

Relationships Between Site Index, and Soil Moisture and Nutrient Regimes for Western Hemlock and Sitka Spruce

17 / 1995



Ministry of Forests
Research Program

Relationships Between Site Index, and
Soil Moisture and Nutrient Regimes
for Western Hemlock and Sitka Spruce

Gordon J. Kayahara and
Audrey F. Pearson



BRITISH
COLUMBIA

Ministry of Forests
Research Program

The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the Government of British Columbia of any product or service to the exclusion of any others that may also be suitable. Contents of this report are presented for discussion purposes only.

Citation:

Kayahara, G.J. and A.F. Pearson 1996. Relationships between site index, and soil moisture and nutrient regimes for western hemlock and Sitka spruce. Res. Br., B.C. Min. For., Victoria, B.C. Work. Pap. 08/1996

Compiled by

Gordon J. Kayahara
Forest Sciences Department
University of British Columbia
Vancouver, BC, V6T 1Z4

for

B.C. Ministry of Forests
Research Branch
31 Bastion Square
Victoria, BC V8W 3E7

Copies of this report may be obtained, depending upon supply, from:

B.C. Ministry of Forests
Forestry Division Services Branch
Production Resources
1205 Broad Street
Victoria, BC V8W 3E7

© 1996 Province of British Columbia

The contents of this report may not be cited in whole or in part without the approval of the Director of Research, B.C. Ministry of Forests, Victoria, B.C.

PREFACE

This working paper summarizes the sections of the Master of Science theses of G. J. Kayahara and A. F. Pearson (see literature cited) concerning the relationship between site index and soil moisture and nutrient regimes for western hemlock and Sitka spruce. This summary was undertaken under Project 1.0 of the South Moresby Forest Replacement Account (SMFRA). Funding for the data collection and student support for the thesis on western hemlock was provided by Canadian Pacific Forest Products Ltd., Fletcher Challenge Canada, the South Moresby Forest Replacement Account, and the B.C. Science Council. Funding for the thesis on Sitka spruce was provided by the South Moresby Forest Replacement Account and the B.C. Ministry of Forests. The South Moresby Forest Replacement Account is a component of the joint South Moresby Agreement of the federal and provincial governments. The purpose of the account is to enhance the productivity of the managed forest lands of the Queen Charlotte Islands, by funding operational silviculture, and related research and extension work.

SUMMARY

Relationships between site index and soil moisture and nutrient regimes were examined to investigate the productivity of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). Stands representing a wide range in ecological site quality were sampled in southwestern British Columbia for western hemlock and the Queen Charlotte Islands for Sitka spruce. For western hemlock on fresh, moist, and very moist sites, increases in mean site index values occurred along the soil nutrient gradient from very poor to poor (18–30 m at 50 years breast height age); site index values were then level at 30 m for poor, medium, and rich sites. Trends in mean site index values along a soil moisture gradient were not well defined because most of the plots occurred on fresh and moist sites. For Sitka spruce, mean site index values increased from the slightly dry soil moisture regime to a maximum on moist and very moist sites, and decreased on wet sites. Along the soil nutrient gradient, mean site index values increased from poor to very rich, with maximum site index values occurring on very rich sites (40 m at 50 years breast-height age). The site index relationships derived for the various combinations of soil nutrient and moisture regimes can be used to estimate a site index for western hemlock in the CWHVM1 variant and Sitka spruce in the CWHWH1 variant. For both species, the relationship between soil nutrient regimes estimated in the field and actual measures of selected soil chemicals was not consistent. Agreement within one soil nutrient class appears to be all that is possible, at least when dealing with closed-canopy, immature plantations having little understorey vegetation.

CONTENTS

Preface	iii
Summary	iv
1 Introduction	1
2 Methods	1
2.1 Study Area	1
2.1.1 Western Hemlock	1
2.1.2 Sitka Spruce	2
2.2 Sampling and Site Description	2
2.3 Soil Chemical Analyses	3
2.4 Analysis of Productivity Relationships	3
3 Results	4
3.1 Western Hemlock	4
3.2 Sitka Spruce	7
4 Discussion	8
4.1 Western Hemlock Site Index Relationships	8
4.2 Sitka Spruce Site Index Relationships	9
4.3 Soil Nutrient Regime Relationships	9
5 Conclusions	10
Literature Cited	11

