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COMPARATIVE GROWTH AND FOLIAR ELEMENT CONCENTRATIONS OF *LARIX LARICINA* OVER A RANGE OF WETLAND TYPES IN MINNESOTA

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SUMMARY

(1) Growth and foliar concentrations of N, P, K, Ca, Mg, Al, Fe, Mn, Zn and B in *Larix laricina* were measured at twenty-two sites in Minnesota, ranging from ombrotrophic, *Sphagnum*-dominated bogs to sandy mineral soils.

(2) Needle and lateral shoot length, stemwood radial increment and site index (the height attainable by dominant 50-year-old trees) were lower in acid, nutrient-poor bogs than in circumneutral, relatively nutrient-rich fens. Variation in these growth measures was positively correlated with foliar concentrations of N and, to a lesser extent, P.

(3) Nitrogen and P concentrations in the foliage were positively correlated with specific conductivity of the soil water at a site, and inversely correlated with site wetness. Foliar concentrations of Ca were also positively correlated with specific conductivity, while Mg concentrations in the foliage were positively correlated with soil water pH and specific conductivity. Manganese concentrations were inversely related to soil water pH.

INTRODUCTION

Larix laricina (Du Roi) K. Koch has one of the widest geographic ranges of all North American gymnosperms, extending from Newfoundland and Labrador west along the northern limit of tree growth to the Yukon Territory and Alaska (Fowells 1965). Its southwestern limit occurs in Minnesota, U.S.A., where it predominates on moist organic soils, although it tolerates a wide range of moisture conditions.

Within the state of Minnesota *L. laricina* is found over a range of wetland habitats, from ombrotrophic, *Sphagnum*-dominated bogs to more minerotrophic sedge fens and forested swamps. A previous study of the seasonal patterns of growth and foliar element concentrations of *Larix laricina* growing in different habitats (Tilton 1977) showed that trees growing in a fen had longer short shoot needles and greater lateral shoot elongation than trees growing in a bog. Furthermore, foliar concentrations of N, P, Ca and Mg were greater in foliage from the fen than from the bog.

The present study examines the growth and foliar element concentrations of *L. laricina* in an extended range of wetland habitats in Minnesota, and seeks to ascertain whether foliar element concentrations are related to particular edaphic factors and whether growth is related to concentrations of elements in the foliage.

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METHODS

The study sites

Twenty-two undisturbed sites were selected which encompassed the range of site conditions in which *Larix laricina* grows in Minnesota (Fig. 1). Sites were rejected if there was evidence of disturbances such as altered drainage patterns by road building or drainage ditches, recent insect infestations, recent fire or recent lumbering.
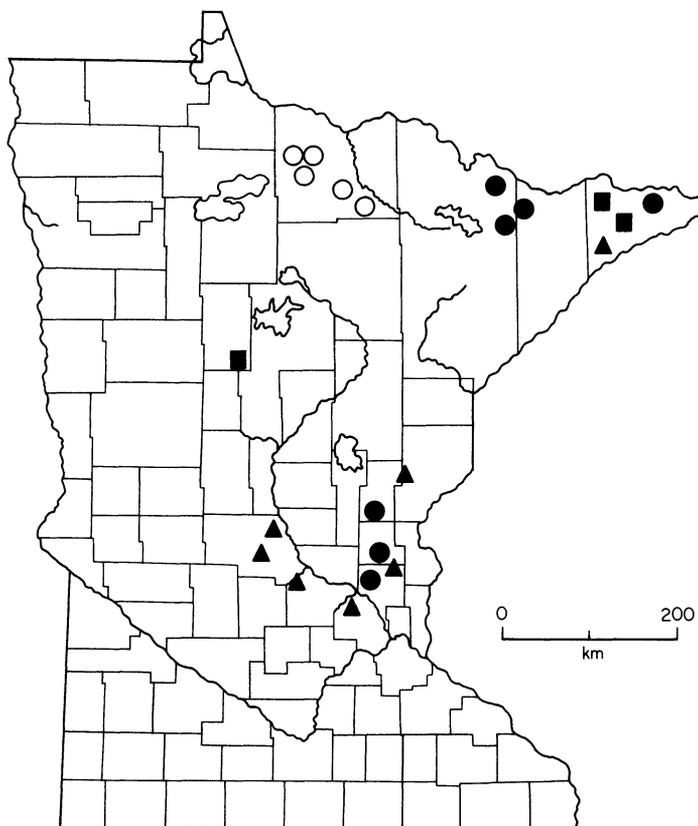

FIG. 1. The location of the study sites within the state of Minnesota. ○, northern peatlands; ●, forested bogs; ▲, fens; ■, sites on mineral soil.

