

SOIL - NUTRIENT RELATIONSHIPS
OF TREE SPECIES COMPOSITION AND DOMINANCE
IN THE FIELD IRRADIATION GAMMA (FIG) AREA,
WHITESHELL NUCLEAR RESEARCH ESTABLISHMENT, PINAWA, MANITOBA.

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Presented to
the Faculty of Graduate Studies and Research
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In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Calvin James Webb
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ABSTRACT

Seven nutrient parameters, hydrogen ion activity, calcium, potassium, phosphate, ammonium, nitrate, and organic matter, were measured in soil samples taken from a transect within the Field Irradiator-Gamma (FIG) area of the Whiteshell Nuclear Research Establishment, Pinawa, Manitoba. The relationship between these nutrients and the tree species composition and dominance of the overlying forest was interpreted using graphs and multiple linear regression equations.

Four major vegetation associations were identified along the transect: 1) larch-black spruce, 2) black spruce, 3) balsam fir-black spruce, and 4) aspen. Most of the nutrient concentrations were highest in the soils of the first two communities, and lowest in the aspen association. The low concentrations in the latter were attributed to the early successional status of the vegetation and the sandy soil. Higher levels within the evergreen communities were probably due to the high cation exchange capacity of the peat soils and to base flow of nutrients. Concentration differences between the evergreen associations were believed to result from variations in the rate of decomposition of organic matter. Tree basal area appeared to be related to a cation complex consisting of organic matter, calcium, and to a lesser extent, potassium and ammonium. The prominence of these parameters, however, was dependent on the

successional status of the vegetation and the depth of the soil sample.

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CHAPTER I
INTRODUCTION

Canada's national wealth is very dependent upon forests and forest-based industries. In 1974 the value added--value of shipments less cost of materials and fuels--by the forest industry was 3,520,000,000 dollars (1974 Canada Year Book, 373). The rapidly increasing demand for timber products necessitates 1) increasing the land under forest management and 2) increasing forest productivity. Most harvested timber occurs on mineral soils, but necessity will probably force harvesting of trees in the marginally productive peatlands. In view of the extensive areas of peatland in Canada, 110 million hectares (Burke and O'Hare 1962, 647 as cited in Reader 1971, 2), knowledge on methods of increasing yield is important. One method which probably holds a good future for increasing yield in the forest industry is the application of chemical fertilizers. This approach can only be economical and effective after studies on the relationships between tree species composition and productivity of forests in relation to the nutrient status of the soil in unfertilized ecosystems have been conducted.

Mueller-Dombois (1964), Dammon (1971), Wali and Krajina (1973), and Page (1974) have documented forest-soil nutrient relationships in Canada, but in view of the extensive nature of the boreal forest (1972 Canada Year Book, 649) and the scarcity of relevant information, more study is necessary. This research was conducted as a pre-irradiation study of forest-nutrient relationships along the 200M cut line in the Field Irradiator-Gamma (FIG) area

of the Whiteshell Nuclear Research Establishment (WNRE)

The objectives of the research were:

1) to characterize differences in the concentrations of selected nutrients between organic and mineral soils along the transect,

2) to determine the relationship between the tree species composition along the transect and the upper 30 cm of soil, and

3) to describe and assess the relationship between the basal areas and the upper soil nutrient status along such a transect.

CHAPTER II

LITERATURE REVIEW

A. Introduction

Ecologists have always been "aware of important correlations between soils and vegetation" (Beals and Cope 1964, 777), but the study of plant-nutrient interactions is a relatively new endeavour. In most cases workers have found that other agents are relatively more important than mineral nutrition in determining the tree species composition and the growth rates of forests (Mitchell and Chandler 1939, 85). Failures to find plant-nutrient interactions in natural ecosystems (e.g. Mitchell, West, and Miller, 1966) may have resulted from the attention paid to moisture and sunlight, among others, at the expense of nutrients. This has retarded the understanding of nutrient circulation so that subsequent evaluation of nutrient levels in the plant's environment is difficult. Although methodological confusion in forest soil analysis (Gessel 1960, 224) may also account for some of the failure, the problem associated with soils analysis in the evaluation of plant-nutrient relationships is even more basic and is succinctly described by Wali and Krajina (1973, 298):

Soils analyses for all essential elements reflect only relative amounts of potentially available nutrients, often not correlated directly with plant response or species specificity. Whether these different levels of nutrients are available to plants in the final analysis is open to discussion.