TABLES

1 Western hemlock site index means, standard deviations, and number of stands	5
2 Means and standard deviations of soil properties	5
3 Comparisons of field-derived and chemically derived soil nutrient regimes	6
4 Sitka spruce site index means, standard deviations, and number of stands	7
5 Means and standard deviations of soil nitrogen measures	8

FIGURES

1 Site index means and standard errors associated with soil nutrient regimes	6
---	---

Knowledge of the ecological characteristics of forest sites and the growth of forest trees on different sites is essential for making silvicultural decisions. In British Columbia, the biogeoclimatic ecosystem classification (BEC) is widely used to recognize forest ecosystems according to the ecological quality (climate, moisture, nutrients) of their sites (Pojar et al. 1987; MacKinnon et al. 1992). Recent research has focused on determining the potential productivity of various tree species on different sites defined by the BEC system. These efforts should assist forest managers to select the most suitable crop species and silvicultural regimes.

Forest productivity is one focus of forest management, and traditionally, site index (height at a reference age) has been the most widely accepted estimate of forest productivity (Mader 1963; Tesch 1981). However, in cases where the site index for a certain species cannot be determined directly, alternative methods of estimating site index are required to estimate forest productivity. For example, alternative methods are required in situations where the species of interest is absent, is too young or too old for site index calculations, or has suffered mechanical or pathogenic damage.

Various combinations of individual environmental measures have been used to estimate site index indirectly (see Jones 1969; Carmean 1975; Spurr and Barnes 1980, Hägglund 1981). In British Columbia, the relationship between the site index of the province's major tree species and site units of the BEC system has been the focus of recent research (Kabzems and Klinka 1987; Green et al. 1989; Carter and Klinka 1990, 1991; Klinka and Carter 1990; Wang 1992; McLennan 1993; Wang 1993; Wang et al. 1994a, b).

This working paper summarizes two studies that were conducted to determine the relationship between site index and soil moisture and nutrient regimes. Samples were from 102 immature western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands in southwestern coastal British Columbia (Kayahara 1992) and 55 immature Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stands in the eastern Queen Charlotte Islands (Pearson 1992).

2 METHODS

2.1 Study Area

2.1.1 Western Hemlock The study sites were located in three areas of southwestern British Columbia, on Vancouver Island, and the adjacent mainland (49° N and 123°–126° W). One area was in the vicinity of the municipalities of Gold River, Tahsis and Zeballos; a second near the municipality of Port McNeill; and the third in the Seymour Valley, near Vancouver. Most stands were within the Submontane Very Wet Maritime Coastal Western Hemlock (CWHVM1) variant, with some in the Southern Very Wet Hypermaritime (CWHVH1) and Western Very Dry Maritime (CWHXM2) variant (Klinka et al. 1984, 1991). The cool mesothermal climate is characterized by cool summers and mild winters, with the heaviest precipitation occurring during the winter. Mean annual precipitation ranges from 1500 to 4400 mm, with less than 15% falling as snow (Valentine et al. 1981). Using Köppen's system

(Trewartha and Horn 1980), this climate would be termed *Cfb* — mild, temperate, and rainy, with mild winters, no distinct dry season (except in the CWHxm2 variant where summer warm dry spells are common), and cool summers.

The soils of the stands were primarily Ferro-Humic Podzols, and Humo-Ferric Podzols, with some Dystric Brunisols and Humic Folisols (Agriculture Canada Expert Committee on Soil Survey 1987). Humimors are the chief humus forms present, with some Mormoders, Leptomoders and Mullmoders (Green et al. 1993). The majority of forest floors were thick (15 cm and greater, up to 60 cm). They included those composed mainly of woody material in various stages of decomposition.

2.1.2 Sitka Spruce The study sites were located on the leeward (eastern) side of the Queen Charlotte Islands, near the municipalities of Sandspit and Queen Charlotte City, in the Submontane Wet Hypermaritime Coastal Western Hemlock (CWHwh1) variant. This climate is also identified as *Cfb* using Köppen's system. However, although the summers are generally relatively cool and wet on the leeward side of the Queen Charlotte Islands, warm, dry spells are not uncommon.

The soils of the stands were (1) Dystric and Sombric Brunisols, and Regosols that occurred on active alluvial landforms with Mormoder, Rhizomoder, Mullmoder, and Rhizomull humus forms; (2) Podzols with Humimors that occurred on inactive alluvial landforms; and (3) Dystric Brunisols and Folisols with Humimor, Hydromor, and Hydromoder humus forms on moist sites of colluvial morainal deposits.