The sites sampled were classified by water chemistry and vegetation characteristics following the method of Heinselman (1970). Northern peatlands, northern forested bogs and southern forested bogs tended to have acid waters (pH 3·8–6·0) and low conductivity (50–150 μS cm^{-1}). These sites were similar floristically in that *Picea mariana* (Mill.) BSP and ericaceous shrubs such as *Ledum groenlandicum* Oeder. and *Chamaedaphne calyculata* (L.) Moench. were frequent associates of *Larix laricina; Sphagnum* spp. formed the dominant ground-cover. Southern forested bogs (at *c.* latitude 45 °N) were distinguished from northern forested bogs (at *c.* latitude 48 °N) because of probable differences in climatic conditions. Sites with neutral soil water pH, relatively high specific

conductivity and an absence of *Sphagnum* spp. as the dominant ground-cover were considered fens. The majority of these sites in Minnesota generally had alder (*Alnus* sp.) or willow (*Salix* spp.) as shrub associates and sedges (*Carex* spp.) were quite common. When a conflict occurred between floristic data and water chemistry information, the classification of a given site tended to rely on floristic data.

Sampling

In late August and early September 1974, five dominant trees, similar in diameter at breast height (1·37 m), crown development and total height (but not necessarily of the same age), were sampled at each site. Foliage and branch samples were obtained by pole pruners from the outer portion of the upper third of the southwest side of each tree, the terminal 20–30 cm of the branch being collected; the samples were kept cool in a portable ice-chest until required. Stemwood increment cores were taken at a height of 1·37 m.

Soil conditions were characterized by field measures of pH, specific conductivity and site wetness. Specific conductivity and pH of mineral soils were determined in a 1:1 mixture of soil and distilled water; water samples from peat sites were obtained by hand-squeezing moist peat samples. Soil pH was determined with a portable battery-operated pH meter (Beckman N) with a reference and glass electrode, and specific conductivity with a battery-operated unit, the readings being corrected to 20 °C (Sjörs 1950). A rating of 1–5 was used to characterize site wetness. The categories recognized were: (1), dry upland soils; (2), moist organic soils with no standing water; (3), less than 30% standing water per 100 m² of surface; (4), between 30 and 60% standing water per 100 m² of surface; and (5), more than 60% standing water per 100 m² of surface. These ratings will be influenced by season, climatic conditions and hydrologic characteristics; sites were accordingly classified at similar times of the year (late August and early September).

Maximum fascicular needle length, that is maximum elongation of short shoot needles, was measured on ten short shoots on different-aged portions of branches from each tree. Lateral shoot elongation was then measured, and the current year's lateral shoots separated from the branch; this minimized the mixing of fascicular and axial needles, the latter being attached to these lateral shoots. A maximum of ten lateral shoots per tree was measured, although not all branches had lateral shoot elongation. Radial wood increment was measured on dry increment cores. Site index, that is the height attainable by dominant trees at an age of 50 years, was determined using site-index curves and the mean age and height of five dominant trees (Gevorkiantz 1957). At three sites (two mineral soil sites and a northern forested bog site), site index could not be determined due to incomplete tree age data as a result of internal bole decay which affected all the mature trees; collection of complete increment cores was thus not possible.

The branch, with attached fascicular needles only, was dried for 16–18 h at 80 °C. Needle dry weight was determined by weighing three samples of 100 needles per tree. These sub-samples were subsequently discarded. The residue from dry-ashing 500 mg of dry needles in a Vycor crucible at 500 °C for 4 h was weighed, and then analysed in the Department of Soil Science in the University of Minnesota by optical emission spectrography for concentrations of P, Ca, Mg, K, Fe, Al, Zn, Mn and B. Total foliar nitrogen was determined in semi-micro Kjeldahl digests by direct Nesslerization (Middleton 1960). All concentrations were expressed as a percentage of needle dry weight.

