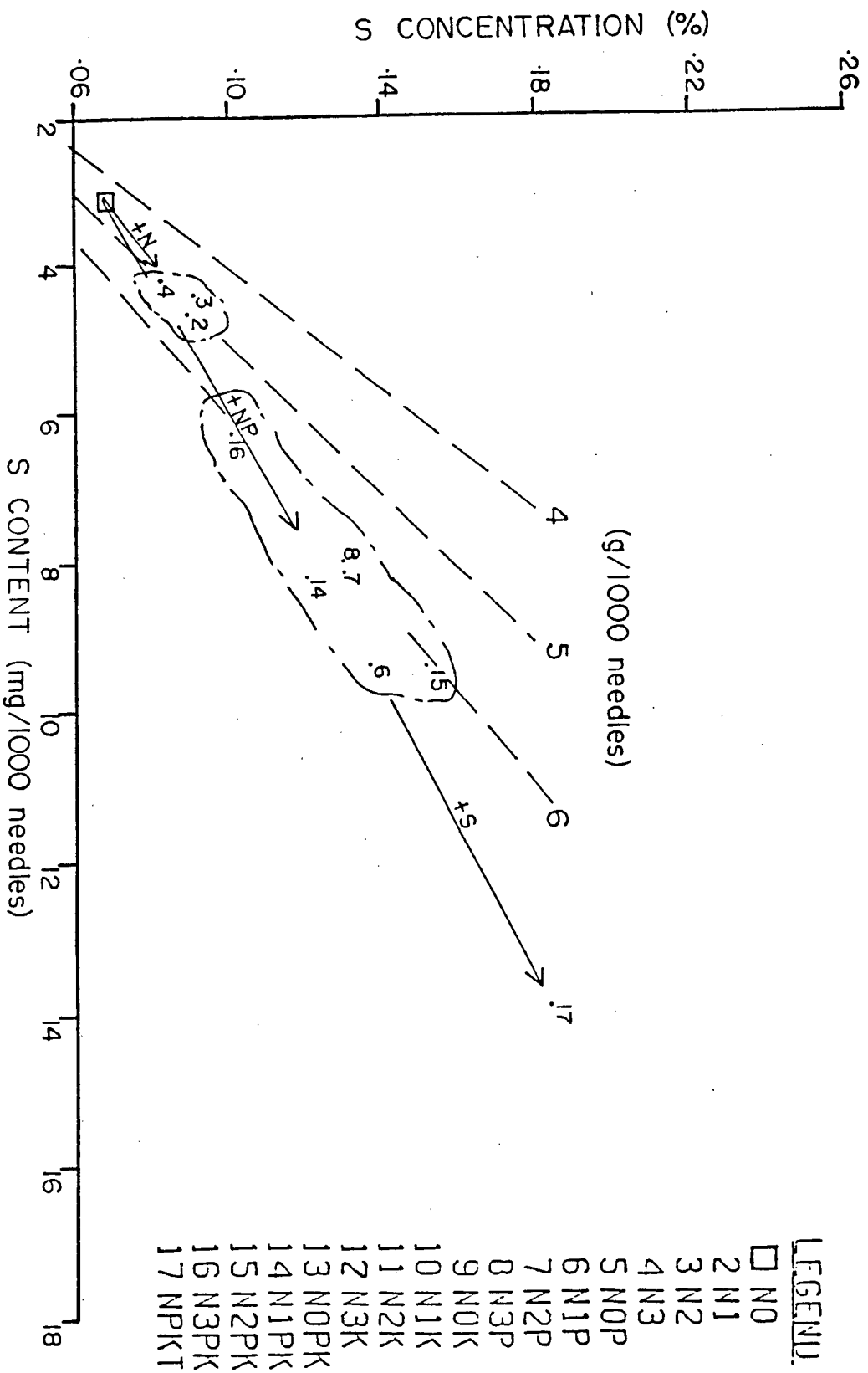


FIGURE 24. Relationship between foliar S concentration, content and dry-weight.

Improvement of the nutritional status of the trees appeared to have resulted in a substantial improvement in the trees' S nutrition even though S was not added. This is clearly evident in Figure 24. Mean foliar S concentrations increased to 0.08% when N alone was added and to 0.13% when N and P were added together. Since control trees were highly deficient in N and P and growth was extremely poor, demand for other nutrients such as S may have been limited even though available sulphate indices were high. This would be somewhat analogous to the "B" shift illustrated in Figure 2. The increase in S concentrations however, may also be related to increases in S mineralization as a result of N and P fertilization. Recent studies have shown mineralization of organic matter is an important source of sulphate for tree species (Davies et al., 1983). Mean foliar S concentration in the trees sampled from the HA-phase were 0.13% and 0.15% for spruce and hemlock, respectively. The higher foliar S levels here may be due to the more "active" organic matter of this phase as indicated by the greater rates of N mineralization.

As sulfur inputs and outputs were not investigated in this study it is not possible to say why foliar S concentrations increased. In any event, it appears that S deficiencies can be overcome through enhanced uptake after N plus P fertilization. If S is indeed deficient, an alternate source of N such as ammonium sulphate may prove to be superior.

Effects on Foliar Micro-nutrients

Application of micro-nutrients in the NPKT treatment resulted in an increase in the foliar concentration and content of all applied nutrients except Zn (Figures 25 to 28). In the case of Zn, concentration decreased but content increased (Figure 28).

Because only limited attention was paid to the micro-nutrients in this study, precise interpretation of the foliar analysis was not possible. In addition, relatively little attention has been paid to micro-nutrient fertilization elsewhere and thus comparisons with other trials are limited. Many organic soils however, are known to be deficient in micro-nutrients, and in particular Cu and B (Veijalainen, 1977). Fertilizer trials with micro-nutrients on peatlands in Scandinavian countries, often result in an increase in foliar concentration of the corresponding nutrients (Veijalainen, 1977) and an improved growth response over plots receiving N, P and K fertilizers only (Veijalainen, 1981). Other studies on micro-nutrients have identified foliar concentrations associated with good and poor growth for various tree species (Table 18). Such values must be compared with caution because of the wide variation encountered.

In general, it appears as if B, Mn and Zn are adequate, whereas, Cu and "active" Fe are low. However, given the range of values in Table 18 it is debatable whether Cu is actually deficient. Cu levels in the HA-phase, while higher, could still be considered low at 4.6 ppm and yet

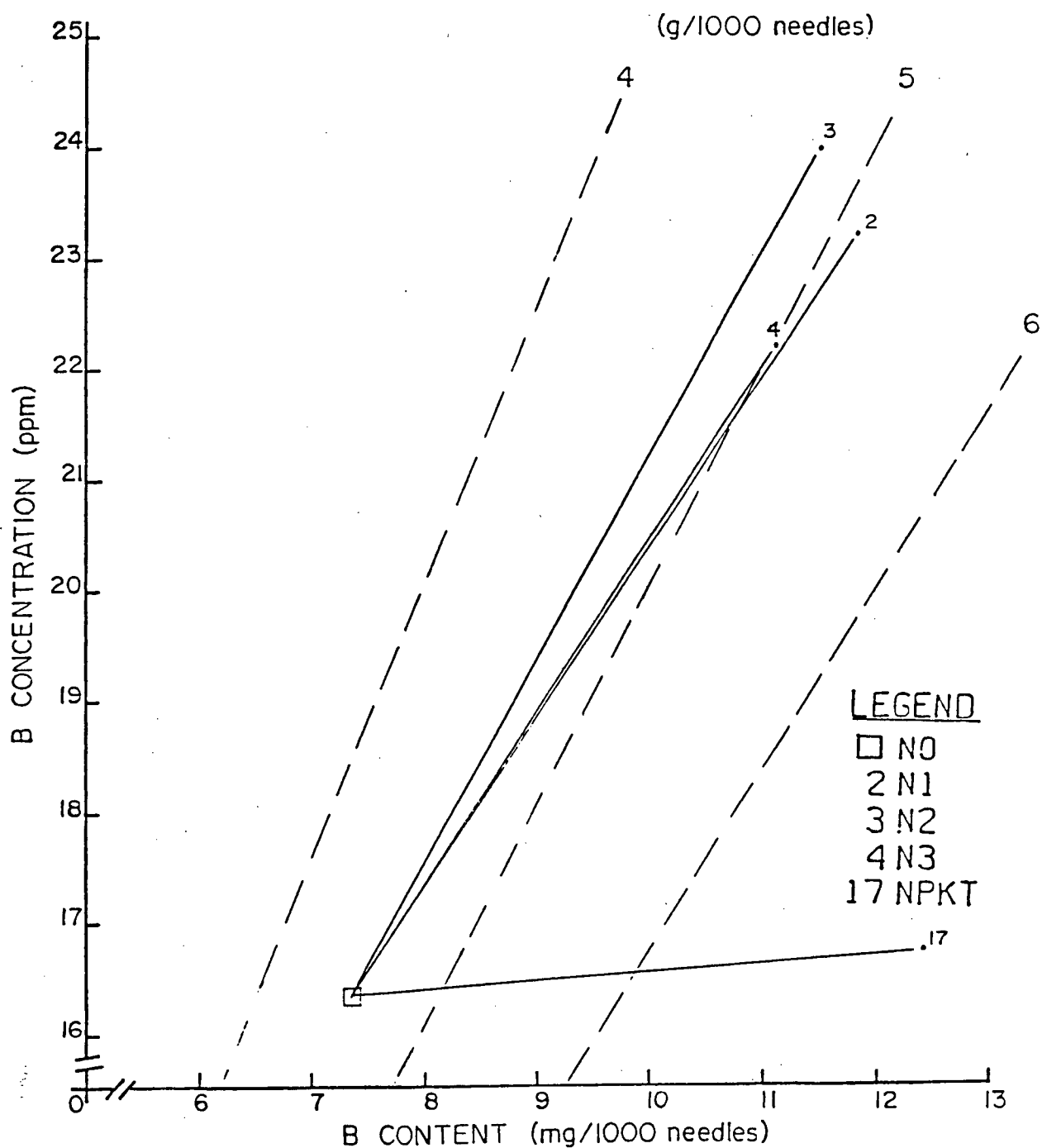


FIGURE 25. Relationship between foliar B concentration, content and dry-weight.

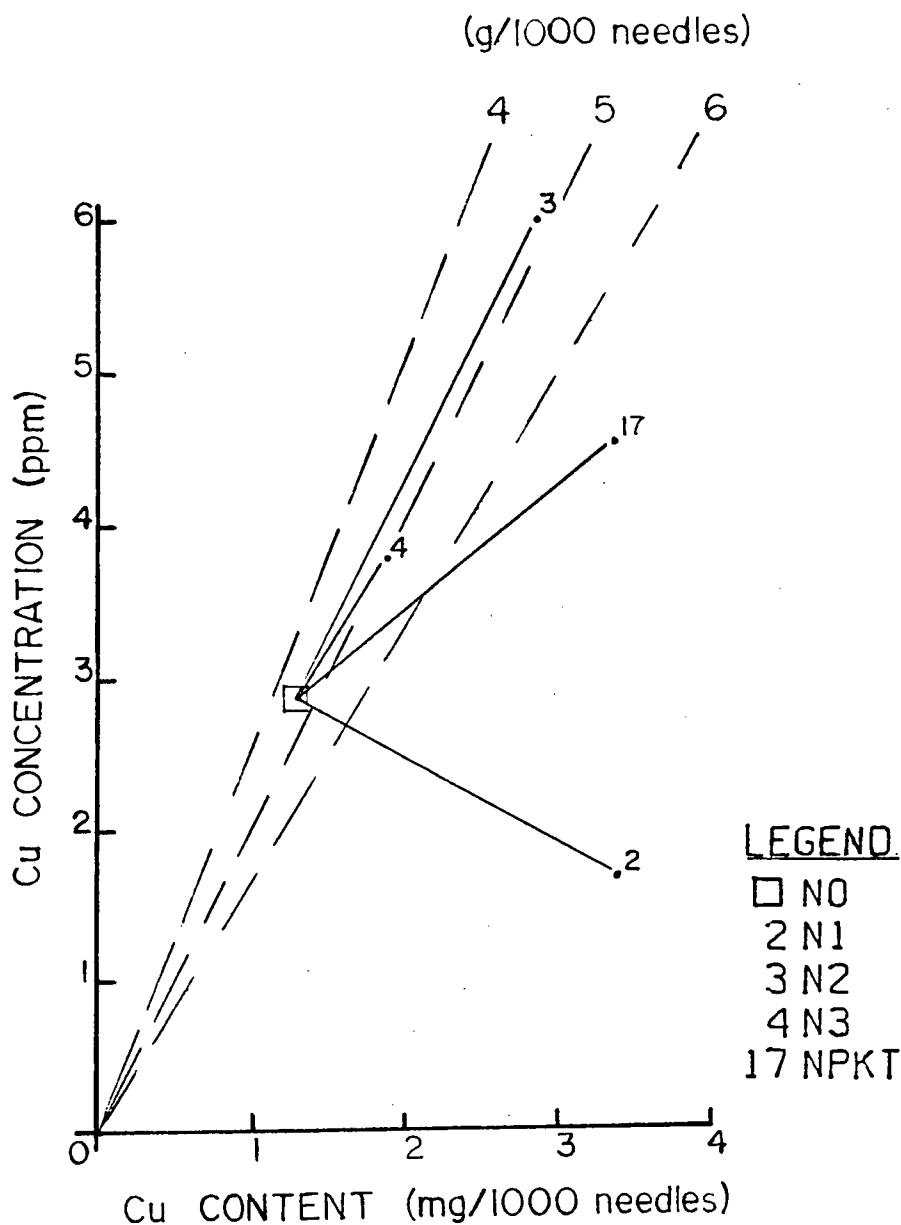


FIGURE 26. Relationship between foliar Cu concentration, content and dry-weight.

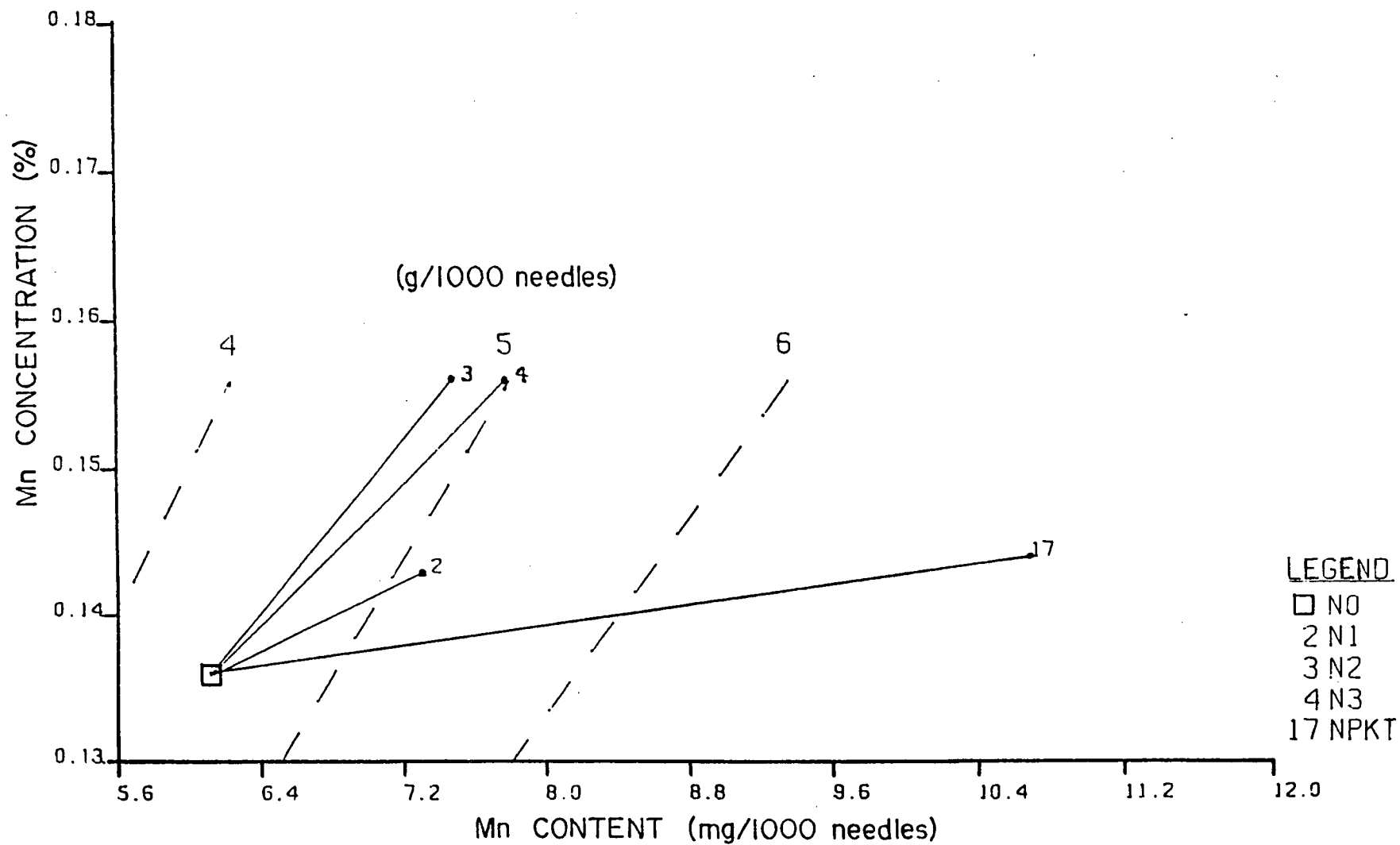


FIGURE 27. Relationship between foliar Mn concentration, content and dry-weight.