2.2 Sampling and Site Description

For western hemlock, 102 stands were sampled; for Sitka spruce, 55 stands were sampled. A wide range of the environments that supported the growth of these species were selected. The majority of these ecosystems supported naturally established, even-aged, mid-successional (30–100 years old), uniformly stocked stands. However, for western hemlock, 14 sample plots were located on extremely low productivity sites in sparsely forested ecosystems to ensure that the study encompassed the full range of sites. Within each stand, a 20×20 m (0.04 ha) sample plot was established that represented an ecosystem judged to be relatively uniform in climate, soil, and plants (Kenkel et al. 1989).

The climate of the site was identified according to its location from the biogeoclimatic maps supplied by the B.C. Ministry of Forests. Soil moisture and soil nutrient regimes were estimated qualitatively in the field using a combination of (1) topographic and soil morphological properties that are synthesized in the field keys of Banner et al. (1990), and (2) understory vegetation with the method of indicator plant analysis (Klinka et al. 1989). The definition of the soil moisture and nutrient regimes are given in Klinka et al. (1989).

Additionally, for western hemlock, soil nitrogen was used to derive soil nutrient regimes. The cluster analysis procedure suggested by Courtin et al. (1988) was performed on standardized scores of mineralizable nitrogen (kg/ha), and forest floor and mineral soil carbon–nitrogen ratios to separate the sample plots into groupings representing soil nutrient regimes. Measures of nitrogen were chosen since nitrogen is considered the most limiting

nutrient in forests of the Pacific Northwest (Jenny 1941; Viets 1965; Heilman 1979; Ballard and Carter 1986). Further, nitrogen has been the one consistent nutrient identified as a good single measure of a soil nutrient gradient (Kabzems and Klinka 1987; Courtin et al. 1988; Klinka and Carter 1990).

Site index (height at 50 years breast-height age) was used as an indicator of productivity. Tree selection was based on top height, defined as the height of the 100 largest-diameter trees per hectare. Thus, for western hemlock, the site index was determined from the heights and ages of the four largest trees per 0.04 ha plot and estimated using height growth curves (Wiley 1978). The heights and ages measured on several of the low-productivity sites were beyond the limits used in the Wiley curves. However, since the general form of the curves was maintained for these lower site index values, site index was determined by extrapolation. For Sitka spruce, site index was determined from the heights and ages of five dominants, and estimated using the height growth curves for second-growth Sitka spruce in the Queen Charlotte Islands.¹

2.3 Soil Chemical Analyses

Composite soil samples of forest floor and mineral soil were taken from three points of an equilateral triangle (2 m each side) at four randomly located positions in the sample plot. Mineral soil samples were taken from a depth of 0–30 cm for western hemlock, and 0–50 cm for Sitka spruce. The bulk density of both forest floor and mineral soil was measured at the centre of the triangle — a core was cut out, its volume measured, and then its mass determined after oven-drying at 105° C to constant weight. The following chemical analyses were undertaken using the methods outlined in Ballard and Carter (1986): total C, total N, and mineralizable N. The soil chemical analysis results were expressed as a mass per unit area. This calculation used bulk density, corrected for coarse fragment and live root content for both forest floor and mineral soil. The results therefore represent the mass of the respective nutrient per hectare in the forest floor, and 0–30 cm (western hemlock) or 0–50 cm (Sitka spruce) of the mineral soil.

2.4 Analysis of Productivity Relationships

Sample plots for the respective species were grouped according to combinations of the determined soil moisture and nutrient regimes. A mean site index value and standard deviation was then calculated for each group. For western hemlock, homogeneity of variance was tested using Bartlett's procedure. If variances were homogeneous, analysis of variance and the Tukey-Kramer multiple-comparison test were used to detect differences in mean site index among the soil moisture and nutrient groups. If variances were not homogeneous even after appropriate transformations, the nonparametric Kruskal-Wallis one-way analysis of variance (Neave and Worthington 1988) was used.

The applicability of using soil nutrient and soil moisture regimes as a method to estimate site index depends on how well these regimes can be identified in the field, and whether the relationship between field identification regimes to available soil nutrients is strong. To clarify the latter point,

1 J. E. Barker and J. W. Goudie. 1987. Site index curves for Sitka spruce. B.C. Min. For., Res. Br. Victoria, B.C. Unpublished report.

the field-derived, soil nutrient regimes were compared to the chemically derived regimes for western hemlock; and between the field-derived regimes and the chemical measures associated with each regime for Sitka spruce.