Statistical analyses were carried out using programs from the social sciences (Nie, Bent & Hull 1970) and biomedical series (Dixon 1974). The relationship between plant growth

and nutrient concentrations in tissue is generally expected to be curvilinear, but graphs of growth parameters and nutrient concentrations for *Larix laricina* indicated linear relationships (Fig. 2). Since the relationships appeared to be linear, correlation coefficients were calculated without data transformations.
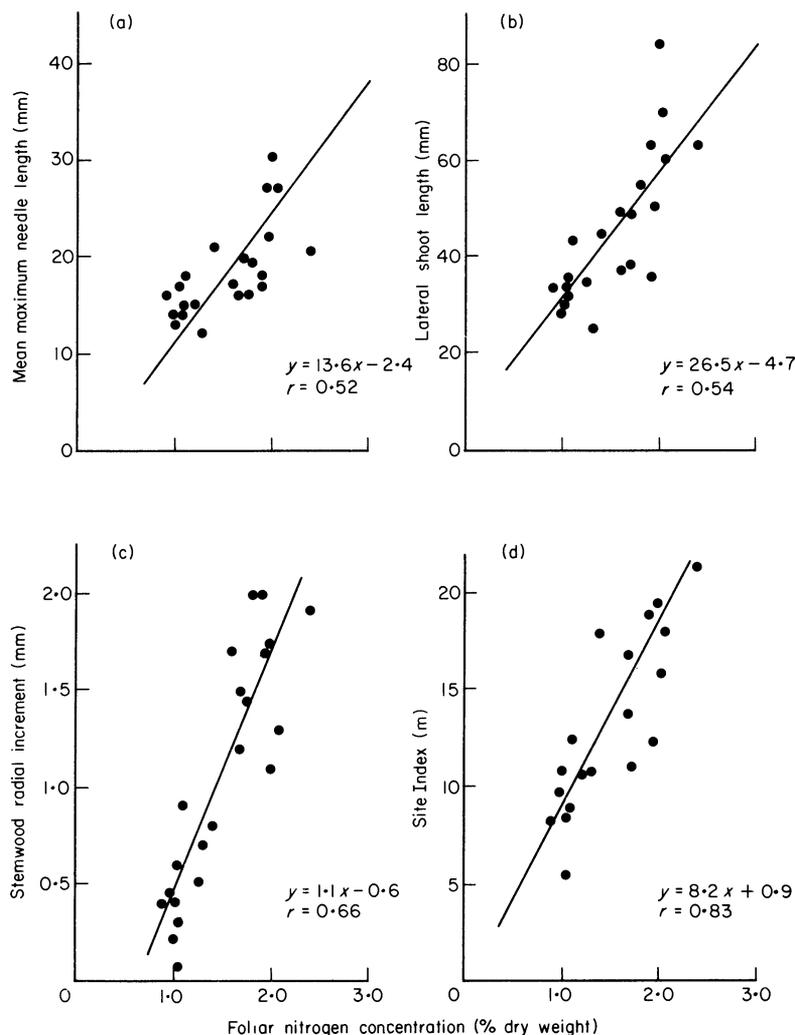

FIG. 2. The relationship between nitrogen concentrations in the leaves of *Larix laricina* and (a) mean maximum needle length, (b) lateral shoot length, (c) stemwood radial increment, and (d) site index (height at 50 years).

Correlation analyses were based on mean site values of tree growth and foliar element concentrations when relating these parameters to edaphic factors. Correlations of growth measures (except site index) with element concentrations were based on individual tree values. Correlation coefficients between site index and foliar element concentrations were based on mean site values of these parameters.

RESULTS

Table 1 shows the range of site conditions, growth and foliar element concentrations sampled at the twenty-two sites. The range of tree age was rather large (20–120 years), but correlation coefficients between tree age and foliar element concentrations were not significant (Table 2). While correlation coefficients between tree age and certain growth parameters were significant, further statistical analysis discussed later suggests that the range of tree age did not bias the growth–foliar element concentration portion of this study.