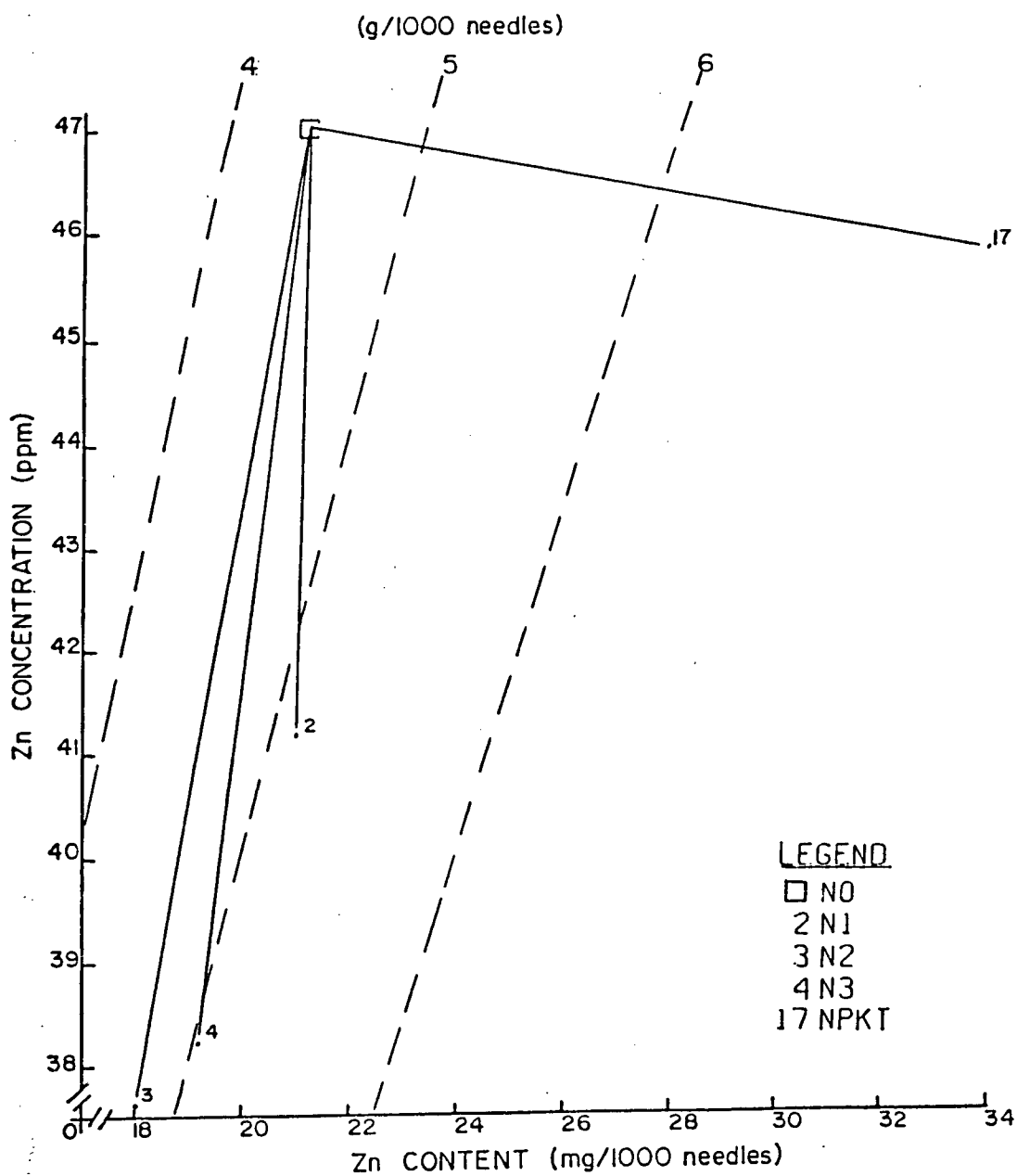


FIGURE 28. Relationship between foliar Zn concentration, content and dry-weight.

there is no evidence, in terms of growth or visual symptoms, to suggest a deficiency exists.

Active Fe, as opposed to total Fe, was considered in this study since Ballard (1981) suggested that it may be more valuable as a diagnostic indicator. It is the Fe that is theoretically active in the formation of chlorophyll (Oserkowsky, 1933). A concentration of less than 30 ppm active Fe is believed to indicate a probable Fe deficiency for several species (Ballard and Carter, 1983). This would suggest that the Sitka spruce in this study, with a mean Fe concentration of 6.1 ppm, was suffering from a severe Fe deficiency, even more so than N or P. However, this seems unlikely since vigorously growing spruce and hemlock in the HA-phase had comparable concentrations (Table 18) and yet showed no signs of deficiency. The limited foliar analysis done by Lewis (1982) found total Fe concentrations to range between 15 and 30 ppm for spruce which is also considered low and possibly deficient (Ballard and Carter, 1983). Thus there is the possibility that a moderate Fe deficiency may exist.

Numerous examples of antagonistic effects on foliar micro-nutrients following macro-nutrient fertilization have been observed (Smith, 1962; Olsen, 1972; Veijalainen, 1977). A limited analysis using foliage from the N only and the N plus P plots of the "phosphorus" trial was done to investigate any possible antagonistic effects. The only apparent antagonistic effects was a negative effect of N and P on Zn and P on B. In general it appears as if uptake of

TABLE 18. Comparison of foliar micro-nutrient concentrations with estimates from Literature. All values are in ppm.

NUTRIENT	LITERATURE VALUES								THIS STUDY			
	DOUGLAS-FIR		NORWAY SPRUCE		WESTERN HEMLOCK		SITKA SPRUCE		CH-PHASE SITKA SPRUCE		HA-PHASE SITKA WESTERN SPRUCE HEMLOCK	
	*ADEQUATE	DEFICIENT	ADEQUATE	DEFICIENT	ADEQUATE	DEFICIENT	ADEQUATE	DEFICIENT	CONTROL	FERTILIZED		
Cu	1.5 ² 4.2-5.9 ¹	1.1 2.4-3.9	0.7-4.2 ³ -	- -	3.9-4.1 ¹ -	- -	2.4 ² 7.0-10.8 ¹ 4.5-6.6 ¹	1.5 2.3-2.8	2.9	4.6	4.6	5.1
B	9-16 ¹	5	10-25 ³	6-8 ⁴	17 ¹	5	17-28 ¹	-	16.3	16.7	19.1	24.5
Fe (total)	39-51 ¹	-	-	-	35-59 ¹	-	-	-	15-30 ⁵	-	15-61 ⁵	46-92 ⁵
Fe (active)	-	-	-	-	-	-	-	-	6.1	6.9	5.7	7.3
Mn	390-1294 ¹	-	300-2300 ¹	-	1583-1876 ¹	-	1598-2043 ¹	-	1355	1439	1374	1663
Zn	-	-	-	-	-	-	42-57 ¹	-	47	46	41	28

* Adequate represents concentrations found in trees exhibiting good growth.

- Sources: 1. Stone, 1967.
 2. Binns et al., 1980.
 3. Braekke, 1979.
 4. Silfverberg, 1980.
 5. Lewis, 1982.

Cu, Mn and B were all enhanced by N fertilization (Figures 25 to 27).

SUMMARY AND CONCLUSIONS

Fertilization significantly increased first-year leader growth, current year needle dry-weight and needle nutrient composition. There were a number of highly significant interactions, usually N x P, which influenced the above responses.

Although N alone or in combination with K had a positive effect on both needle weight and leader growth, the addition of P had a strong synergistic effect when applied with N and resulted in a 27% and 41% increase in leader growth and needle weight, respectively, over that of N alone. Similar, although somewhat greater response patterns were noted for hemlock.

Fertilization with N resulted in a dramatic increase in foliar N concentrations, well in excess of the optimum for spruce. As a result, there tended to be a progressive decline in response with increasing rates of N application. N also had a strong antagonistic effect on K concentrations to the extent that a severe K deficiency was induced in all plots receiving N whether K was added or not. A similar effect was not noted for P, Ca or Mg.

Although the design did not adequately test all nutrients, the methods used were useful in interpreting foliar analysis and identifying potentially limiting

nutrients and responsive treatments. Based on the interpretation of the results, the following conclusions can be drawn:

- (1) N and P are severely deficient in both spruce and hemlock and are partly restricting growth. Cedar, while having sufficient P, appears to have a moderate N deficiency.
- (2) K is presently moderately deficient in spruce, but, a severe N-induced K deficiency is likely if an N fertilization program is undertaken without additional K.
- (3) Of other nutrients tested, S, Cu and Fe remain questionable as to their adequacy. Further testing is required, particularly with respect to S; it is the only element of the three where large differences in foliar concentrations between the two phases were noted. In addition to these three elements however, further testing of K and different types of N fertilizers should also be considered.
- (4) Changes in needle weight and first-year leader growth responses suggest that both spruce and hemlock will be highly responsive to N and P fertilization. Although some response to N alone is possible, additional growth benefits from P suggest that economical gains can only be obtained by N and P together. No benefits were apparent from K, but the induced deficiency may have a negative impact in subsequent years. Since no growth estimate for cedar were determined, it is unknown how this species will respond, however, the positive changes in the foliar nutrient concentrations after fertilization suggest that it also will respond favourably to fertilization.
- (5) All five plantations responded similarly indicating that the results from this study will be applicable to other plantations established on the CH-phase.
- (6) Further fertilization trials are required to quantify responses and determine their economic viability. However, results of this study suggest that, under operational conditions, an initial fertilizer application of 200 kg N/ha, 75 kg P/ha and 125 kg K/ha appears to be optimum.

GENERAL CONCLUSIONS

The poor growth of Sitka spruce and western hemlock on the CH-phase of the salal-moss ecosystem association can be attributed to multiple nutrient deficiencies, and in particular, N and P. In addition, there was a possible S and K deficiency. Moreover, a severe K deficiency was also induced by N fertilization. Despite this N induced deficiency however, no apparent growth benefits from K fertilization were evident.

With the exception of mineralizable N, the dramatic difference in productivity between the two phases does not appear to be a reflection of differences in soil nutrient content. Even in the case of mineralizable N, relatively high amounts were released during the incubation of samples from the non-productive CH-phase.

The high amounts of N found in the incubated samples raises questions as to the validity of using mineralizable N as a measure of N availability on these sites. However, the fact that cedar had relatively high foliar N concentrations and exhibited good growth suggested an adequate supply of N was available. Most studies on N mineralization and its relationship to tree growth have used mineral soil when determining mineralization rates. On sites with thick organic accumulations, such as those found in the

CH-phase, further research is required into the relationships between N mineralization rates, N availability, and tree growth before the results from incubation studies on these sites can be interpreted with confidence.

In addition to differences in soil nutrients, other factors, such as a salal effect and/or differences in soil physical properties, must be considered as possible contributing agents to the decline of these plantations. Eradication of salal and amelioration of site conditions through scarification have been suggested as an alternative to fertilization for the management of these sites. However, the benefits derived from scarification may not last the entire rotation and subsequent fertilization with N may be necessary to maintain site productivity. In addition, scarification while increasing N availability on these sites, may have only a modest or even a negative influence on the availability of other nutrients. Improvement in the N nutrition without a corresponding improvement in the P nutrition may only compound the present P deficiency. Therefore, fertilization must be considered as an integral part of the overall management regime selected for these sites.

All the evidence of this study suggest that spruce, hemlock and in all likelihood, cedar, will be highly responsive to N and P fertilization. Despite the lack of response to K, any fertilization program undertaken on these sites should also include this element since a severe deficiency is readily induced by N.

At present, the methods used in this study only allow a qualitative estimate of the potential responsiveness of these plantations. In order to quantify the response and determine whether or not fertilization will be economically viable, conventional fertilizer trials must be established and their development followed. The results of this study however, have narrowed considerably, those treatments which should be considered in subsequent fertilizer trials. Moreover, it has been shown that the plantations of the CH-phase exhibit very similar response patterns, thus the results of this and other studies should be applicable to other plantations established on the CH-phase.

Not all of the objectives of this study have been met since some elements such as S and K, as well as, other sources and rates of N require further testing. In addition, more questions were raised than possibly were answered. While it has been shown that fertilization is a promising silvicultural management tool for plantations established on the CH-phase, more research is required, not only into the nutritional aspects of these potentially highly productive sites, but also into the processes responsible for their development.

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APPENDIX I

The analysis of variance and Student-Newman-Keuls' multiple range test of individual stands.

STAND - 1

SOURCE OF VARIATION:	TREATMENT EFFECTS						
	N	P	K	NP	NK	PK	NPK
DEGREES OF FREEDOM:	3	1	1	3	3	1	3
Needle Weight	**	**		*			
1983 Leader Growth	**	*		*			
Needle Concentration							
N	**				*		
P		**	**		*		**
K	**				**	**	
Ca							
Mg	*			*			**
Nutrient Content							
N	**	**					
P	**	**	*		*		
K	**	*	*				
Ca	**	**					
Mg	*	**					

* Significant at 0.05 level.

** Significant at 0.01 level.

STAND - 2

SOURCE OF VARIATION:	TREATMENT EFFECTS						
	N	P	K	NP	NK	PK	NPK
DEGREES OF FREEDOM:	3	1	1	3	3	1	3
Needle Weight	**	**		*			
1983 Leader Growth	**	**		**	*		
Needle Concentration							
N	**	**		*		*	*
P		**			*		
K	**	**	**	*	*		*
Ca							
Mg			**	**		**	
Nutrient Content							
N	**	**		*			
P		**					
K	**		**				
Ca	**	**					
Mg		**	**				*

* Significant at 0.05 level.

** Significant at 0.01 level.

STAND - 3

SOURCE OF VARIATION:	TREATMENT EFFECTS						
	N	P	K	NP	NK	PK	NPK
DEGREES OF FREEDOM:	3	1	1	3	3	1	3
Needle Weight	**	**		**			
1983 Leader Growth	**	**		**			
Needle Concentration							
N	**			**	*		
P		**			*		
K	**		**	*	**		
Ca	**				**		
Mg		**					
Nutrient Content							
N	**	**		**			
P	**	**			*		
K	**	**	**	*	**		*
Ca	**	**		*	**		
Mg	**	*		*			

* Significant at 0.05 level.

** Significant at 0.01 level.

STAND - 4

SOURCE OF VARIATION:	TREATMENT EFFECTS						
	N	P	K	NP	NK	PK	NPK
DEGREES OF FREEDOM:	3	1	1	3	3	1	3
Needle Weight	**	**					
1983 Leader Growth	**	**	**			*	
Needle Concentration							
N	**			**			
P		**		**			
K	**	*	**		**		**
Ca	*	*					
Mg							
Nutrient Content							
N	**	**					
P	**	**		*			
K	**	**	*	*	**		**
Ca	**	**					
Mg	**	**			*		

* Significant at 0.05 level.

** Significant at 0.01 level.

STAND - 5

SOURCE OF VARIATION:	TREATMENT EFFECTS						
	N	P	K	NP	NK	PK	NPK
DEGREES OF FREEDOM:	3	1	1	3	3	1	3
Needle Weight	**	**		**			
1983 Leader Growth	**	**		**	*		**
Needle Concentration							
N	**		**				
P	*	**		**			
K	**	**		**	**		**
Ca			**			**	**
Mg							
Nutrient Content							
N	**	**	*				
P	**	**					*
K	**	**			**	*	**
Ca	**	**	**	**		**	
Mg	**	**					

* Significant at 0.05 level.
 ** Significant at 0.01 level.

I. 1983 Leader Growth (cm).

STAND - 1		STAND - 2		STAND - 3		STAND - 4		STAND - 5	
NO	10.5	NOP	6.1	NOPK	8.1	NOK	7.4	NO	8.4
NOPK	10.6	NOK	8.6	NOP	9.3	NOP	9.7	NOP	8.7
NOP	11.2	N2K	9.1	N1	9.6	NOPK	10.7	NOPK	8.9
NOK	12.1	N3K	9.2	NOK	10.5	NO	11.6	NOK	11.2
N3	14.7	N3	9.3	N3	11.4	N1	12.2	N2K	11.4
N1	15.3	N2	9.4	N2	11.7	N3K	12.5	N1K	11.4
N2	15.3	N1K	9.6	N3K	11.8	N2K	12.7	N3K	12.1
N2K	15.3	NOPK	9.7	N2K	12.5	N1K	13.5	N1	12.2
N3K	16.3	NO	9.8	N1K	12.5	N3	15.3	N2	12.4
N2P	18.0	N1	11.2	N1	14.0	N3PK	16.5	N3	13.5
N1K	18.7	N1PK	12.8	N3PK	16.1	N2	16.8	N3P	14.9
NPKT	19.6	N2PK	13.8	N2P	16.1	N3P	19.2	N1PK	15.1
N2PK	21.1	N3P	13.8	N1P	16.2	N1PK	19.6	N2PK	15.3
N3PK	21.9	N3PK	14.1	NPKT	18.6	N2PK	20.1	N2P	16.7
N1P	22.6	N2P	14.7	N1PK	18.8	N2P	20.3	N3PK	18.8
N3P	23.0	N1P	18.2	N3P	19.4	NPKT	21.1	N1P	20.0
N2PK	23.2	NPKT	18.3	N2PK	19.6	N1P	21.2	NPKT	20.6

Treatments connected by the same line are not significantly different at $p=.01$.