3 RESULTS

3.1 Western Hemlock

Four soil nutrient regimes were identified using cluster analysis, and seven soil moisture regimes were identified using field-based measures, resulting in a total of 18 unique combinations. However, several of these combinations were poorly represented (Table 1). The measures used to characterize the soil nutrient regimes are given in Table 2.

Western hemlock most commonly occurred on poor to rich soil nutrient regimes in combination with fresh to moist soil moisture regimes. The very poor, moderately dry sites consisted of a thin organic layer over bedrock and included some sparsely forested ecosystems. The slightly dry, very poor, and poor sites were either located in the drier subzone (CWHxm), or were from upper slopes, with shallow soils containing a large proportion of coarse fragments. Very few sample plots were located on wet to very wet sites, having a water table close to the surface; the few that were had very low productivity. No plots occurred on very rich soil nutrient regimes.

Only the fresh and moist soil moisture regimes, in combination with the four soil nutrient regimes, had enough plots to test for statistically significant differences in mean site index values. The Kruskal-Wallis test indicated that no significant differences ($p = 0.16$) in site index occurred between the fresh and moist soil moisture regimes within the respective soil nutrient regimes (for example, the site index between fresh–medium and moist–medium were the same). Because fresh and moist soil moisture regimes are defined as sites not having a water deficit or water excess (Klinka et al. 1989), these two moisture regimes were combined and then comparisons between soil nutrient regimes were made. Analysis of variance indicated that at least one combination of nutrient regimes was significantly different ($p < 0.001$). A Tukey-Kramer multiple-range test showed that the very poor nutrient regime site index was different from those on nutrient poor, medium, and rich sites. No significant differences occurred between the site indexes of the poor, medium, and rich regimes. This relationship is illustrated in Figure 1.

When soil chemical-derived and field-derived soil nutrient regimes were compared, only 45% of the sample plots could be identified to the same soil nutrient class (Table 3); 47% deviated by one nutrient regime class, and 8% deviated by two classes.

TABLE 1 *Western hemlock site index means (in bold face), standard deviations (in parentheses), and number of stands stratified according to soil moisture and nutrient regimes.*

Soil moisture regime	Soil nutrient regime			
	Very poor	Poor	Medium	Rich
Moderately dry	8.3 (4.1) n=10			
Slightly dry	16.5 (3.1) n=3	18.7 (6.4) n=3		
Fresh	18.1 (3.6) n=3	31.9 (5.2) n=21	32.4 (3.3) n=16	28.8 (1.9) n=6
Moist	18.1 (6.4) n=2	30.7 (6.9) n=9	34.4 (4.0) n=16	32.6 (6.1) n=6
Very moist		36.7 (na) n=1		29.4 (na) n=1
Wet		7.7 (na) n=1	8.3 (na) n=1	10.6 (na) n=1
Very wet	2.5 (na) n=1	3.6 (na) n=1		

TABLE 2 *Means and standard deviations (in parentheses) of soil properties used to stratify actual soil nutrient regimes for the western hemlock stands. Different lowercase letters indicate significant differences at $p < 0.05$ using the Tukey-Kramer multiple range test.*

Property	Soil nutrient regime			
	Very poor (n=19)	Poor (n=36)	Medium (n=33)	Rich (n=14)
Mineralizable N (kg/ha)	24a (13)	90b (31)	105b (27)	182c (56)
Forest floor C–N ratio	50a (5)	48a (8)	36b (4)	29c (5)
Mineral soil C–N ratio	44a (7)	31b (5)	23c (3)	24c (2)

TABLE 3 Comparison of field-derived and chemically derived soil nutrient regimes. The matrix shows the percentage of plots identified to the same soil nutrient regime (**boldface**) and the number identified to different regimes using the two methods.