The wide discrepancy between concentrations of nutrients commonly found in the soil and the lower levels at which toxicity occurs in culture solutions is evidence

that often the concentrations of nutrient extracted from the soil are not immediately available to the plant. Until a fraction that can be termed "plant available" is determined, progress in the study of plant-nutrient relationships in the ecosystem will be slow.

Nevertheless, valuable insights into the interaction between plants and nutrients have been defined and these suggest that correlations in the field can be found. By analyzing the nutrient concentrations within the plant Dijkshoon (1968, 201) concluded that minerals are needed in minimal amounts to permit plant growth and that the requirement is species specific; exclusion of plants from soils of relatively low nutrient concentration can, therefore, be expected. Mitchell (1939, 98) found that the correlation between internal nutrient concentration and the yield of white pine is true for other tree species also; since there is evidence that the internal concentration of nutrients is proportional to the nutrient-supplying capacity of the soil (Mitchell and Chandler 1939), a relationship between yield and extractable nutrients is likely.

Given the existence of such fundamental relationships between trees and soil nutrient levels, studies of their interaction may well bear on the generic aspects of ecology. For instance, differences in yields between species under varying and generally intermediate conditions of nutrient availability could result in overlapping bell-shaped species distribution curves as described by

Whittaker (1967). Principles of species diversity too (Whittaker 1965, 253) might be explained by differential growth responses under varying conditions of nutrient availability. The roughly asymptotic response of tree species with differing nutrient demands to the fertility levels of the soil (Mitchell and Chandler 1939, 65), suggests that the greatest number of species would be found at intermediate nutrient levels. Differences in yield between species are most pronounced at the extremes of the nutrient gradient; on relatively infertile soils because of differences in the extractive ability of the roots (Mitchell 1939, 105; Childers 1959, 54) and at higher levels because of differences in the optimum concentrations for each species (Mitchell and Chandler 1939, 65). Dominance by only a few tree species would be the logical result of the exaggerated differences in production under these conditions, thereby confirming the thesis of Monk (1967) and McNaughton and Wolf (1969) that species dominance is greatest at environmental extremes.

While most of the previous discussion has centered on interaction at the species level, relationships at the association level can also be expected. Page (1974, 229) observed that the availability of all nutrients (with the exceptions of sodium and phosphorus) that he studied was greatest under the hardwoods, and Rennie (1955, 59) calculated that hardwoods remove four times, and other species two times, the quantities of nitrogen, phosphorus

and potassium removed by pine. Only, however, by measuring the quantities of nutrients beneath each association and, perhaps more important, identifying the proportions of nutrients within each component of the ecosystem will ecologists be able to associate nutrient levels with vegetation associations, or vice versa.

What follows is a summary of the importance of seven soil variables on plant autecology, and a recapitulation of varied aspects of the relationship between vegetation type and the soil concentrations of each nutrient. Only seven parameters were selected for analysis because of the limited time and resources available. Moisture was not measured because the soils were saturated along most of the transect during sampling making measurement and analysis very difficult. Those selected are commonly tested in soils analysis laboratories and are quantitatively important to plant growth. Attention is centered on the more northerly forest ecosystems.

B. Soil pH

Although pH is commonly defined as the negative logarithm of hydrogen ion concentration, it actually "expresses the activity rather than the concentration of hydrogen or hydroxyl ions" (Wilde 1958, 212) and thus, is regarded as "simply a number read on a potentiometer....." (ibid. 213). The numerical aspect of a pH reading invites statistical tests of the correlation between pH and various vegetation attributes. Rarely, however, have these tests assumed significance (e.g. Loucks 1962, 150) because, except at the extremes of acidity or alkalinity (Wilde 1954, 89), the effects of pH on plant distribution and production are indirect (Gordon 1964, 182); Gordon (ibid.) found the lower limit to be the more ecologically significant extreme in natural stands of common ash, but the general applicability of this finding is unknown.