TABLE 1. Mean values, ranges and standard deviations of certain edaphic parameters at twenty-two sites in Minnesota, and the growth (site index) and foliar element concentrations (on a dry-weight basis) of *Larix laricina* in those sites

	Maximum	Minimum	Mean	S.D.
Conductivity (μS cm^{-1})	600	33	200	175
Site wetness	4	1	2·8	0·9
Site pH	7·6	3·2	5·5	1·5
Needle length (mm)	34	11	18	5·0
Needle dry weight (mg per 100 needles)	137	38	73	22
Shoot length (mm)	110	29	45	21
Stemwood radial increment (mm)	3·8	0·1	1·0	0·7
Site index (m at 50 years)*	21·3	5·5	13·1	14·4
Tree height (m)	20·7	4·6	13·4	12·2
Tree age (years)	120	30	53	20
Needle ash (%)	5·2	2·1	3·3	0·8
Total nitrogen (%)	3·05	0·75	1·50	0·50
Total phosphorus (%)	0·50	0·09	0·18	0·07
Calcium (%)	0·79	0·15	0·42	0·15
Magnesium (%)	0·42	0·06	0·16	0·07
Potassium (%)	0·97	0·34	0·55	0·13
Aluminium (μg g^{-1})	240	20	88	46
Iron (μg g^{-1})	280	40	130	49
Manganese (μg g^{-1})	1950	20	420	371
Boron (μg g^{-1})	90	20	40	12
Zinc (μg g^{-1})	70	20	30	9

*Mean height of five tallest trees at 50 years.

TABLE 2. Correlation coefficients for *Larix laricina* between age of tree and foliar concentrations of certain elements, and between age and certain growth parameters ($n = 94$)

	r		r
Nitrogen	−0·14	Needle length	−0·14
Phosphorus	−0·15	Shoot length	−0·16
Potassium	−0·14	Radial increment	−0·36*
Calcium	−0·04	Site index ($n = 19$)†	−0·69*
Magnesium	−0·11		

*Significant at the 5% level.
†Total height at 50 years estimated from site index curves.

TABLE 3. Mean concentrations and ranges of certain elements in the foliage of *Larix laricina* in different habitats in Minnesota

Wetland type	Conductivity (μS cm^{-1})	Site wetness*	pH	N	P	K	Ca	Mg	Al	Fe	Zn	Mn	B
						(% dry weight)					(μg g^{-1} dry weight)		
Northern peatlands (n=5)	59 (54–71)	3·4 (3–4)	4·8 (3·8–6·3)	1·03 (0·91–1·11)	0·12 (0·11–0·17)	0·52 (0·47–0·58)	0·24 (0·21–0·29)	0·13 (0·08–0·17)	82 (63–102)	121 (97–151)	31 (26–34)	470 (250–780)	36 (33–41)
Northern forested bogs (n=4)	109 (33–245)	3·2 (3–4)	5·1 (4·2–5·9)	1·41 (1·05–1·70)	0·14 (0·12–0·17)	0·50 (0·46–0·54)	0·39 (0·34–0·48)	0·15 (0·08–0·25)	49 (23–80)	93 (68–130)	25 (22–28)	400 (100–760)	35 (29–42)
Southern forested bogs (n=3)	77 (36–136)	3·3 (3–4)	5·0 (3·2–7·6)	1·39 (1·07–1·85)	0·18 (0·13–0·25)	0·56 (0·47–0·62)	0·42 (0·37–0·46)	0·12 (0·09–0·14)	86 (53–133)	139 (108–200)	34 (25–46)	600 (116–1180)	48 (35–58)
Fens (n=7)	368 (73–600)	2·7 (2–4)	6·6 (4·5–7·5)	1·90 (1·74–2·40)	0·20 (0·16–0·24)	0·57 (0·40–0·72)	0·55 (0·48–0·65)	0·23 (0·16–0·34)	108 (80–178)	156 (100–222)	28 (21–46)	170 (20–610)	38 (27–44)
Mineral soil sites (n=3)	267 (200–310)	1·0 (–)	3·9 (3·6–4·1)	1·91 (1·81–2·00)	0·27 (0·18–0·33)	0·58 (0·49–0·64)	0·48 (0·46–0·51)	0·13 (0·12–0·14)	109 (54–142)	104 (85–116)	31 (27–33)	670 (260–1140)	31 (22–40)

*On a 1–5 scale (see text).

Growth and foliar element concentrations in relation to habitat

Foliage of *Larix laricina* from northern peatlands and bogs (Table 3) had uniformly lower concentrations of N, P, Ca and Mg than foliage from fens, while K varied very little among wetland sites. The remaining elements, Al, Fe, Mn, B and Zn, were highly variable among sites. Compared to fens, foliage from sites on mineral soil had similar concentrations of N, K, Al, Zn and B, but lower concentrations of Ca, Mg and Fe. Phosphorus and Mn concentrations were higher in foliage from mineral sites than from any other habitat type.