Field-derived nutrient regimes	Chemically derived nutrient regimes				
	Percent Correct	Very poor	Poor	Medium	Rich
Very poor	84	16	3	1	0
Poor	25	2	9	3	3
Medium	48	1	21	16	5
Rich	36	0	3	13	5
Very Rich	0	0	0	0	1
Total		19	36	33	14

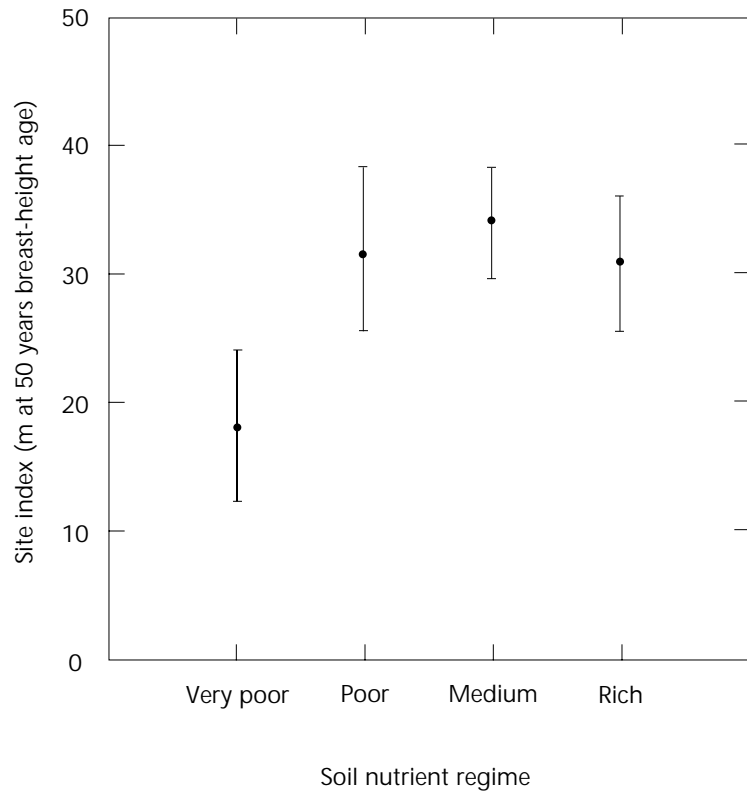


FIGURE 1 Site index means and standard errors associated with soil nutrient regimes on fresh and moist sites for western hemlock.

3.2 Sitka Spruce

Four soil nutrient regimes and five soil moisture regimes were identified in the study plots, with a total of 18 unique combinations. Several combinations were poorly represented, however (Table 4). No plots occurred on very poor nutrient regimes. A comparison of the measured soil chemicals associated with each nutrient regime is given in Table 5. In general, the only significant differences in the selected soil chemicals and the various soil nutrient regimes were the broad differences between the poor and medium classes compared to the rich and very rich classes.

TABLE 4 *Sitka spruce site index means (in boldface), standard deviations (in parentheses), and number of stands stratified according to soil moisture and soil nutrient regimes.*

Soil moisture regime	Soil nutrient regime			
	Poor	Medium	Rich	Very rich
Slightly dry	16.5 (3.1) n=2	22.6 (2.1) n=5	30.3 (1.5) n=3	28.5 (0.6) n=4
Fresh		29.7 (2.1) n=3	35.5 (3.3) n=6	34.0 (0.0) n=2
Moist		34.6 (3.6) n=7	37.0 (0.7) n=5	41.0 (1.0) n=3
Very moist	22.0 (na) n=1	26.0 (na) n=1	34.7 (na) n=1	40.0 (na) n=1
Wet	23.0 (na) n=1	25.0 (1.4) n=2	34.0 (na) n=1	25.0 (na) n=1

TABLE 5 Means and standard deviations (in parentheses) of soil nitrogen measures associated with the field-derived soil nutrient regimes identified for the Sitka spruce stands. Different lowercase letters indicate significant differences ($p < 0.05$) using the Tukey-Kramer multiple-range test.

Property	Soil nutrient regime			
	Poor (n=4)	Medium (n=18)	Rich (n=22)	Very rich (n=11)
Mineralizable N (kg/ha)	87a (7)	141a (48)	165a (62)	243b (116)
Total N (kg/ha)	2777a (857)	5770a (1429)	8811b (3578)	10844b (3262)
Forest floor C–N ratio	49a (7)	43a (5)	35b (3)	32b (2)

4 DISCUSSION

4.1 Western Hemlock Site Index Relationships

The stands sampled in this study primarily represented western hemlock ecosystems without a water deficit or a water table close to the surface. The difficulty in finding study sites that had a water deficit or excess was expected. Western hemlock has limited drought stress avoidance and tolerance mechanisms (Ballard and Dosskey 1985; Livingston and Black 1987 a, b), and is poorly suited to sites that have a high water table (Minore and Smith 1971) or that flood during the growing season (Brink 1954; Minore 1968).