II. Needle Weight (g/100 needles).

STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
NOP	.414	(.051)	N3K	.441	(.085)	NOPK	.465	(.107)	NOK	.347	(.058)	NOP	.362	(.141)
NO	.421	(.092)	N2	.448	(.090)	N3K	.485	(.089)	N1	.397	(.020)	NOPK	.414	(.056)
N3	.456	(.051)	N3	.450	(.088)	NOP	.487	(.115)	NO	.408	(.092)	NO	.439	(.061)
NOPK	.464	(.072)	NO	.474	(.025)	N2	.504	(.105)	NOPK	.413	(.109)	N3K	.439	(.094)
NOK	.478	(.062)	NOP	.476	(.096)	NO	.508	(.025)	NOP	.415	(.063)	N2	.481	(.076)
N2K	.485	(.120)	NOK	.479	(.085)	N1K	.518	(.088)	N2	.466	(.102)	N2K	.488	(.074)
N2	.498	(.130)	NOPK	.485	(.067)	NOK	.528	(.079)	N3K	.472	(.109)	N1K	.515	(.082)
N1K	.507	(.104)	N1K	.498	(.140)	N1	.539	(.121)	N1K	.494	(.088)	NOK	.517	(.088)
N3K	.521	(.154)	N2K	.515	(.104)	N3	.556	(.113)	N3PK	.507	(.139)	N3	.529	(.107)
N1	.540	(.091)	N1	.531	(.074)	N2K	.565	(.096)	N2K	.516	(.122)	N3P	.529	(.065)
N2P	.602	(.036)	N3PK	.588	(.065)	N1P	.653	(.077)	N3	.516	(.120)	N1	.543	(.112)
N3P	.616	(.112)	N3P	.591	(.141)	N2PK	.650	(.071)	N2P	.557	(.056)	N2PK	.605	(.085)
N3PK	.616	(.059)	N2PK	.629	(.091)	N2P	.654	(.112)	N3P	.571	(.116)	N2P	.606	(.072)
N1PK	.657	(.146)	N2P	.648	(.116)	N3PK	.668	(.075)	N2PK	.572	(.114)	N1P	.611	(.097)
N2PK	.681	(.213)	N1PK	.678	(.133)	N3P	.706	(.116)	N1P	.626	(.166)	N1PK	.617	(.093)
NPKT	.716	(.170)	N1P	.691	(.162)	N1PK	.728	(.114)	N1PK	.637	(.136)	NPKT	.663	(.108)
N1P	.775	(.198)	NPKT	.786	(.172)	NPKT	.877	(.169)	NPKT	.675	(.139)	N3PK	.698	(.113)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis ± 1 SD.

III. Nitrogen concentration (% oven-dry weight).

STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
NOK	0.78	(.101)	NO	0.84	(.134)	NOPK	0.74	(.112)	NO	0.64	(.108)	NO	0.81	(.096)
NO	0.78	(.075)	NOK	0.87	(.063)	NOP	0.77	(.082)	NOK	0.79	(.243)	NOK	0.84	(.106)
NOP	0.81	(.100)	NOPK	0.92	(.086)	NOK	0.83	(.087)	NOPK	0.86	(.198)	NOP	0.89	(.188)
NOPK	0.97	(.182)	NOP	1.00	(.184)	NO	0.87	(.058)	NOP	0.96	(.152)	NOPK	1.03	(.208)
N1	2.66	(.537)	N1	2.89	(.331)	N1P	2.60	(.374)	N1PK	3.28	(.424)	N1P	2.92	(.242)
N1P	2.68	(.477)	N1K	2.98	(.715)	N1PK	2.95	(.677)	NPKT	3.39	(.559)	N1	2.95	(.379)
N1K	2.89	(.506)	N1P	3.48	(.577)	NPKT	3.19	(.567)	N1P	3.50	(.444)	N1K	3.21	(.428)
NPKT	3.03	(.369)	NPKT	3.58	(.699)	N1	3.39	(.400)	N1K	3.62	(.630)	N1PK	3.35	(.670)
N1PK	3.25	(.787)	N2K	3.70	(.513)	N3K	3.43	(.807)	N1	3.68	(.446)	N2P	3.53	(.527)
N2K	3.41	(.623)	N1PK	3.73	(.236)	N2K	3.58	(.709)	N2K	4.05	(.303)	NPKT	3.84	(.596)
N2PK	3.53	(.580)	N3K	3.90	(.592)	N2	3.77	(.490)	N2PK	4.06	(.342)	N3	3.84	(.596)
N3K	3.55	(.544)	N2P	4.00	(.279)	N1K	3.87	(.508)	N2	4.26	(.215)	N2PK	3.86	(.545)
N2	3.66	(.902)	N3P	4.09	(.490)	N2PK	3.91	(.269)	N3K	4.30	(.286)	N2	3.95	(.576)
N3P	3.69	(.498)	N2	4.22	(.255)	N3P	3.96	(.504)	N3PK	4.39	(.297)	N2K	4.04	(.342)
N3PK	3.70	(.456)	N3PK	4.26	(.426)	N3	4.05	(.792)	N2P	4.43	(.314)	N3P	4.09	(.201)
N2P	3.96	(.410)	N2PK	4.49	(.319)	N3PK	4.12	(.499)	N3P	4.50	(.258)	N3PK	4.38	(.322)
N3	3.97	(.336)	N3	4.56	(.496)	N2P	4.46	(.515)	N3	4.55	(.437)	N3K	4.41	(.279)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis ± 1 SD.

IV. Phosphorus concentration (% oven-dry weight).

STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
N1	.10	(.014)	N2K	.09	(.016)	NO	.10	(.013)	NOK	.12	(.014)	NO	.10	(.023)
NO	.10	(.021)	NOK	.09	(.010)	N3K	.11	(.025)	NO	.13	(.021)	N1K	.11	(.016)
NOK	.10	(.026)	N1	.10	(.015)	N2K	.11	(.020)	N2	.13	(.014)	N1	.11	(.016)
N2K	.11	(.010)	N1K	.10	(.025)	N1	.12	(.021)	N1K	.13	(.018)	NOK	.11	(.021)
N2	.11	(.022)	NO	.11	(.014)	N1K	.12	(.018)	N1	.14	(.012)	N2K	.11	(.016)
N3	.11	(.006)	N2	.11	(.017)	NOK	.13	(.023)	N3K	.14	(.015)	N3K	.12	(.018)
N3K	.12	(.016)	N3K	.11	(.026)	N3	.13	(.036)	N2K	.14	(.021)	N3	.12	(.015)
N1K	.13	(.026)	N3	.11	(.022)	N2	.14	(.029)	N3	.14	(.021)	N2	.14	(.014)
NOP	.16	(.025)	N2PK	.17	(.015)	NPKT	.18	(.011)	N3PK	.18	(.013)	N2P	.17	(.019)
N3P	.17	(.016)	N1P	.17	(.020)	N1P	.19	(.016)	N2P	.19	(.026)	N1PK	.17	(.020)
N2PK	.17	(.017)	NPKT	.17	(.019)	N3PK	.20	(.014)	NPKT	.19	(.019)	NPKT	.18	(.010)
NPKT	.18	(.020)	N3P	.18	(.018)	N1PK	.20	(.028)	N2PK	.19	(.021)	N3P	.18	(.019)
N3PK	.18	(.015)	N3PK	.19	(.025)	N3P	.20	(.017)	N1PK	.20	(.016)	N1P	.18	(.024)
N1P	.18	(.017)	NOPK	.19	(.022)	NOP	.20	(.046)	N3P	.20	(.015)	N3PK	.18	(.018)
N2P	.18	(.018)	N1PK	.20	(.025)	N2P	.20	(.033)	NOP	.22	(.037)	N2PK	.19	(.016)
N1PK	.18	(.021)	N2P	.20	(.020)	N2PK	.20	(.020)	NOPK	.24	(.048)	NOPK	.21	(.044)
NOPK	.21	(.028)	NOP	.21	(.036)	NOPK	.23	(.046)				NOP	.23	(.032)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis \pm 1 SD.

V. Potassium concentration (% oven-dry weight).

STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
N2P	.30	(.064)	N2	.30	(.077)	N3P	.32	(.052)	N3	.27	(.038)	N3K	.27	(.054)
N3PK	.31	(.049)	N3PK	.31	(.053)	N2	.33	(.076)	N2K	.28	(.028)	N3P	.29	(.049)
N3P	.31	(.067)	N1P	.31	(.063)	N3PK	.34	(.055)	N1	.28	(.045)	N1K	.31	(.101)
N3K	.34	(.076)	N2P	.31	(.082)	N2P	.34	(.064)	N2	.29	(.048)	N3PK	.32	(.041)
N2	.36	(.065)	N2PK	.31	(.082)	N2PK	.35	(.051)	N3PK	.29	(.072)	N2K	.33	(.113)
N2PK	.38	(.107)	N3P	.35	(.054)	N1	.37	(.064)	N3K	.32	(.053)	N2P	.33	(.066)
N3	.39	(.064)	N3	.40	(.123)	N3	.40	(.051)	N2PK	.33	(.068)	N3	.34	(.073)
N1	.41	(.123)	N3K	.40	(.095)	N3K	.40	(.110)	N3P	.35	(.041)	N2	.37	(.063)
N1PK	.42	(.085)	N1	.41	(.054)	N1P	.41	(.063)	N2P	.36	(.051)	N2PK	.38	(.043)
N2K	.43	(.107)	N1PK	.43	(.063)	N2K	.42	(.099)	N1PK	.40	(.089)	N1P	.39	(.046)
N1P	.46	(.116)	N2K	.44	(.098)	NPKT	.45	(.042)	N1P	.41	(.072)	N1PK	.39	(.042)
N1K	.49	(.103)	N1K	.48	(.079)	NO	.47	(.046)	N1K	.43	(.077)	NPKT	.42	(.052)
NPKT	.53	(.037)	NPKT	.55	(.047)	N1K	.49	(.055)	NPKT	.47	(.061)	N1	.42	(.057)
NOP	.63	(.097)	NOP	.59	(.048)	N1PK	.53	(.139)	NOP	.52	(.020)	NO	.47	(.017)
NO	.64	(.094)	NO	.60	(.071)	NOP	.59	(.134)	NO	.68	(.183)	NOK	.75	(.079)
NOK	.75	(.149)	NOK	.67	(.102)	NOPK	.79	(.068)	NOK	.74	(.083)	NOP	.75	(.083)
NOPK	.84	(.058)	NOPK	.76	(.096)	NOK	.84	(.067)	NOPK	.91	(.098)	NOPK	.82	(.093)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis ± 1 SD.

VI. Calcium concentration (% oven-dry weight).

STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
N3P	.40	(.086)	NPKT	.34	(.078)	NOK	.45	(.081)	N3PK	.45	(.094)	NOP	.36	(.070)
N2PK	.41	(.141)	NOK	.44	(.071)	N3PK	.46	(.064)	N3	.46	(.106)	N2P	.37	(.073)
NOK	.43	(.099)	N2K	.44	(.070)	N2	.46	(.092)	NO	.47	(.084)	N3	.40	(.037)
N2	.44	(.069)	N3P	.46	(.065)	N3K	.47	(.059)	N2P	.48	(.120)	NO	.43	(.090)
N2P	.44	(.071)	NO	.46	(.069)	NOP	.48	(.041)	N2	.50	(.077)	N1P	.43	(.078)
N1	.44	(.093)	N1P	.46	(.082)	N1	.49	(.069)	NOK	.50	(.146)	N1K	.46	(.059)
N1K	.45	(.069)	N1	.47	(.062)	NPKT	.50	(.063)	N3P	.51	(.086)	N2	.50	(.106)
N3PK	.49	(.116)	NOPK	.48	(.082)	NO	.50	(.057)	N1K	.51	(.051)	N1	.51	(.106)
NO	.49	(.112)	N2PK	.48	(.092)	N3	.51	(.092)	N3K	.51	(.135)	N3P	.51	(.043)
N1P	.50	(.124)	N2P	.48	(.082)	N2PK	.51	(.058)	N1	.52	(.076)	NOK	.52	(.174)
NOP	.50	(.096)	N2	.49	(.061)	N3P	.52	(.117)	NOPK	.53	(.066)	N3K	.53	(.070)
N2K	.50	(.070)	N3PK	.49	(.083)	N1P	.53	(.062)	N2K	.54	(.127)	N3PK	.55	(.108)
N3K	.50	(.105)	N3	.49	(.075)	NOPK	.53	(.064)	NOP	.54	(.105)	N2PK	.56	(.127)
N1PK	.50	(.138)	N3K	.49	(.071)	N2P	.53	(.086)	NPKT	.55	(.037)	N2K	.56	(.132)
NOPK	.51	(.079)	NOP	.50	(.105)	N1PK	.61	(.093)	N1P	.57	(.111)	NPKT	.60	(.164)
N3	.51	(.073)	N1PK	.50	(.056)	N1K	.66	(.109)	N2PK	.59	(.079)	NOPK	.60	(.113)
NPKT	.58	(.069)	N1K	.51	(.101)				N1PK	.63	(.059)	N1PK	.62	(.086)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis ± 1 SD.

VII. Magnesium concentration (% oven-dry weight).

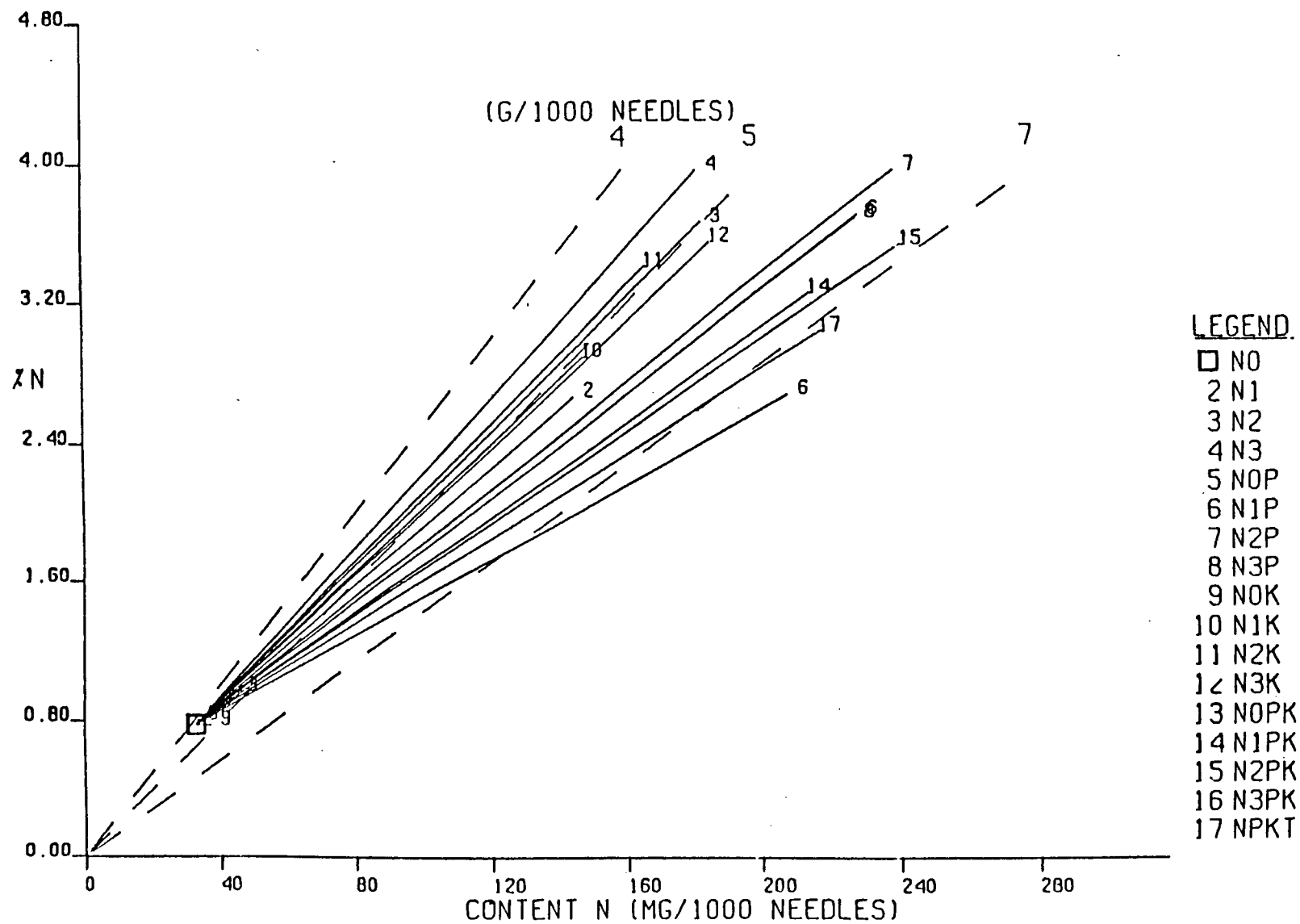
STAND - 1			STAND - 2			STAND - 3			STAND - 4			STAND - 5		
N2	.07	(.015)	N2K	.07	(.010)	N1P	.08	(.020)	N3K	.09	(.029)	N1K	.07	(.019)
N2PK	.07	(.017)	N3PK	.08	(.007)	NOPK	.09	(.008)	NOP	.09	(.019)	N3PK	.07	(.016)
N3P	.07	(.013)	NOK	.08	(.011)	NOK	.09	(.004)	N2K	.09	(.023)	NOK	.08	(.022)
N1K	.08	(.017)	N2PK	.08	(.004)	N3PK	.09	(.011)	N3PK	.10	(.020)	NO	.08	(.007)
N1PK	.08	(.019)	N3K	.09	(.011)	N3P	.09	(.011)	NO	.10	(.018)	N3K	.08	(.014)
N1	.08	(.016)	N1PK	.09	(.016)	N2PK	.09	(.008)	NOPK	.10	(.016)	N2PK	.08	(.032)
N1P	.08	(.022)	N1K	.09	(.011)	N1PK	.09	(.019)	N1PK	.10	(.016)	N1P	.09	(.015)
N3PK	.09	(.012)	N3P	.09	(.013)	N3K	.10	(.028)	N2P	.10	(.020)	N1K	.09	(.033)
NOK	.09	(.023)	NOPK	.10	(.012)	NPKT	.10	(.014)	N2PK	.10	(.028)	N3	.09	(.015)
NO	.09	(.016)	N1P	.10	(.022)	NOP	.10	(.009)	N1P	.10	(.027)	N2P	.09	(.014)
N2P	.09	(.021)	N1	.10	(.016)	N2P	.10	(.014)	N3P	.10	(.025)	NOPK	.09	(.013)
N2K	.09	(.017)	N2P	.11	(.020)	NO	.10	(.012)	N2	.11	(.026)	N3P	.09	(.013)
NOPK	.09	(.014)	NOP	.11	(.015)	N1K	.10	(.026)	NOK	.11	(.017)	NPKT	.09	(.015)
N3K	.09	(.014)	N2	.11	(.022)	N1	.10	(.013)	N1K	.11	(.020)	N1	.10	(.025)
NOP	.10	(.012)	NO	.11	(.009)	N2	.10	(.016)	N3	.11	(.029)	NOP	.10	(.013)
N3	.10	(.013)	NPKT	.11	(.017)	N3	.10	(.016)	N1	.11	(.022)	N2	.10	(.023)
NPKT	.11	(.010)	N3	.13	(.019)	N1K	.10	(.016)	NPKT	.13	(.011)	N1PK	.11	(.041)

Treatments connected by the same line are not significantly different at $p=.01$. Values in parenthesis ± 1 SD.