Mean maximum needle length, lateral shoot length, stemwood radial increment and site index were also lower in forested bogs and ombrotrophic peatlands than in fens (Fig. 3). The growth of *L. laricina* in mineral sites was generally similar to that in fen sites. Since *L. laricina* is known to be a shade-intolerant species (Duncan 1954), competition from other tree species probably inhibits its growth in mineral sites.
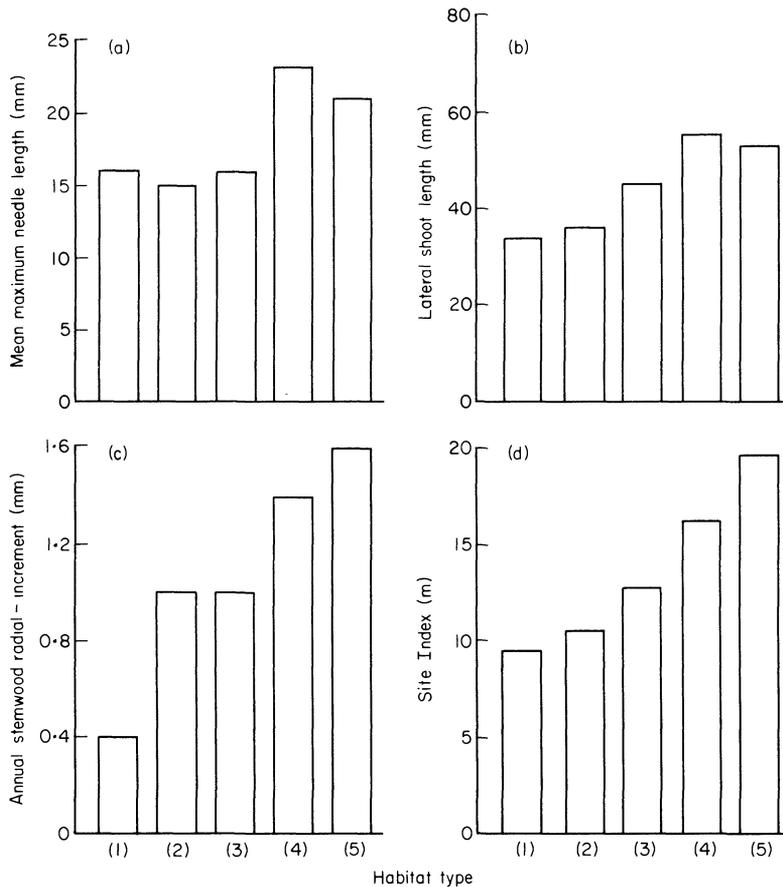

FIG. 3. Mean values of four growth parameters of *Larix laricina* growing in five different habitats in Minnesota; (a) mean maximum needle length, (b) lateral shoot length, (c) stemwood radial increment, (d) site index (height at 50 years). The habitat types are (1) northern peatlands ($n = 5$), (2) northern forested bogs ($n = 4$), (3) southern forested bogs ($n = 3$), (4) fens ($n = 7$), and (5) sites on sandy mineral soil ($n = 3$).

Relationships between foliar element concentrations and edaphic factors

Correlation coefficients of edaphic factors with foliar element concentrations indicated that several of the elements measured were closely associated with site pH, specific conductivity and site wetness (Table 4). Specific conductivity was positively correlated with concentrations of N, P, Ca and Mg in the foliage, while site wetness was inversel·· related to foliar concentrations of N and P. Site pH was positively correlated with Mg concentrations and inversely related to Mn concentrations in leaves. Relationships between site pH and foliar concentrations of N and P were not detected, nor were Al and Fe concentrations in the needles related to any of the edaphic factors measured. Table 4 shows that the proportion of the variance of foliar element concentrations accounted for by all three edaphic factors in combination (r^2) varied for different elements, but ranged from 69% (Mg) to 7% (Fe).