No positive correlation was observed between soil nutrients and the site index values of western hemlock for sites considered as nutrient poor to rich as defined by Kabzems and Klinka (1987) and Klinka et al. (1989). Although past studies show significant regression relationships between site index and various soil or foliar chemical measures (Wooldridge 1961; Meurisse 1972, 1976; Heilman 1976; Radwan and DeBell 1980), there is no consistency to the measures that are related to site index. The weak, positive relationship of site index to soil nutrient regimes for western hemlock is in contrast to the response of Sitka spruce and other species in British Columbia (Carter and Klinka 1990, 1991; Klinka and Carter 1990; Wang 1992; McLennan 1993; Wang et al. 1994 a, b; Wang et al. 1994; Wang 1995).

The silvics of western hemlock indicate that it is associated with the nutritionally poor substrates of Mor humus forms and decaying wood, with their associated ammonium sources of nitrogen (Taylor 1935; Swan 1960; Krajina 1969; Van den Driessche 1971; Krajina et al. 1973, 1982; Turner and Franz 1985). The mycorrhizal associations formed with western hemlock (Kropp and Trappe 1982; Molina and Trappe 1982) could enhance the acquisition of nitrogen and phosphorus on nutritionally poor sites (Marks and Kozlowski 1973; Lundberg 1970). If western hemlock is adapted to sites of lower

nutrient availability — sites considered poor by the biogeoclimatic ecosystem classification — then greater nutrient availability may not lead to increased productivity for this species. Indeed, results from fertilization studies show an inconsistent growth response of western hemlock to increased availability of nitrogen (Chappell et al., 1992).

4.2 Sitka Spruce Site Index Relationships

The positive correlation of site index with nutrient regimes having increased nutrient availability is in agreement with the known silvics of Sitka spruce. In a descriptive study of ecological requirements of Sitka spruce in the Queen Charlotte Islands, the dominance of spruce was largely associated with the site characteristics related to soil water supply and drainage (Day 1957). The best growth development of Sitka spruce is reported on moist, well-aerated soils, with the poorest on swampy sites (Harris 1990). For nutrient relationships, nitrogen is shown to be important (Blyth and MacLeod 1981; Green 1989). Using sand cultures, Krajina (1959) found that Sitka spruce, although it tolerates ammonium as a source of nitrogen very well, grows better where nitrates prevail over ammonium compounds. The species also requires relatively high amounts of available calcium, magnesium, and phosphorus (Krajina 1959). Sitka spruce often grows on sites with a relatively high nutrient status and is associated with sites having a high degree of nitrification (Day 1957). The results of the present study quantified site index values on different soil moisture and nutrient regimes of this part of the Queen Charlotte Islands.

4.3 Soil Nutrient Regime Relationships

The applicability and confidence in using the mean site index values estimated for the edatopic grid will depend on the relationship of the field identified nutrient regimes to actual nutrient availability. For western hemlock, the lack of agreement between field-derived and chemically derived soil nutrient regimes suggests that identification to a single regime may not be very reliable, at least for the conditions in this study. Only the very poor soil nutrient regime showed close agreement between the two methods of derivation; most others were within one nutrient class. For Sitka spruce, field-derived nutrient regimes and measured soil chemicals also failed to agree. One problem with the field-identified nutrient regimes was that second-growth stands were chosen for study. The lack of suppression associated with these plantations was useful for the calculation of site index; however, the closed canopy and resulting lack of understorey plants prevented the use of indicator plant species. It is expected that closer agreement between field-derived nutrient regimes and actual soil chemical measures would be achieved with old-growth stands.

The site index relationships derived for the various combinations of soil nutrient and moisture regimes can be used to estimate site index for western hemlock in the CWHvm1 variant and for Sitka spruce in the CWHwh1 variant. However, because of the lack of significant agreement between field-derived and chemically derived nutrient regimes, and additionally for Sitka spruce, the small sample size, site index estimates for these two species should be used only as a relative productivity measure for tree species selection. Since western hemlock does not show an increase in site index with poor to rich nutrient regimes, further research is needed before deciding to fertilize western hemlock on poor or medium sites.