pH regulates plant-nutrient relationships in two ways. First, acid conditions reduce the life functions of bacteria and fungi which promote the decomposition of organic matter (Moizuk and Livingstone 1966, 949), thereby retarding the mineralization of nutrients. In contrast, alkaline conditions may either stimulate the activity of micro-organisms which compete with plants for available nutrients or increase the virility of fungi which attack tree roots, especially those of conifers (Wilde 1958, 216). The second method relates to the form and ultimately the quantity of nutrients available to the plant. One example

of this is that the effective hydroxyl concentration in the soil regulates the production of ammonia gas (du Plessis and Kroontje 1964). The greatest impact on nutrient availability, however, generally occurs at extremes of soil acidity. Phosphate is fixed as slowly soluble iron and aluminum phosphate in acid soils deficient in organic matter, and under alkaline conditions, phosphorus as calcium phosphate is also unavailable to plants (Wilde 1958, 231). Nitrogen and bases are also unavailable at low pH values (Wali and Krajina 1973, 302) and the availability of iron, boron, zinc, and manganese may decrease above pH 8.0 (Wilde 1958, 216). Harmful effects on plants at pH extremes may also result from toxic accumulations of elements; manganese accumulates to poisonous levels in soils of low pH and restricted aeration (Gotoh and Patrick 1972, 738), while compounds such as sodium carbonate may exist at toxic concentrations in alkaline soils (Wilde 1954, 89; Wilde 1958, 215).

Cases of serious harm caused by low or high pH levels are probably rare. Most plants can grow over a range of pH from 4 to 8 (Heinselman 1963, 329), but additional considerations such as the length of the growing season, the supply of total moisture available (Wilde 1954, 90; Wilde 1958, 214) and the concentrations of nutrients in the rooting medium (Wali and Krajina 1973, 302) ameliorate the strictness of these boundaries.

Despite the inability to set precise limits of pH to plant growth, soil acidity does have sociological

significance (Heinselman 1963, 342) which is best illustrated where sufficient time has elapsed for the plants to come to a relative state of equilibrium with their "total ecological requirements" (ibid 329). The soils beneath hardwoods are generally less acid than those under softwoods. This may be explained by differences in the nutrient requirements, or in the root patterns of the overlying vegetation. Challinor (1968, 288-289) accounted for higher pH values of the surface layers under red oak than those under three conifer species by the relatively high exchangeable calcium levels in the oak litter; alternatively, the shallow rooting systems of species such as spruce causes rapid recycling of calcium near the soil surface, so that the deeper soil beneath them may be slightly more acid than that from equivalent depths under other species (ibid. 289). Ovington (1953, 32) found little difference between species in the pH of fresh leaves of coniferous and hardwood species growing on alkaline soils, but on acid soils he found that the leaf pH of individual tree species varied from site to site and was closely related to the acidity of the underlying mineral soil (ibid.). Differences in pH levels between tree species of the same form also exist and may be attributed to differences in leaf acidity; Page (1974, 12), for instance, found that the pH at depths of 2.5 and 15 cm was higher under balsam fir than under black spruce.

Since correlations between pH, tree species, and vegetation types have been documented, it is logical to

expect changes coincident with ecosystem succession. Although Burgess, Johnson, and Keammerer (197, 78) found little difference in soil acidity along an age gradient, Page (1974, 24) observed such changes. For all soil and cover types the pH increased by about 0.5 units after clear cutting. The pH steadily decreased until minimum values were reached under stands 6.1 to 9.1 m high, then small increases were noticed in stands exceeding 9.1 m. The similarity in this pattern to the nutrient trends associated with succession that were described by Vitousek and Reiners (1975) suggests that the changes in pH are closely linked with the status of calcium in the soil.

To summarize the ecological correlations of pH, three trends were observed in the literature reviewed. One is that pH readings are usually higher under hardwoods than softwoods. Second, close associations between tree species and hydrogen ion activity may be found, but the strength of the association apparently depends on 1) the nature of the rooting system, 2) the calcium requirements of the species, and 3) the depth at which the pH measurement was taken. The third trend is that small changes in pH associated with the age of the forest ecosystem do occur, and may result from simultaneous changes in the status of other nutrients. Since calcium may be especially important in this respect, a general review of the ecological importance of calcium follows.