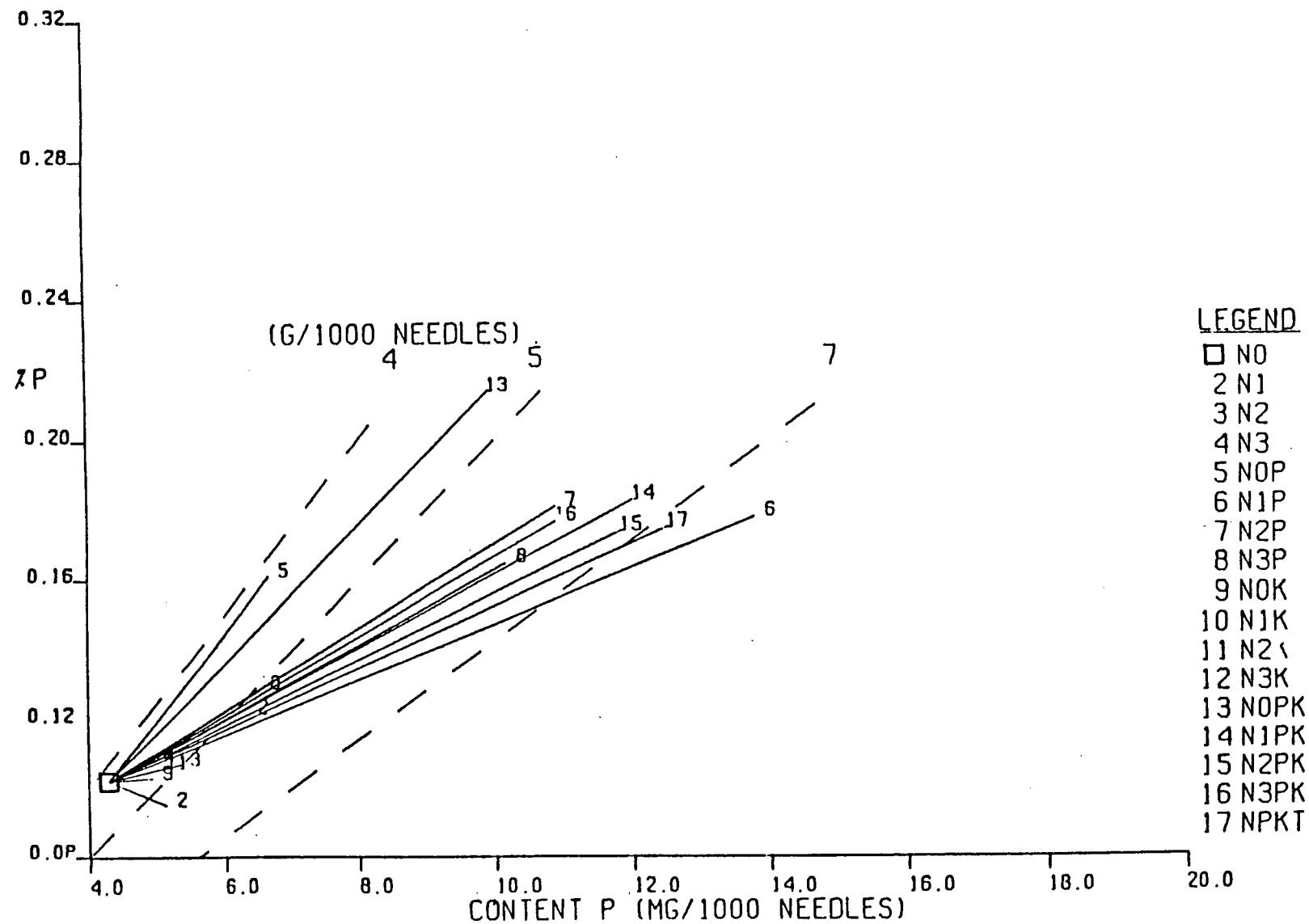
APPENDIX II

Effects of fertilization on needle nutrient composition and
needle weight for each stand.

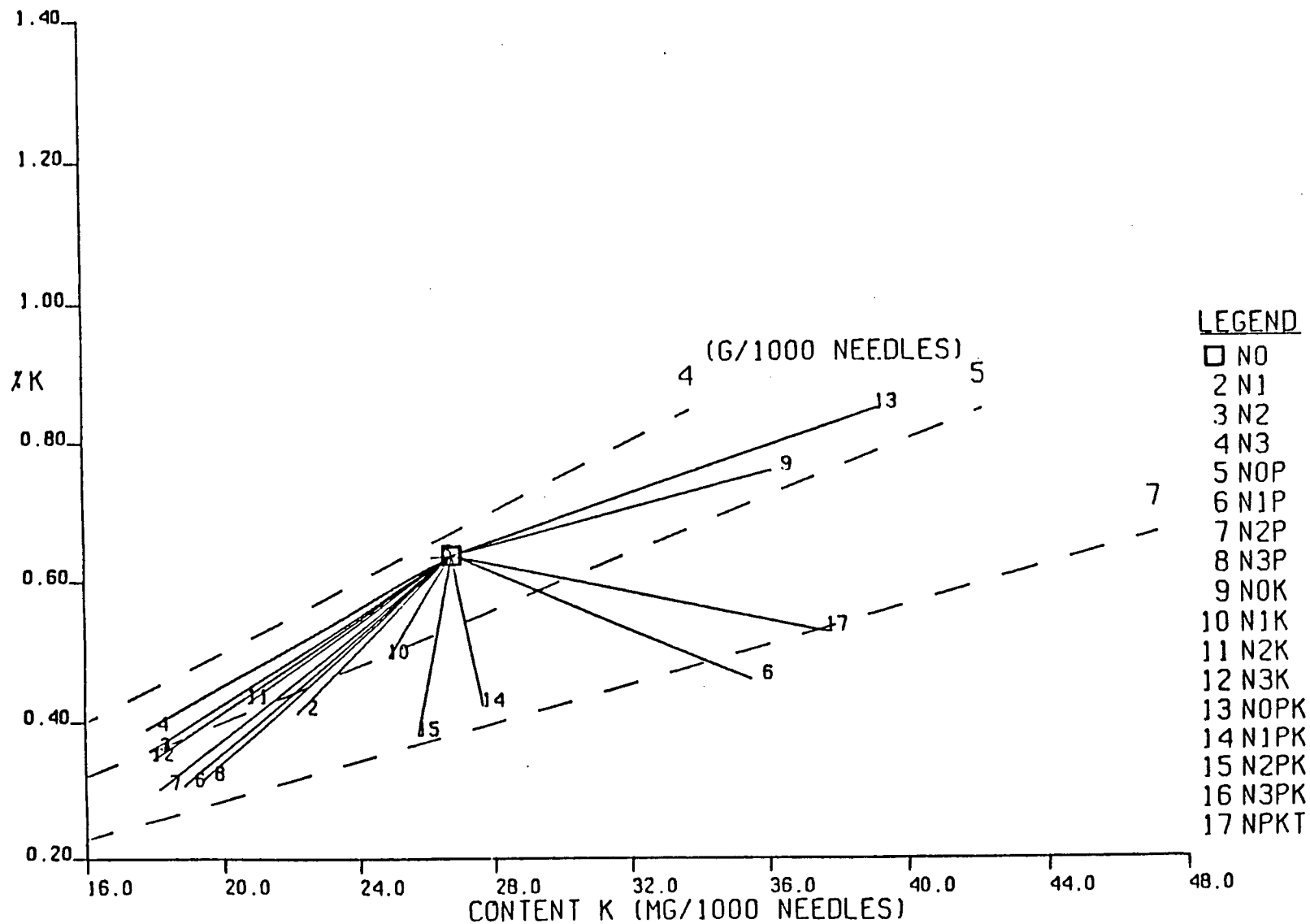
STAND 1



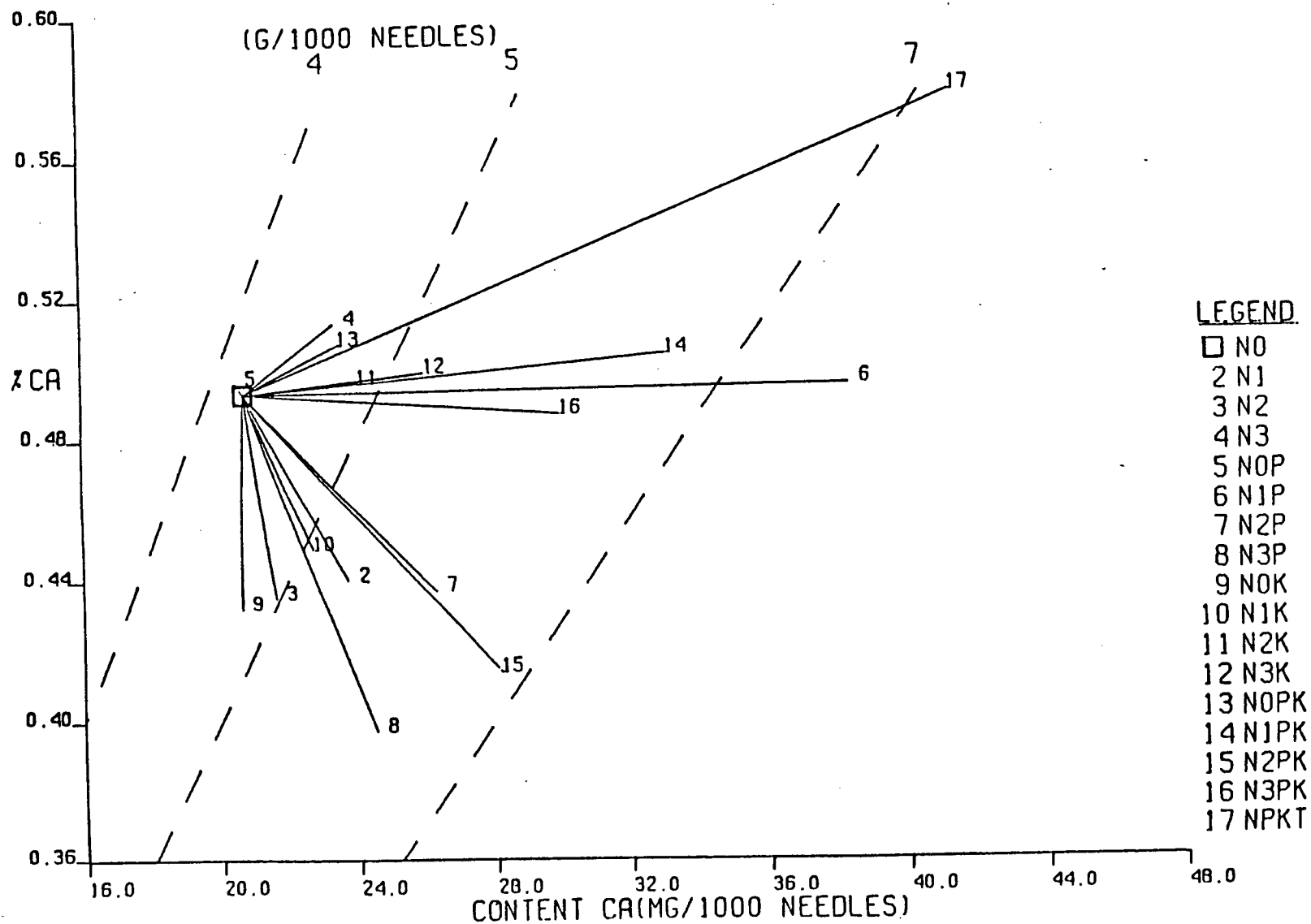
STAND 1



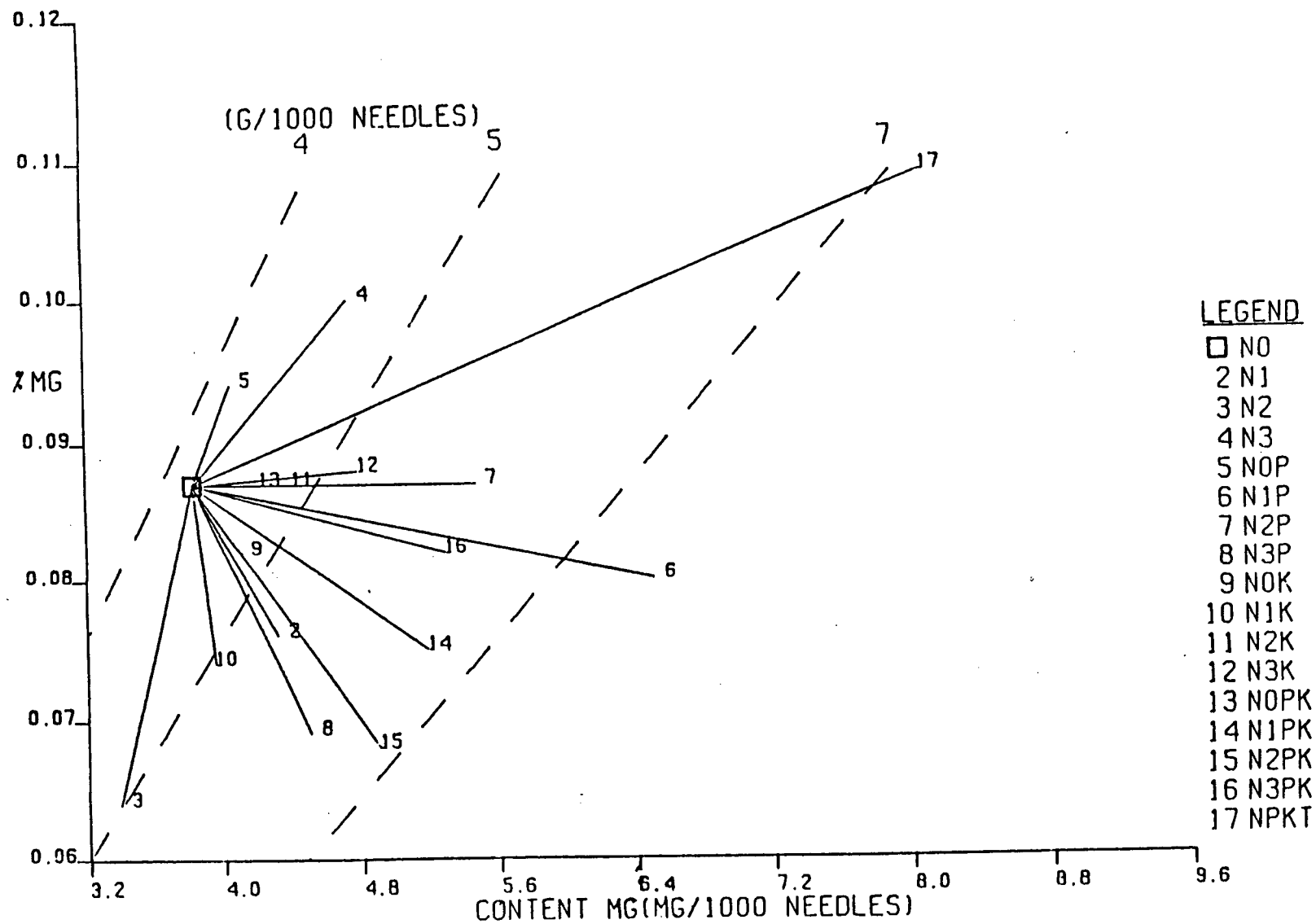
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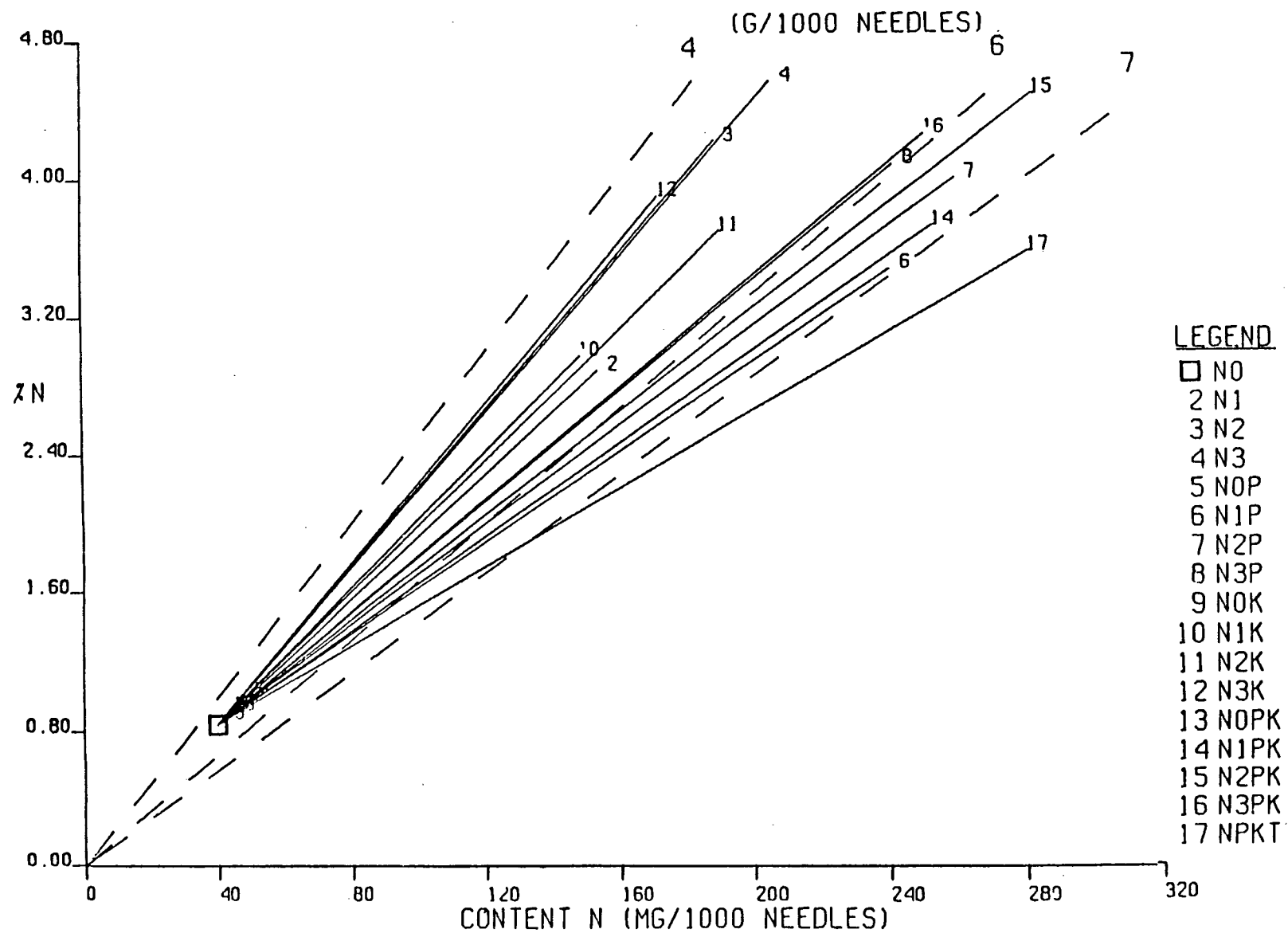
STAND 1