LITERATURE CITED

- Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification. 2nd ed., Supply and Services Can., Ottawa, Ont. Agric. Can. Publ. No. 1646. 164 pp.
- Ballard, T.M. and R.E. Carter. 1986. Evaluating forest stand nutrient status. B.C. Min. For. and Lands, Victoria, B.C. Land Manage. Rep. No. 20. 60 pp.
- Ballard, T.M. and M.G. Dosskey. 1985. Needle water potential and soil-to-fo- liage flow resistance during soil drying: a comparison of Douglas-fir, western hemlock and mountain hemlock. Can. J. For. Res. 15:185–88.
- Banner, A., R.N. Green, K. Klinka, D.S. McLennan, D.V. Meidinger, F.C. Nuszdorfer, and J. Pojar. 1990. Site classification for coastal British Columbia: a first approximation. B.C. Min. For., Victoria, B.C. 2 pp. (a coloured pamphlet).
- Blyth, J.F. and D.A. MacLeod. 1981. Sitka spruce (*Picea sitchensis*) in north- eastern Scotland. I: Relationships between site factors and growth. Forestry 54:41–62.
- Brink, V.C. 1954. Survival of plants under flood in the lower Fraser River Valley, British Columbia. Ecology 35:94–95.
- Carmean, W.H. 1975. Forest site quality evaluation in the United States. Adv. Agron. 27:209–69.
- Carter, R.E. and K. Klinka. 1990. Relationships between growing-season soil water deficit, mineralizable soil nitrogen, and site index of coastal Douglas-fir. For. Ecol. Manage. 30:301–11.
- . 1991. Use of ecological site classification in the prediction of forest productivity and response to fertilization. In A.P.G. Schonau (editor). Intensive forestry – the role of eucalypts. Pietersmaritzburg, South Africa, pp. 382–92.
- Courtin, P.J., K. Klinka, M.C. Feller, and J.P. Demaerschalk. 1988. An ap- proach to quantitative classification of nutrient regimes of forest soils. Can. J. Bot. 66:2640–53.
- Day, W.R. 1957. Sitka spruce in British Columbia – a study in forest relation- ships. For. Comm. Bull. No. 28. Imperial For. Inst., Oxford, England.
- Green, R.N. 1989. Site–forest productivity relationships and their manage- ment implications in coast lowland ecosystems of east Graham Island, Queen Charlotte Islands. M.Sc. thesis. Univ. B.C., Vancouver, B.C. 169 pp.

- Green, R.N., P.L. Marshall, and K. Klinka. 1989. Estimating site index of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) from ecological variables in southwestern British Columbia. *For. Sci.* 35:50–63.
- Green, R.N., R.L. Trowbridge, and K. Klinka. 1993. Towards a taxonomic classification of humus forms. *For. Sci. Monogr. No.* 29.
- Hägglund, B. 1981. Evaluation of forest site productivity. *For. Abstr. Rev.* 42(11):515–27.
- Harris, A.S. 1990. *Picea sitchensis* (Bong.) Carr. Sitka spruce. *In* *Silvics of North America*. R.M. Burns and B.H. Honkala (technical co-ordinators). U.S. Dep. Agric. For. Serv., Washington, D.C. Agric. Handb. No. 654, pp. 260–67.
- Heilman, P.E. 1976. Soils and site index in coastal western hemlock forests of Washington and Alaska. *In* *Western hemlock management conf. proc.* W.A. Atkinson and R.J. Zasoski (editors). Univ. Wash., Seattle, Wash., pp.39–48.
- . 1979. Minerals, chemical properties, and fertility of forest soils. *In* *Forest soils of the Douglas-fir region*. P.E. Heilman, W.H. Anderson, and D.M. Baumgartner (editors). Wash. State Univ., Pullman, Wash., pp. 121–36.
- Jones, J.R. 1969. Review and comparison of site evaluation methods. U.S. Dep. Agric. For. Serv., Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colo. Res. Pap. RM–51. 27 pp.
- Kabzems, R.D. and K. Klinka. 1987. Initial quantitative characterization of soil nutrient regimes. I. Soil properties. *Can. J. For. Res.* 17:1557–64.
- Kayahara, G.J. 1992. Ecological site quality and productivity of western hemlock in the Coastal Western Hemlock zone of British Columbia. M.Sc. thesis. Fac. For., Univ. B. C., Vancouver, B.C. 164 pp.
- Kenkel, N.C., P. Juhász-Nagy, and J. Podani. 1989. On sampling procedures in population and community ecology. *Vegetation* 82:195–207.
- Klinka, K. and R.E. Carter. 1990. Relationships between site index and synoptic environmental variables in immature coastal Douglas-fir stands. *For. Sci.* 36:815–30.
- Klinka, K., V.J. Krajina, A. Ceska, and A.M. Scagel. 1989. Indicator plants of coastal British Columbia. Univ. B.C. Press, Vancouver, B.C. 288 pp.
- Klinka, K., J. Pojar, and D.V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. *Northwest Sci.* 65(1):32–47.
- Krajina, V.J. 1959. Ecological experiments on Douglas-fir, western hemlock, Sitka spruce, and western redcedar. 1958 Progr. Rep., NRC Grant No. T-92:2–5.