TABLE 4. Correlation coefficients of edaphic factors (site means) with mean element concentrations in foliage of *Larix laricina* in Minnesota ($n=22$); the multiple correlation coefficients *(r)* were calculated using all three edaphic factors

	Ash	N	P	Ca	Mg	K	Al	Fe	Zn	Mn	B
Conductivity	0·74**	0·44*	0·47*	0·66**	0·76**	0·27	0·27	0·24	−0·29	−0·44*	−0·19
Site wetness	−0·32	−0·58**	−0·52**	−0·41	−0·04	−0·04	−0·27	0·07	−0·07	−0·10	−0·28
Site pH	0·53**	0·03	0·14	0·33	0·67**	0·04	−0·12	0·11	−0·32	−0·61**	−0·14
r	0·82	0·71	0·67	0·75	0·83	0·30	0·44	0·26	0·35	0·63	0·35

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

Since the three edaphic factors are clearly interrelated, second-order partial correlation coefficients were also calculated (Table 5). With the influence of site wetness and pH controlled, then conductivity of soil and water were positively associated with foliar concentrations of N, P, Ca and Mg. Site wetness was inversely related to foliar N, P and Ca independent of pH and conductivity, while site pH, independent of site wetness and conductivity, was inversely related to Mn concentrations and positively related to Mg concentrations in *Larix* needles.

TABLE 5. Second-order partial correlation coefficients of edaphic factors (site means) with mean element concentrations in foliage of *Larix laricina* ($n=22$)

	N	P	Ca	Mg	K	Al	Fe	Zn	Mn	B
Conductivity	0·46*	0·43*	0·58*	0·63*	0·29	0·36	0·23	−0·15	−0·19	−0·08
Site wetness	−0·58*	−0·54*	−0·49*	−0·13	0·02	−0·18	0·11	−0·04	−0·01	0·29
Site pH	−0·10	0·03	0·14	0·52*	−0·12	−0·26	−0·05	−0·20	−0·48*	−0·14

*Significant at the 5% level.

The relationships between growth of L. laricina *and foliar element concentrations*

The correlation matrix of foliar element concentrations and the various growth measures indicated a number of significant relationships (Table 6). Site index was not significantly related to foliar P levels, nor were any relationships detected between growth

TABLE 6. Correlation coefficients of growth parameters of *Larix laricina* with foliar element concentrations; the multiple correlation coefficients (*r*) were calculated using all elements but excluding ash

	r	Ash	N	P	Ca	Mg	K	Al	Fe	Zn	Mn	B
Fascicular needle length (*n* = 108)	0·63	0·42**	0·52**	0·45**	0·48**	0·37**	0·08	0·08	0·04	−0·07	−0·16	−0·08
Fascicular needle dry weight (*n* = 108)	0·46	0·03	0·32	0·35**	0·33**	0·28**	0·09	0·01	−0·01	−0·07	0·12	0·05
Lateral shoot length (*n* = 102)	0·60	0·42**	0·54**	0·44**	0·45**	0·32**	0·12	−0·01	−0·05	0·05	−0·08	0·13
Site index (*n* = 19)	0·91	0·51*	0·83**	0·37	0·74**	0·50*	0·32	0·13	0·14	0·20	−0·19	0·10
Stemwood radial increment (*n* = 93)	0·64	0·37*	0·66**	0·22**	0·42**	0·27**	0·08	0·02	−0·01	−0·12	−0·35*	0·17

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

TABLE 7. First- and second-order partial correlation coefficients of growth parameters of *Larix laricina* with foliar element concentrations

Growth parameter	Independent of	N	P	Ca	Mg	K
Fascicular needle length (*n* = 108)	Age	0·51**	0·43**	0·48**	0·36**	0·06
	N	–	0·33**	0·22**	0·19*	0·01
	P	0·44**	–	0·33**	0·28**	−0·03
	N,P	–	–	0·10	0·14	−0·07
Fascicular needle dry weight (*n* = 108)	Age	0·31**	0·35**	0·33**	0·28**	0·08
	N	–	0·27**	0·17*	0·17*	0·04
	P	0·23*	–	0·19*	0·20*	0·00
	N,P	–	–	0·01	0·13	−0·02
Lateral shoot length (*n* = 10)	Age	0·53**	0·43**	0·45**	0·31**	0·10
	N	–	0·22**	0·10	0·12	−0·08
	P	0·42**	–	0·25**	0·22**	−0·09
	N,P	–	–	0·01	0·08	−0·13
Site index (*n* = 19)	Age	0·73**	0·26	0·74**	0·35	0·17
	N	–	0·01	0·28	0·21	0·37
	P	0·79**	–	0·69*	0·43	0·21
	N,P	–	–	0·31	0·21	0·39
Stemwood radial increment (*n* = 93)	Age	0·66**	0·57**	0·43**	0·25**	0·03
	N	–	0·02	−0·04	−0·01	−0·04
	P	0·64**	–	0·36**	0·22**	0·02
	N,P	–	–	−0·06	−0·02	−0·05