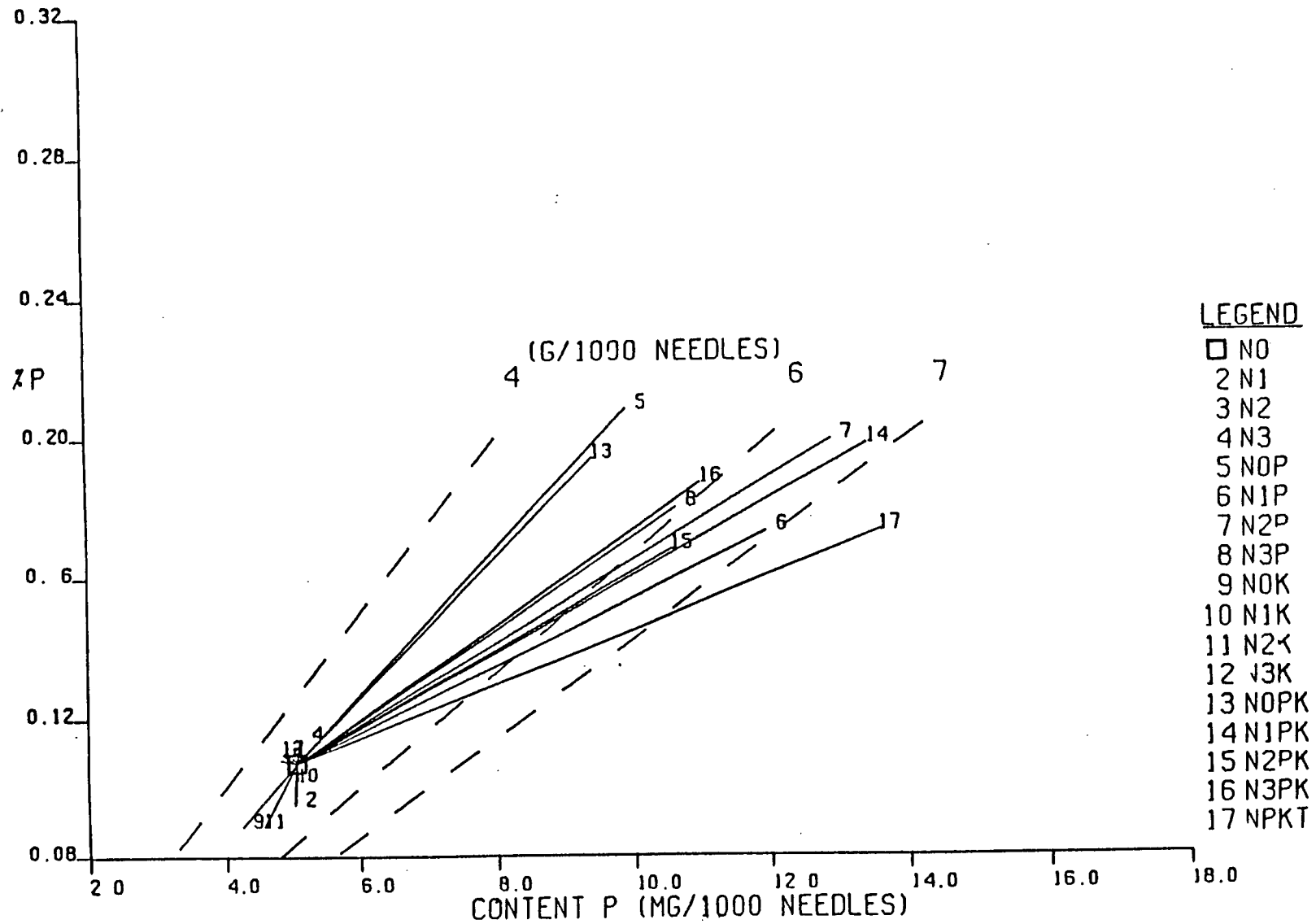
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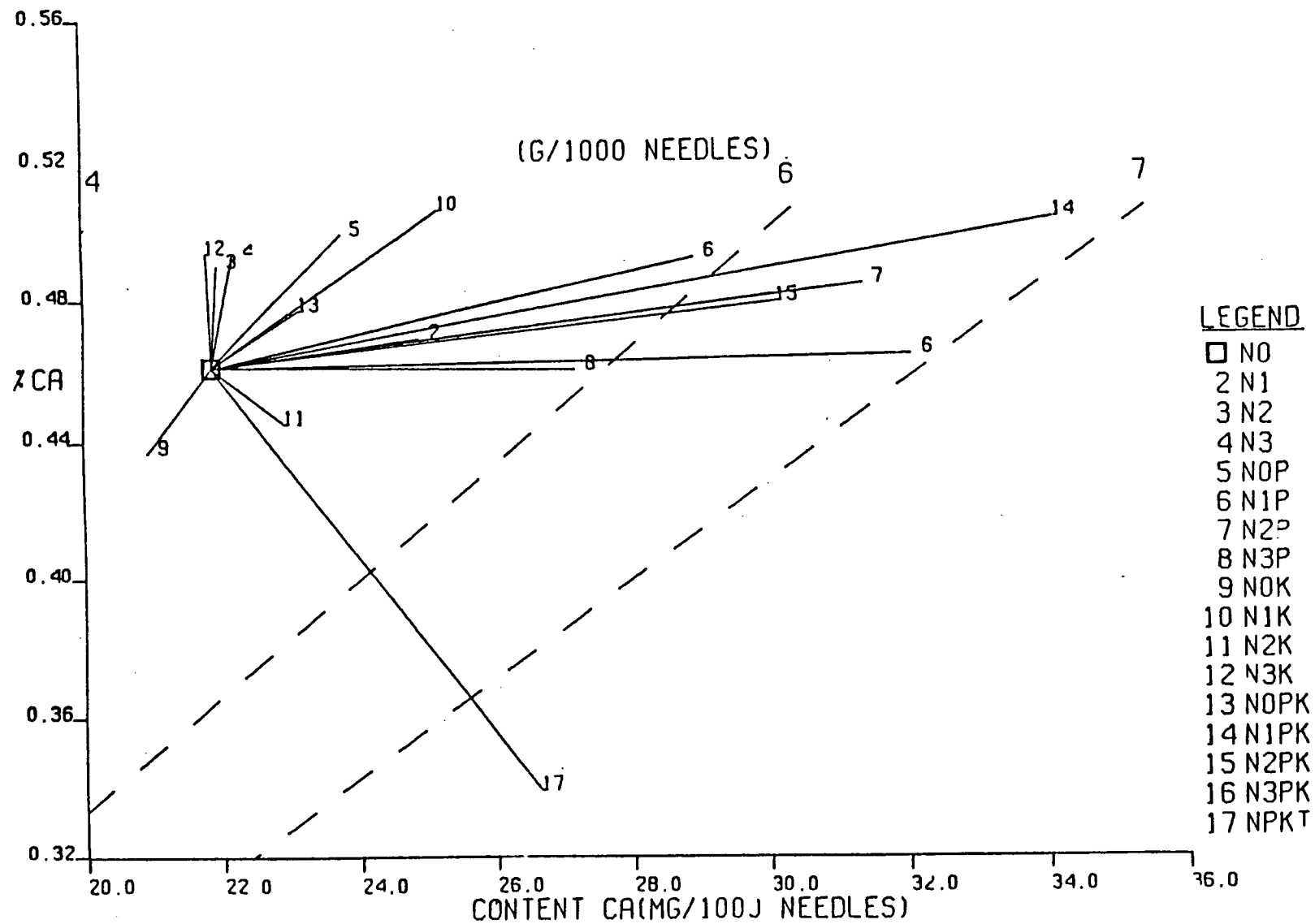
STAND 2



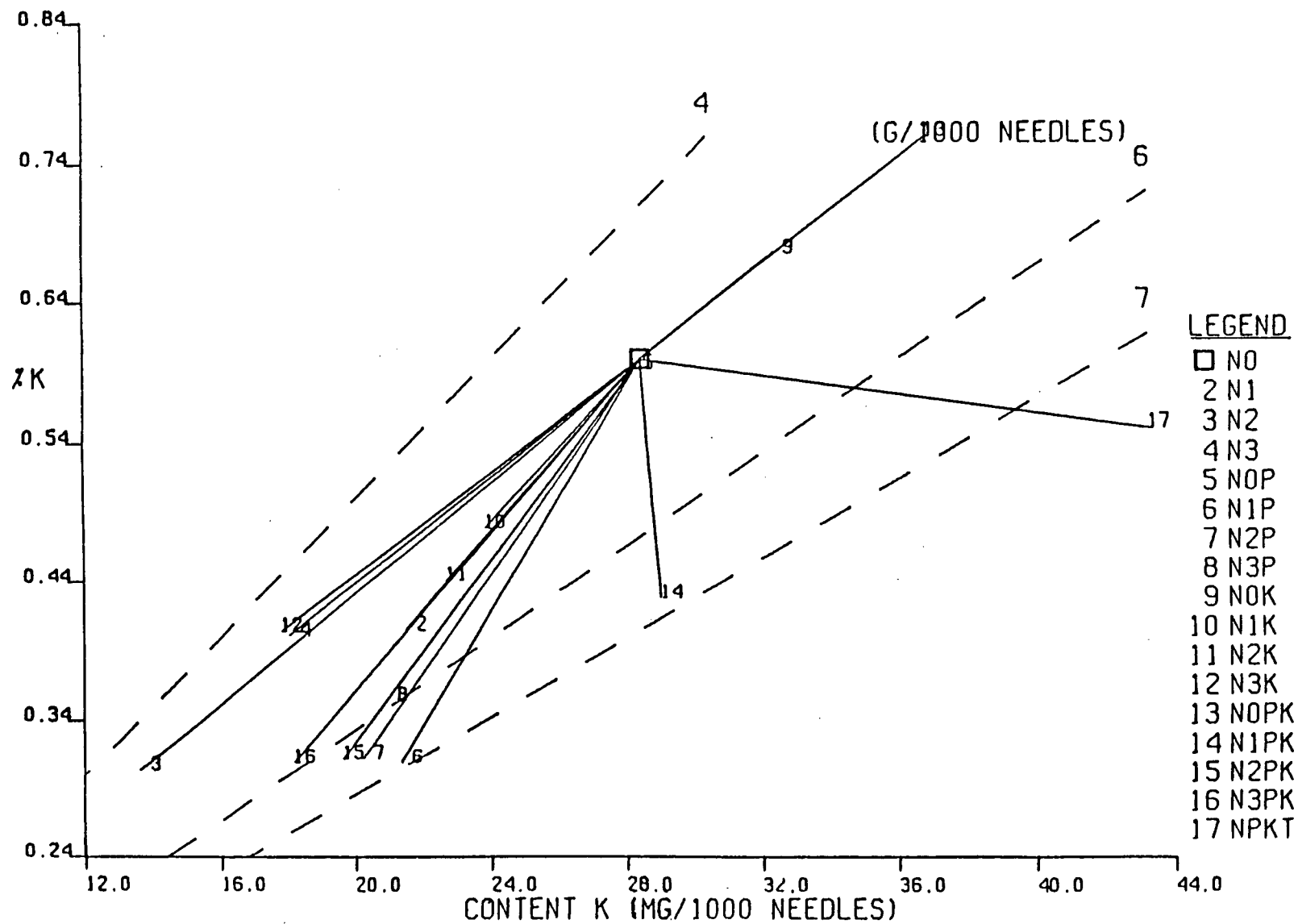
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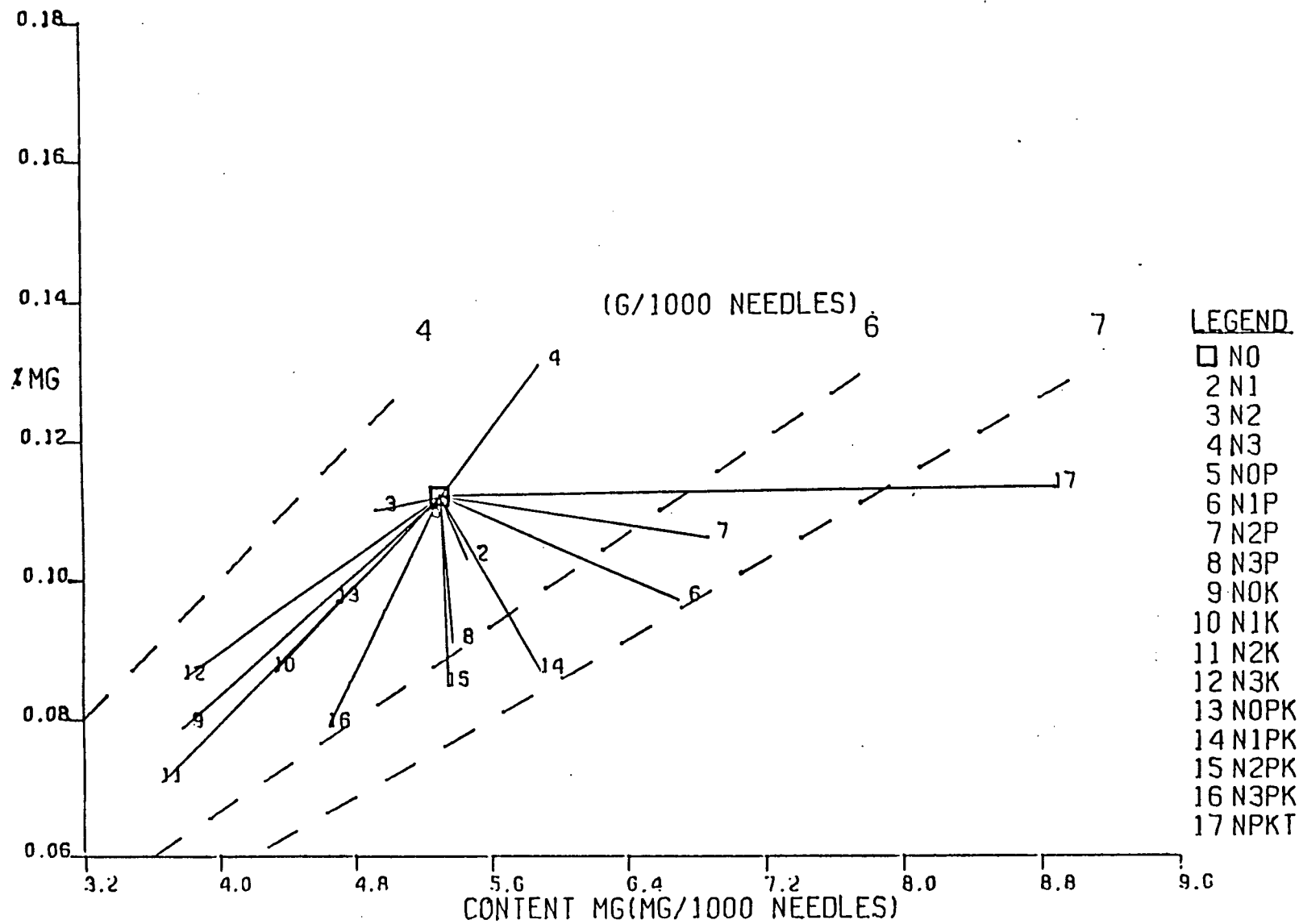
STAND 2