C. Calcium

The ecological significance of calcium is reflected by its use to characterize the cation-exchange-capacity of the soils and as an "index to general nutrient availability" (Beals and Cope 1964, 781) on the basis that calcium is the dominant macronutrient cation (Broyer and Stout 1959, 288; Buckman and Brady 1960, 74 and 347) and has a high energy of adsorption (Wilde 1958, 237). Two citations illustrate its ecological importance: 1) Wali and Krajina (1973, 307) in a study of vegetation change along a nutrient gradient found that replaceable calcium was one of five (from a total of thirty-nine variables) that was retained after step-wise elimination regression, and 2) Jeglum (1974, 122) using principal components analysis demonstrated a close relationship between calcium and the growth of black spruce.

The importance of calcium on plant distribution and production often results from the alleviation of the harmful effects of acidity by keeping the absorption and selectivity mechanisms involved in cation uptake intact (Black 1968, 327). Calcium "tends to overcome the injurious effects of excessive amounts of sodium, potassium, magnesium, aluminum, manganese and other constituents which may become toxic to the plants" (Wilde 1958, 226). Sufficient calcium must also be present to meet the heavy physiological demands of the plant community. The main function of calcium is to serve as a cementing agent (as calcium pectate for the cells of all tissues, but it also functions in the extension of

roots and root hairs, neutralizes toxic by-products formed during the growth processes (ibid.), and aids in the absorption of water and nutrients (Minotti, Williams and Jackson 1968, 692) by enhancing the permeability of the cell walls. The overall physiological importance of calcium is indicated by Mitchell's (1939, 91) finding that the differences in calcium concentration between the root and shoot of white pine seedlings were not as great as the differences for nitrogen, phosphorus, and potassium; the distribution of calcium within the plant varies with tree type (Rennie 1965, 62) and probably with the age of the tree.

Approximately thirty per cent of the cation exchange complex should be occupied by calcium if a plant's need for this element are to be met (Broyer and Stout 1959, 281). Many species have limited calcium demands and "their physiological requirements are fulfilled on most sites" (Tamm 1964, 154), while calcium toxicity is not common because most of it is absorbed by the soil (Mitchell 1939, 62). The extraction of much calcium from the soil does not mean that the physiological requirements of the overlying vegetation has been fulfilled. Low base saturation may lessen the availability of calcium (and other nutrients) to the plant (Wali and Krajina 1973, 260). Quantitative relationships between vegetation and the calcium status of the soil may, therefore, be difficult to detect.

Some general trends of the nutrient demands of tree types have been recognized. Rennie (1955, 65) calculated

that the uptake of calcium by pines is approximately one-fifth, and by other conifers one-half that of hardwood species; Ovington (1958b, 403) also notes the lesser demands of pines and larch than hardwoods (ash). A clear pattern between forest association and the calcium status of the soil, though, has not been established. Ovington found a lower per cent calcium in the organic layers (ibid. 393) under conifers than under hardwoods, but the difference in the upper mineral soil was insignificant (ibid. 398). The surface soils of treeless plots contained more exchangeable calcium than those that were forested (ibid.). Page (1974, 13) observed no significant differences beneath hardwoods and softwoods growing on mineral soils. Challinor (1968, 289) found significantly greater calcium concentrations in the top inch of soil under white spruce than under red oak and pine which was attributed to the ability of spruce roots to concentrate this element at the soil surface and to earthworm activity. Wali and Krajina (1973, 303) found that patterns of association varied with the form of calcium extracted. The values of water soluble and replaceable calcium, though, were high under aspen and low under pine. Dammon (1971, 259) found more calcium returned in the litter of balsam fir than in that of black spruce, but under both species the calcium was cycled rapidly and only five times the annual supply of calcium was contained in the raw humus (ibid. 265).

Insufficient research and the failure to eliminate variation among soil type, age--soil calcium levels increase along an age gradient (Burgess et al., 1973, 72)-- and tree composition of the forest may explain the inefficacy in recognizing a consistent pattern between the calcium status of the soil and the overlying vegetation associations. In this respect calcium is similar to another metallic nutrient, potassium.