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

and K concentrations. The low multiple correlation coefficients emphasized that foliar element status was only one of many factors accounting for between-site variation in growth measures.

Since interactions among elements exist and the trees sampled were of different ages, first- and second-order partial correlation coefficients were calculated (Table 7). Calculations were limited to those elements which had already been shown to be significantly correlated with the growth parameters (N, P, Ca and Mg), and indicated that when N and P were controlled the relationships of Ca and Mg to growth became non-significant. It thus appears that the correlations of Ca and Mg with certain aspects of *L. laricina* growth were spurious, and that levels of N and P accounted for more of the variation in tree growth in freshwater wetlands than other elements. The partial correlation coefficients of foliar element concentrations and certain growth parameters independent of tree age indicate that the relationship between growth and foliar elements was not unduly affected by variation in the age of sample trees.

DISCUSSION

A statistically significant correlation coefficient indicates that there is a linear relationship between two variables; proof of causative relationships between such variables, however, requires experimental evidence. Nevertheless, an assumption of causality may be inferred with reasonable certainty if correlation coefficients obtained from field data are supported by experimental evidence in related fields.

The use of soil water conductivity as a measure of plant nutrient supply in wetland soils is based on the known relationship between conductivity and the concentrations of dissolved ions in peatland waters (Gorham 1956; Malmer 1963; Heinselman 1970; Summerfield 1974). The positive correlation coefficients obtained in the present study between foliar concentrations of N, P, Ca and Mg and conductivity suggest that this factor may be a suitable index of plant nutrient availability for *Larix laricina*. However, only few other authors have correlated concentrations of foliar elements in wetland species with conductivity, as in this study. Malmer (1962) detected standing crop differences of *Narthecium ossifragum* at three sites with different nutrient supply, but found no correlation between standing crop and foliar concentrations of N, P and K.

Site wetness reflects many variables which comprise the moisture–aeration status of a freshwater wetland ecosystem (Jeglum 1974), and this in turn controls the nutrient cycling and primary production. The rather qualitative approach to site wetness adopted in this study, however, was sufficient to demonstrate the inverse relationship between site wetness and foliar concentrations of certain elements, primarily N and P. This association could have been due to several factors. Waterlogged peats with little surface water flow are generally depleted of dissolved oxygen (Sparling 1966), and, therefore, represent a soil environment in which absorption of many ions is inhibited (Epstein 1972). In addition, poor soil aeration accompanying wet soils reduces microbial activity and, consequently, nutrient mineralization in the peat (Latter, Cragg & Heal 1967; Avnimelech 1971). Poor soil aeration also reduces root absorptive capacity by retarding root growth (Gore & Urquhart 1966). Nutrient limitations in freshwater wetlands with poor soil aeration and low pH are further aggravated by the formation of insoluble precipitates such as iron and aluminium phosphates (Lucas & Davis 1961).

In contrast to the relatively low amounts of available N and P, some elements, primarily Mn, Fe and Al, are more available in waterlogged peats than in better aerated, circumneutral organic soils (Lucas & Davis 1961; Jones & Etherington 1970). While this is apparent for Mn (Table 4), Fe and Al concentrations in *Larix laricina* needles were not apparently related to site wetness. This may have been due to selective exclusion of these elements at root surfaces by precipitation or adsorption (Dykeman & de Sousa 1966; Armstrong & Boatman 1967). The value of such an adaptation has been discussed by Jones (1972).

The absence of a relationship between soil pH and foliar concentrations of N, P and Ca (Tables 4 and 5) suggests that pH may not be as closely related to nutrient availability in wetlands as previously supposed (Gasser & Bloomfield 1955; Verry 1975). Soil pH affects the availability of certain elements, but Collins & Buol (1970) showed that soil redox potential was also influential. It is not clear whether soil pH is a primary controlling factor, or a result of other factors such as poor soil aeration and low redox potential.