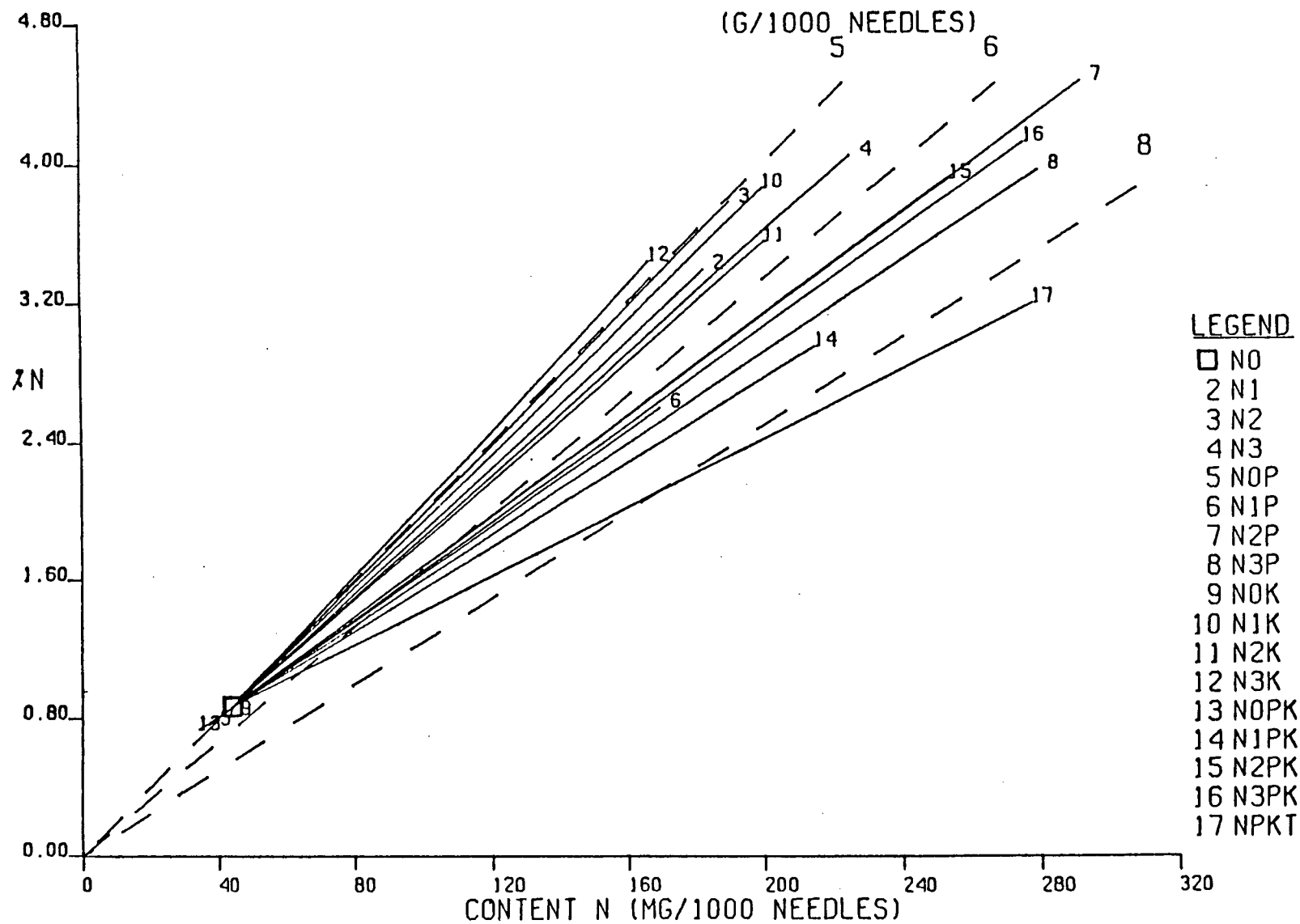
STAND 2



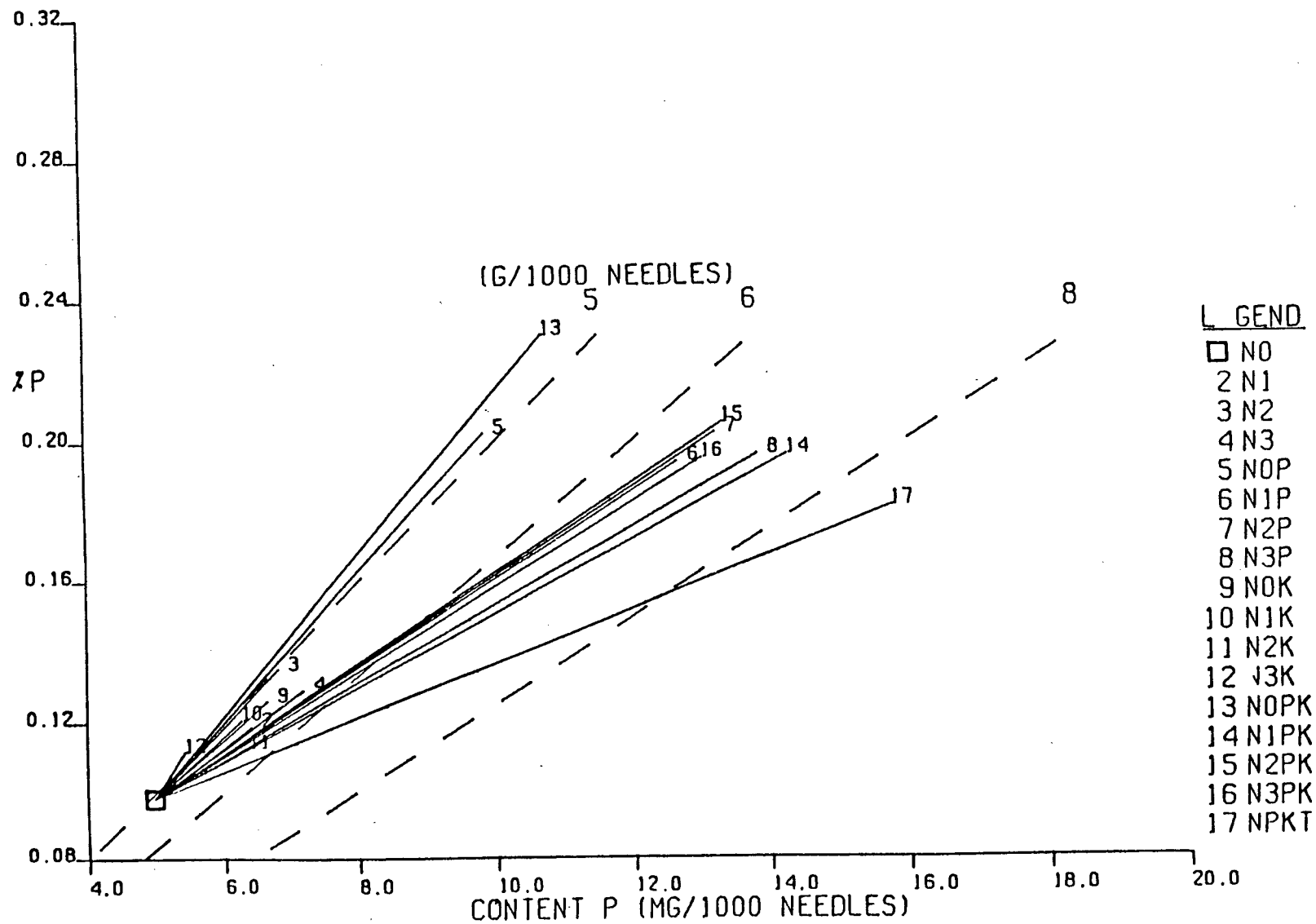
STAND 2



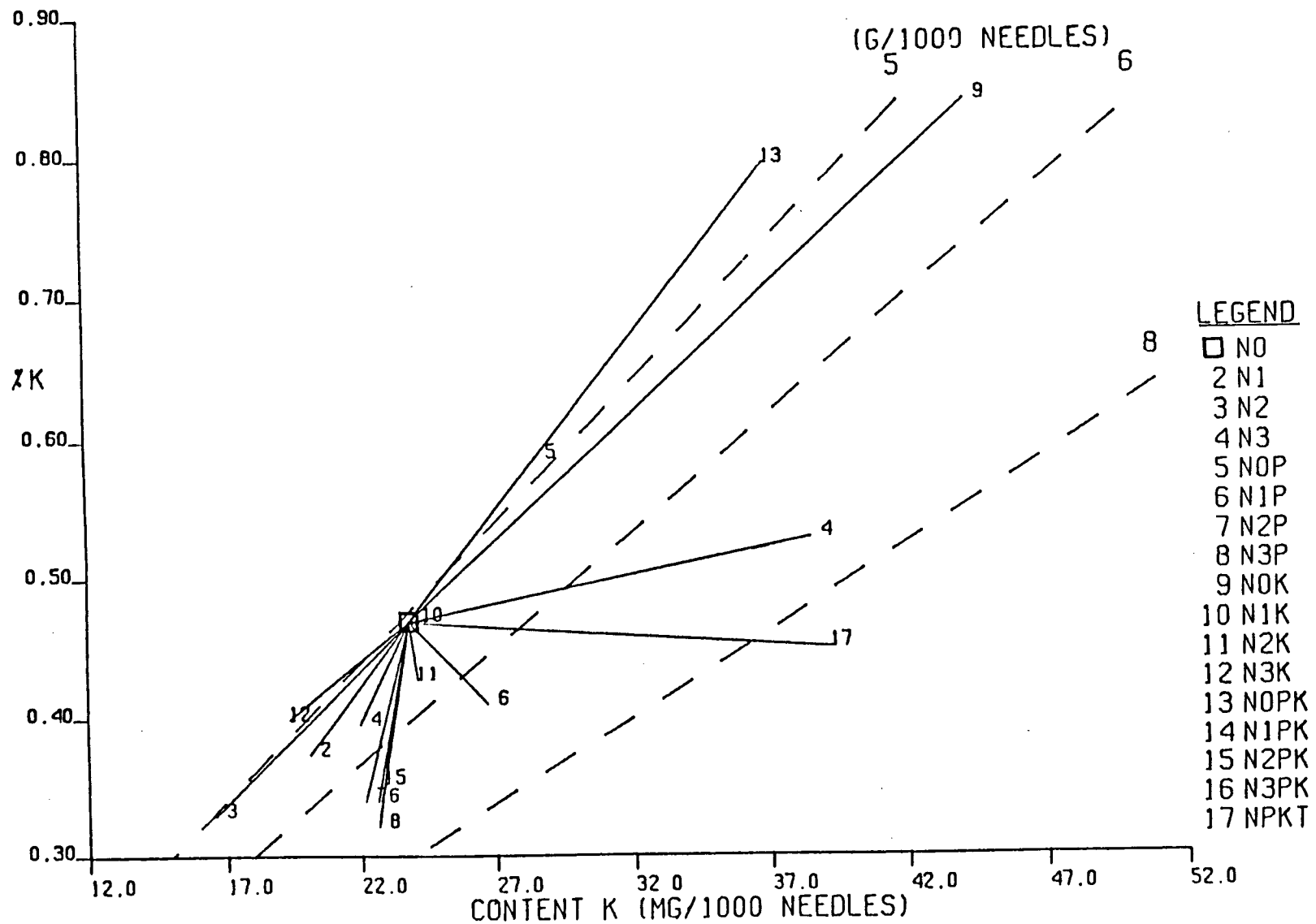
STAND 3



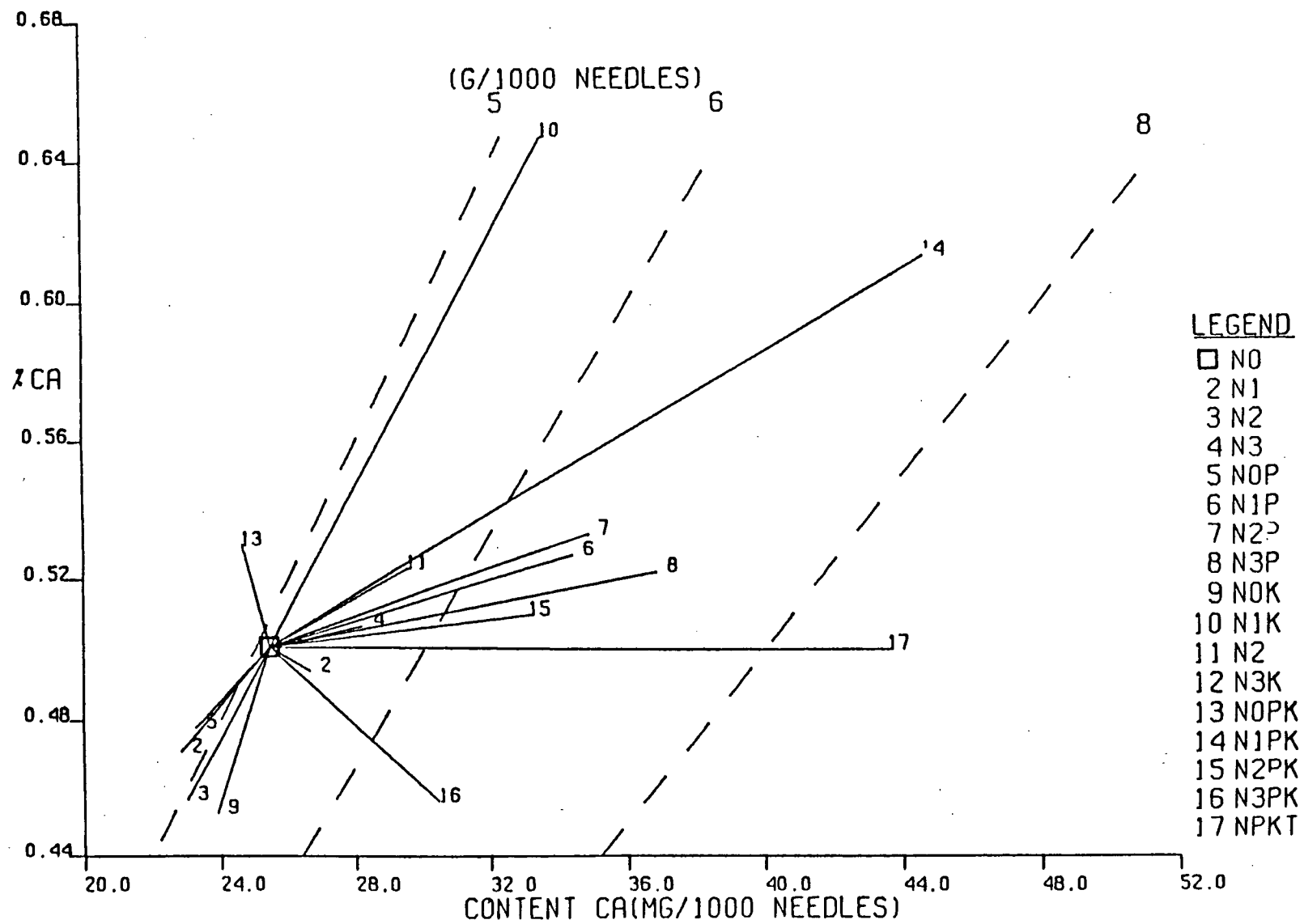
STAND 3



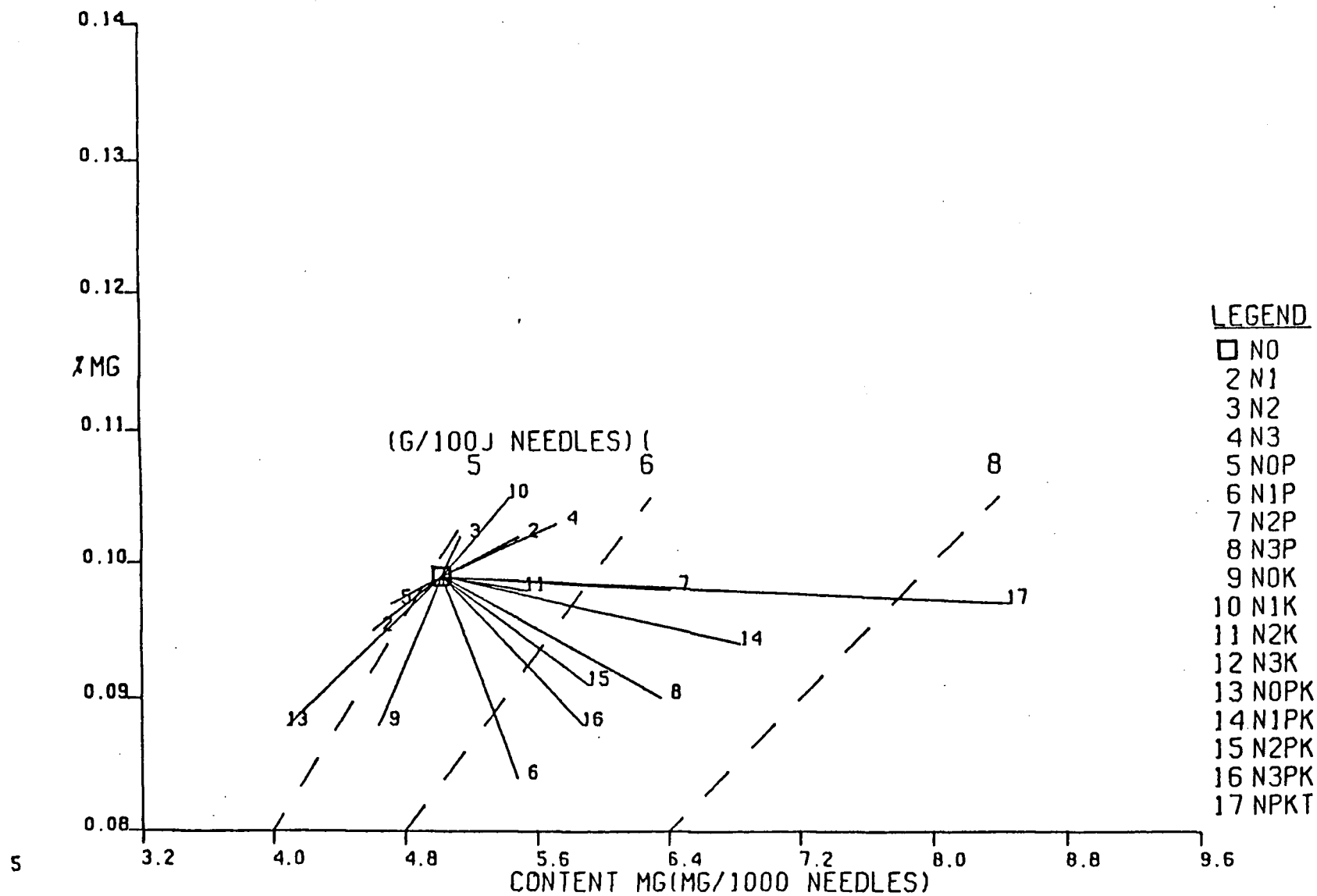
STAND 3



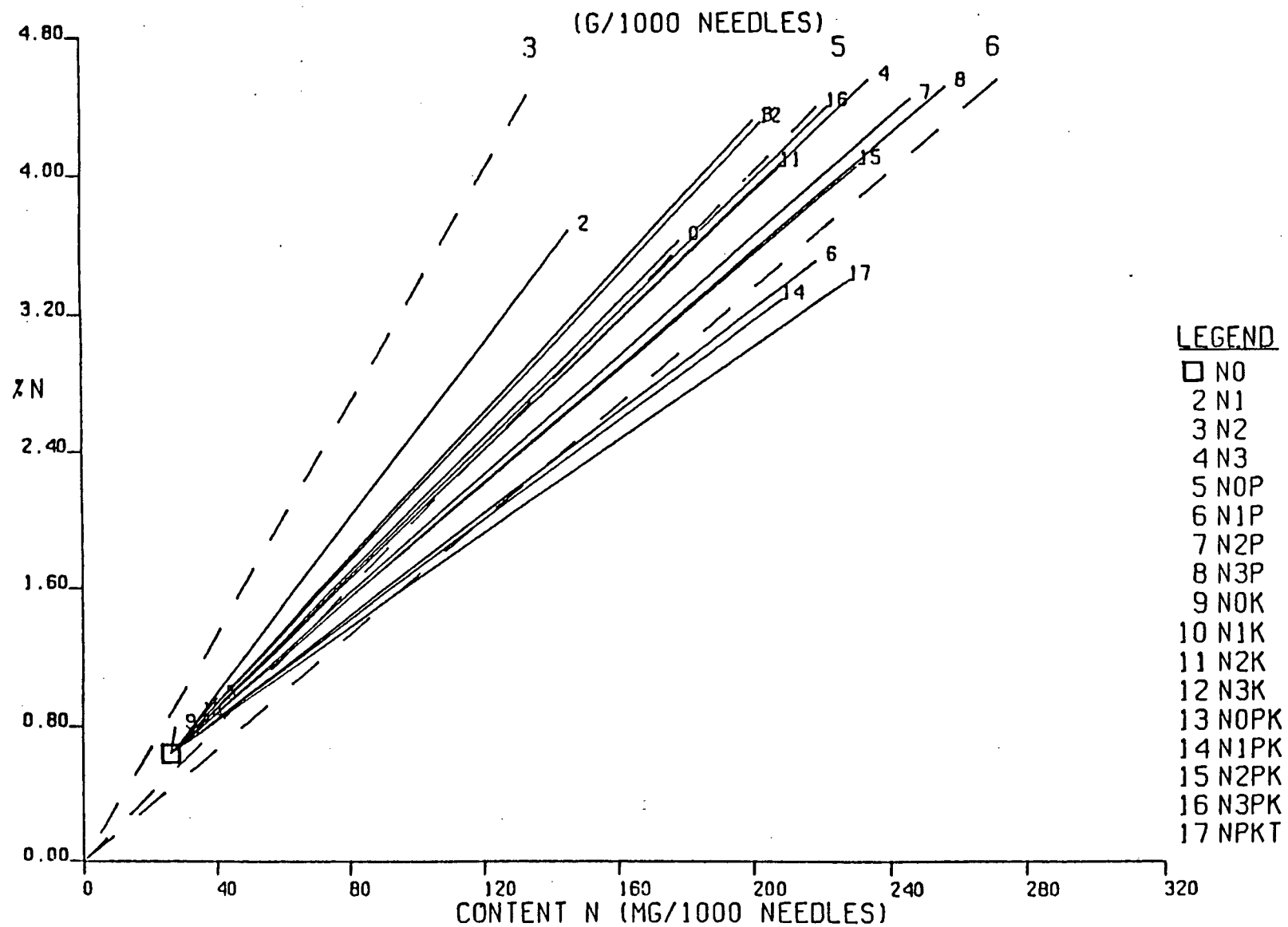
STAND 3



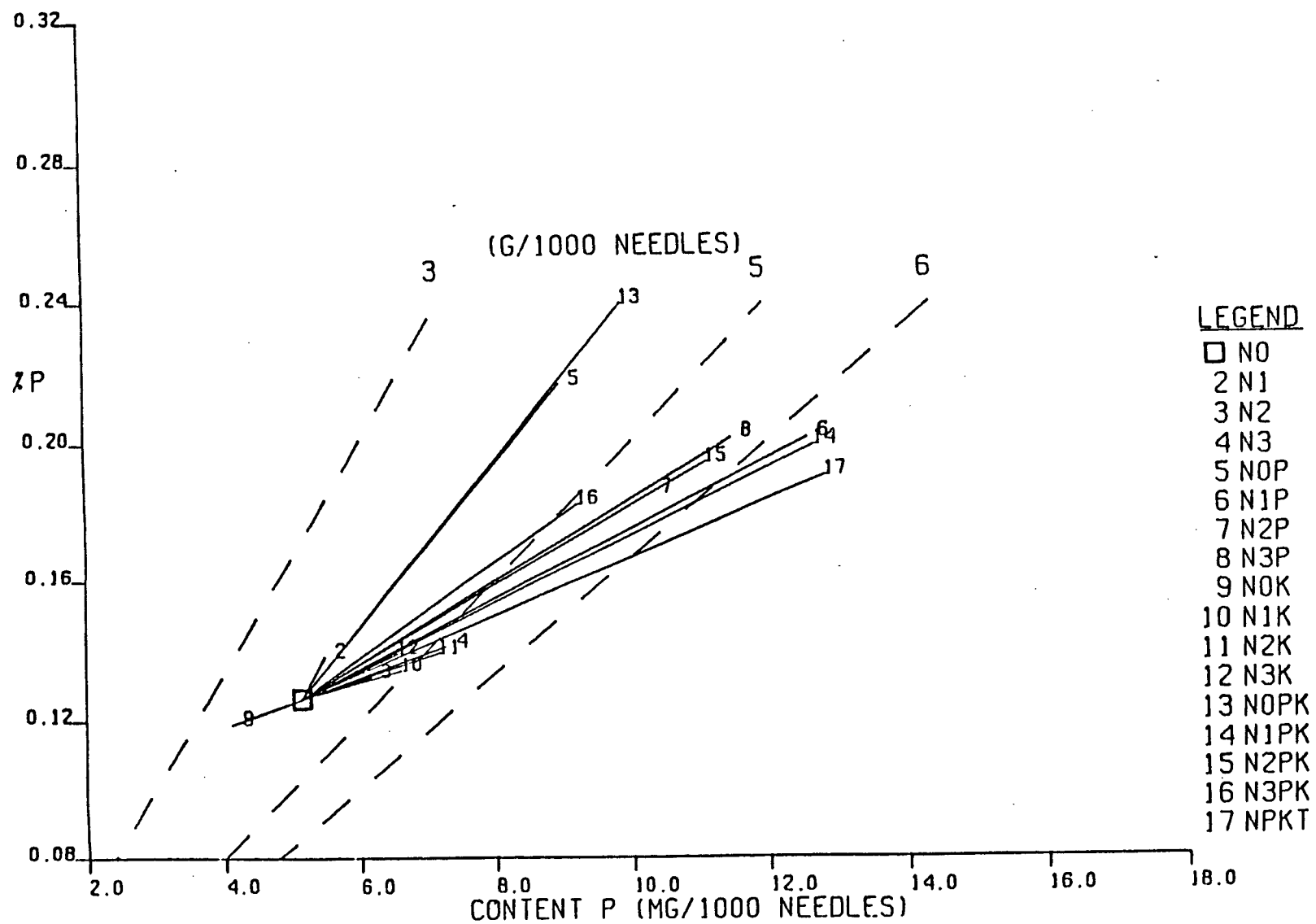
STAND 3



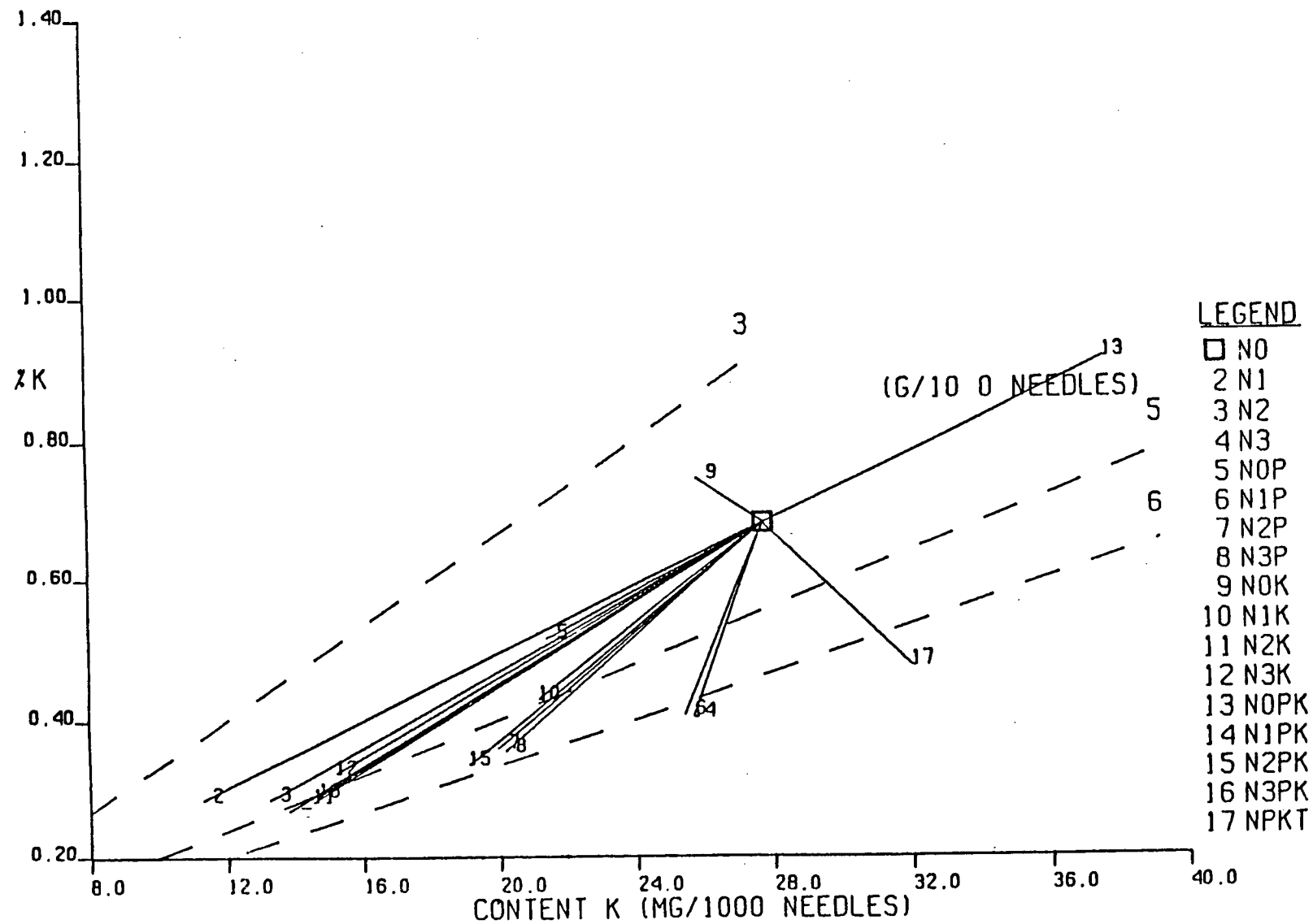
STAND 4



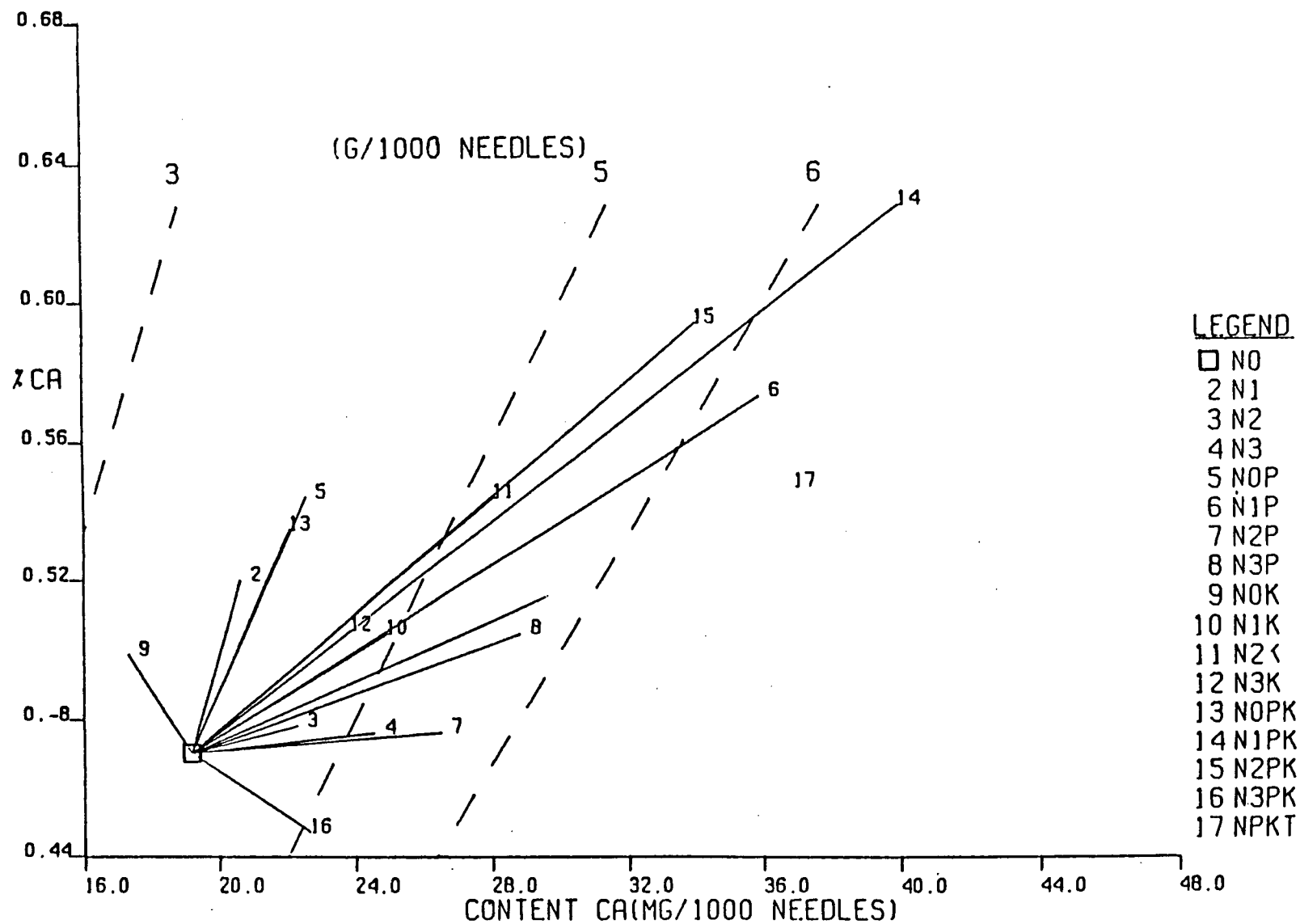
STAND 4



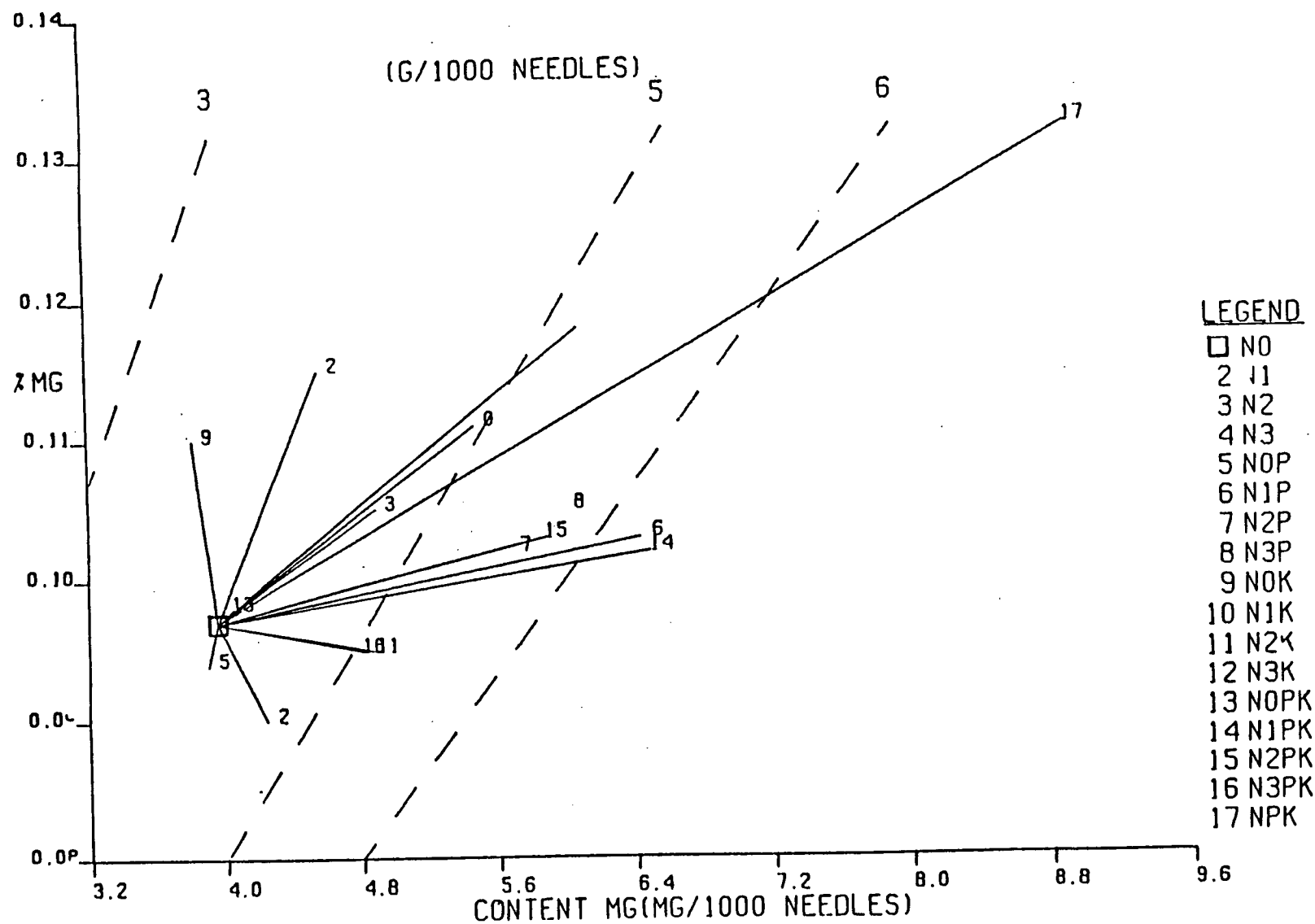