Additional factors may affect the concentrations of foliar elements in *L. laricina* besides those previously considered. Haag (1974) showed low soil temperature to be important in tundra wetland ecosystems in that it limited microbial activity but not ion uptake. However, Heinselman (1963) found summer soil temperatures to be highest on sites with poor tree growth. The mycorrhizal symbionts of *L. laricina* (How 1940) may be an additional factor influencing foliar nutrient concentrations.

Waterlogged sites may have higher foliar nutrient concentrations than expected if there is rapid surface water flow. Sparling (1966) has shown that at flow rates above 0.4 cm s^{-1} peatland waters are replenished with oxygen, thus preventing anaerobiosis. The resultant oxygen supply and consequent increase in microbial activity generally produces shallower peats and improved nutrient status (Watt & Heinselman 1965). Furthermore, as a result of greater water flow, ion uptake by plant roots is facilitated and the supply of ions to roots is increased (Gorham 1950).

Some workers have related tree growth and nutrient status on peatlands to various site factors such as depth of peat and of water-table, water-table fluctuations and rate of surface water movement (Boggie 1972; Lowry 1972; Payandeh 1973). The effects of many of these factors, however, can be explained in terms of soil aeration and nutrient availability. Deep peats do not limit growth *per se*, but are related to poor growth because peat accumulation is favoured under conditions of low nutrient availability and low organic matter decomposition (Heinselman 1963). Similarly, edaphic factors such as site wetness, depth of water-table and water-table fluctuations, do not in themselves control growth or nutrient availability in wetland ecosystems. These factors, however, do influence soil aeration, which in turn affects the processes controlling nutrient cycling and primary production.

Interpretation of foliar element data with regard to determining element deficiencies is difficult without fertilizer trials. However, when foliar nutrient data are combined with growth analyses and some measure of soil nutrient supply, nutrient limitations may be determined with more assurance than by foliar nutrient data alone. Under conditions of an element deficiency, increasing the supply of that element generally increases growth as well as foliar element concentrations (Leyton 1958; van den Driessche 1974). In Minnesota, deficiencies of N and P at sites where *L. laricina* showed poor growth can be assumed, since increased tree growth was associated with higher foliar concentrations of N and P. However, fertilizer trials would be required to confirm such a conclusion. On the

other hand, similar foliar concentrations of K among trees with different growth rates suggest that this element was not limiting growth.

Apparently, no fertilizer trials using *L. laricina* have been published, although *L. leptolepis* has been studied by this approach (Leyton 1957). Results showed foliar N and K concentrations to explain about 81% of the variation in tree height (Leyton 1956), while pot culture studies have related total shoot dry weight to N and P supply (van Goor 1953).

The importance of N, P, and sometimes K, to the growth of tree species in wetland ecosystems is well documented. *Picea mariana* site index has been shown to be significantly related to foliar concentrations of N and P (Watt & Heinselman 1965; Lowry 1972); N, P and K limited *Acer rubrum* growth in a Massachusetts upland bog (Moizuk & Livingstone 1966). Larch and pine growth in Scotland was improved by additions of N and, sometimes, P and K to surface peats (Binns 1962), while *Picea sitchensis* growth on organic soils in Ireland was limited by nitrogen availability (Parker 1962). Peatland fertilization experiences in Sweden have generally demonstrated that tree growth on drained peats responds to P + K additions, but only if N is already in sufficient supply in the peat (Tamm 1965).

The lack of relationship between growth and foliar K concentrations found in this study of *Larix laricina* seems to contradict preceding studies which obtained a response to K fertilization. The fact that *Larix* needles from ombrotrophic peatlands have similar K concentrations to those from nutrient-rich fens (Table 3) seems to suggest that K is sufficiently available on peatlands so as not to limit *Larix* growth.

However, nutrient supply is only one of several factors accounting for variation in the growth of wetland plant species. Additional factors such as soil and air temperatures may account for differential growth of plants among different wetlands. Further, ecotypic variation among species may also explain between-site variation in plant growth. Indeed, ecotype development among wetland plant species would seem to be favoured by the generally scattered distribution of wetland communities, especially in Minnesota. There is clearly a need for studies designed to evaluate the relative importance of each of these factors in controlling primary production of wetland plant species.

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