STAND 4



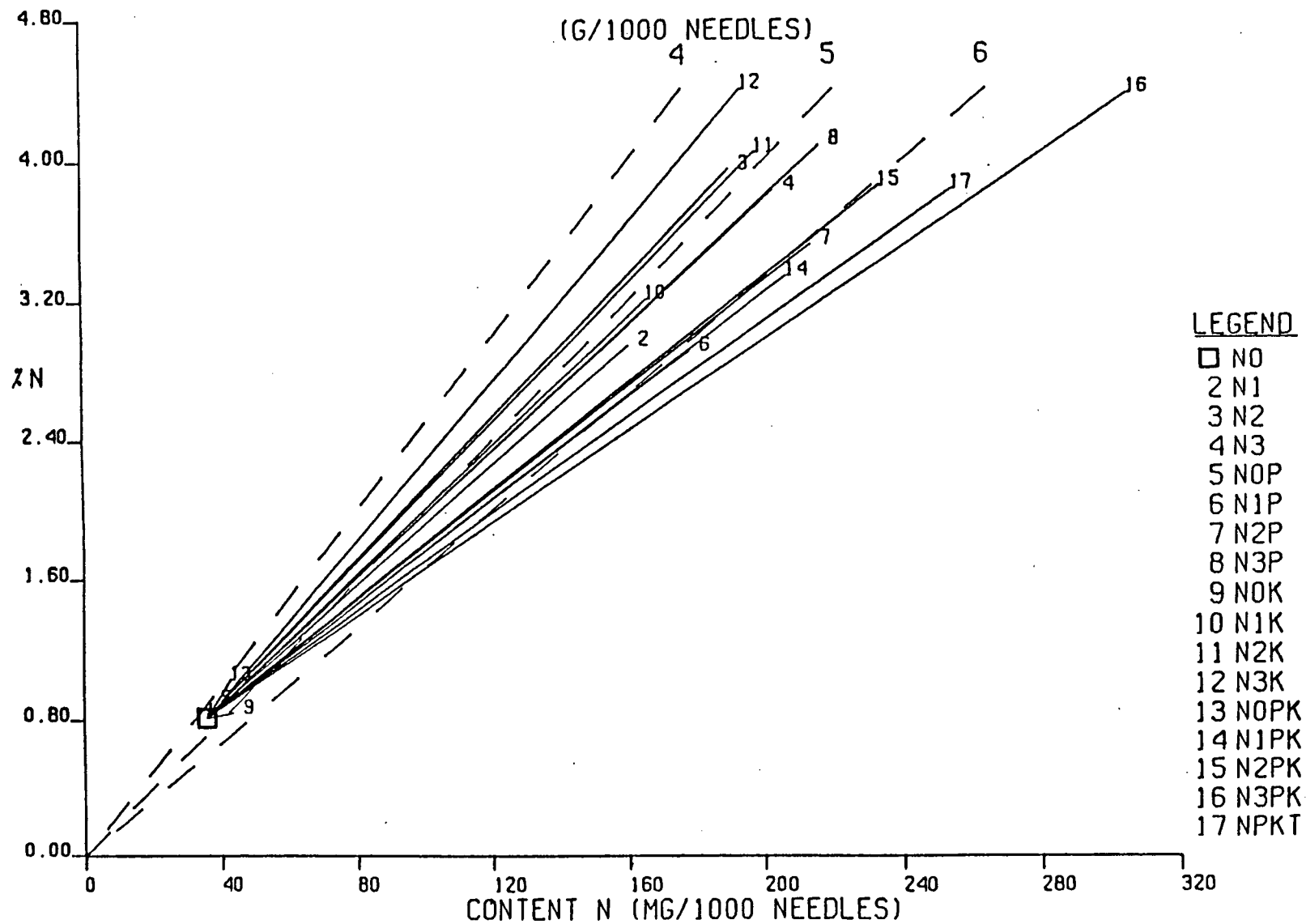
STAND 4



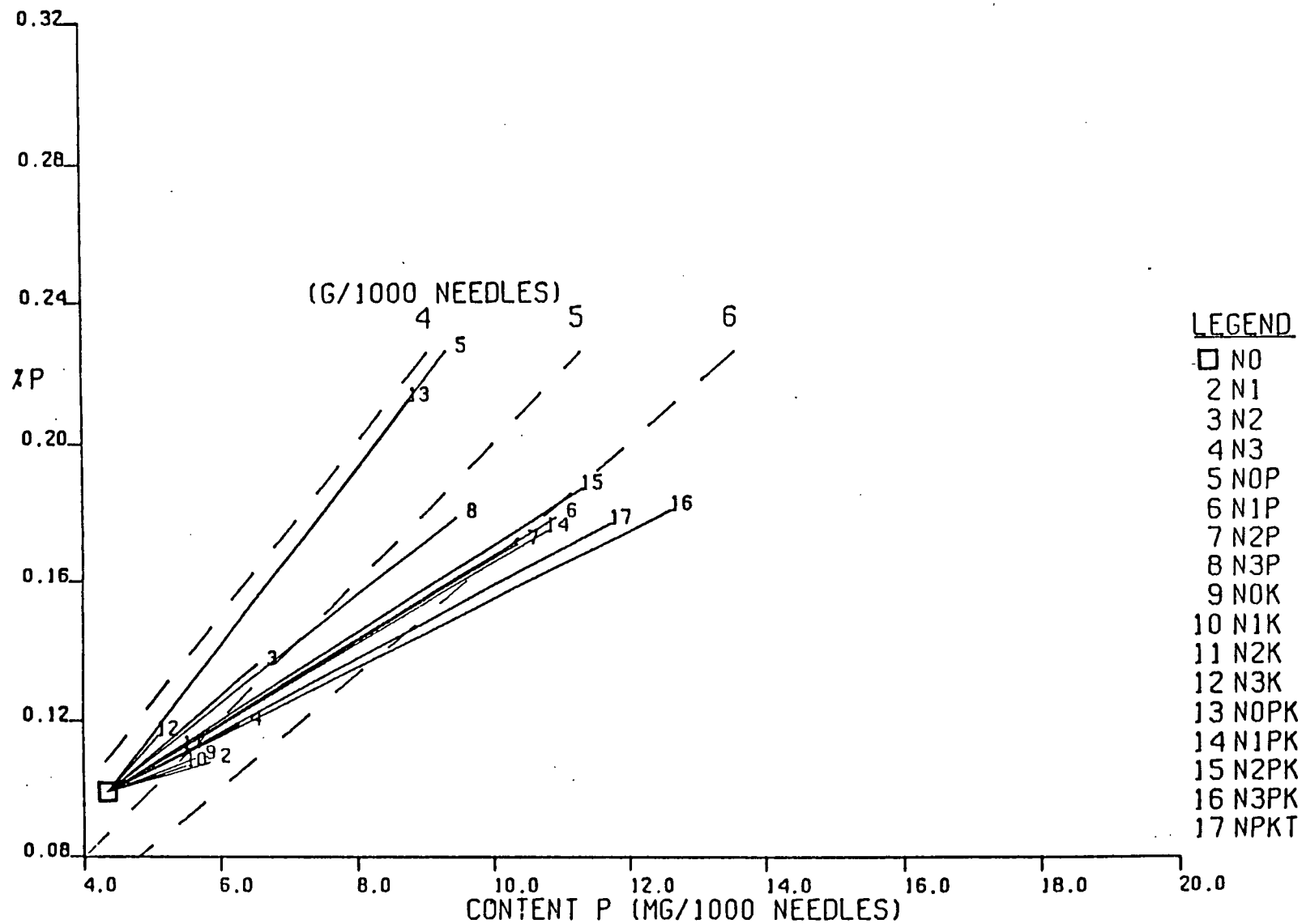
STAND 4



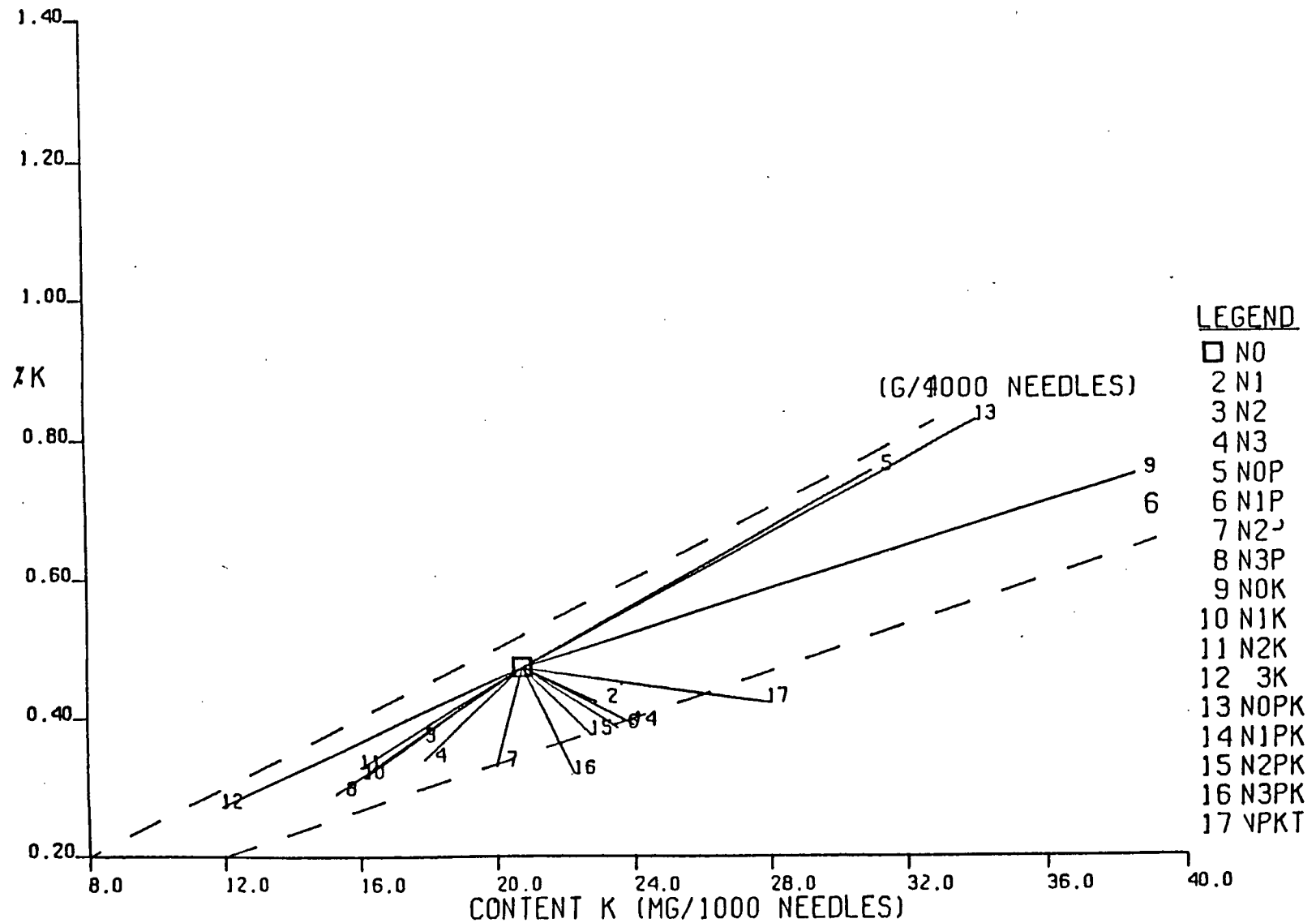
STAND 5



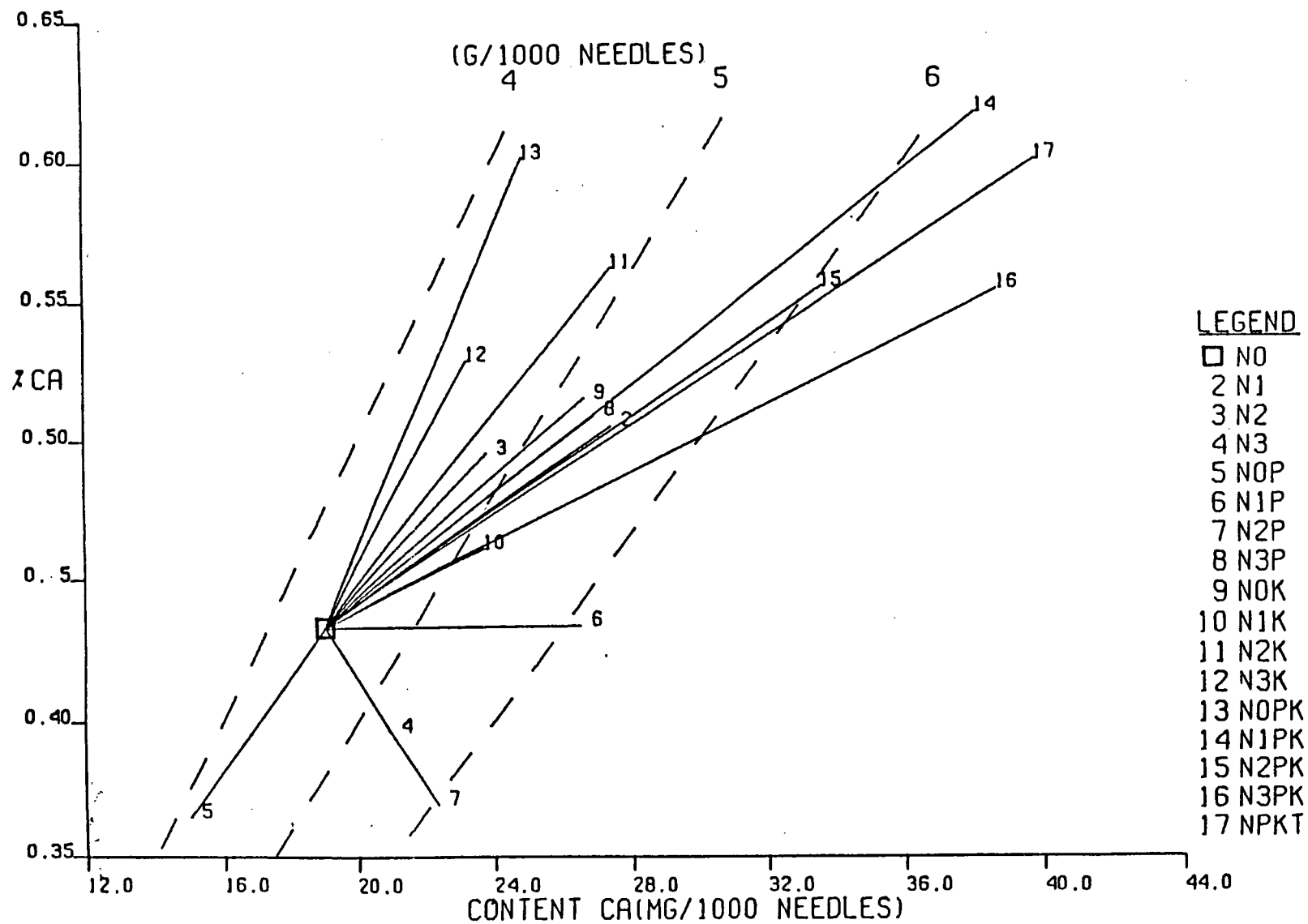
STAND 5



STAND 5



STAND 5



STAND 5