- . 1969. Ecology of forest trees in British Columbia. *Ecol. West. North Amer.* 2(1):1–146.
- Krajina, V.J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. *Fac. For., Univ. B.C., Vancouver, B.C.* 131 pp.
- Krajina, V.J., S. Madoc-Jones, and G. Mellor. 1973. Ammonium and nitrate in the nitrogen economy of some conifers growing in Douglas-fir communities of the Pacific Northwest of America. *Soil Biol. Biochem.* 5:143–47.
- Kropp, B.R. and J.M. Trappe. 1982. Ectomycorrhizal fungi of *Tsuga heterophylla*. *Mycologia* 74(3):479–88.
- Livingston, N.J. and T.A. Black. 1987a. Water stress and survival of three species of conifer seedlings planted on a high elevation south-facing clear-cut. *Can. J. For. Res.* 17:1115–23.
- . 1987b. Stomatal characteristics and transpiration of three species of conifer seedlings planted on a high elevation south-facing clear-cut. *Can. J. For. Res.* 17:1273–82.
- Lundberg, G. 1970. Utilization of various nitrogen sources, in particular bound soil nitrogen, by mycorrhizal fungi. *Stud. For. Suecica* 79:1–95.
- MacKinnon, A., D. Meidinger, and K. Klinka. 1992. Use of the biogeoclimatic ecosystem classification system in British Columbia. *For. Chron.* 68:100–20.
- McLennan, D.S. 1993. Growth and nutrient relations in black cottonwood in south-coastal British Columbia. Ph.D. thesis. *Fac. For., Univ. B.C., Vancouver, B.C.* 187 pp.
- Mader, D.L. 1963. Volume growth measurement – an analysis of function and characteristics in site evaluation. *J. For.* 61(3):193–98.
- Marks, G.C. and T.T. Kozlowski (editors). 1973. *Ectomycorrhizae: their ecology and physiology*. Academic Press, New York, N.Y. 444 pp.
- Meurisse, R.T. 1972. Site quality of western hemlock and chemical characteristics of some western Oregon andic soils. Ph.D. thesis. *Oreg. State Univ. Corvallis, Oreg.* 164 pp.
- . 1976. Some chemical and other properties of western hemlock soils in Oregon – their relationship to productivity. *In* Western hemlock management conf. proc. W.A. Atkinson and R.J. Zasoski, (editors). *Univ. Wash., Seattle, Wash.*, pp. 49–55.
- Minore, D. 1968. Effects of artificial flooding on seedling survival and growth of six northwestern tree species. *U.S. Dep. Agric. For. Serv., Pac. NW For. Res. Sta., Portland, Oreg. Res. Note PMW-92.*

- Minore, D. and C.E. Smith. 1971. Occurrence and growth of four northwestern tree species over shallow water tables. U.S. Dep. Agric. For. Serv., Pac. NW Res. Sta., Portland, Oreg. Res. Note PNW-160.
- Molina, R. and J.M. Trappe. 1982. Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. *For. Sci.* 28(3):423-58.
- Neave, H.R. and P.L. Worthington. 1988. *Distribution-free tests*. Unwin, Hyman Ltd., London, Eng. 430 pp.
- Pearson, A.F. 1992. Relationships between site index of Sitka spruce and measures of ecological site quality in the eastern Queen Charlotte Islands. M.Sc. thesis. Fac. For., Univ. B.C., Vancouver, B.C. 92 pp.
- Pojar, J., K. Klinka, and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* 22:119-54.
- Radwan, M.A. and D.S. DeBell. 1980. Site index, growth, and foliar chemical composition relationships in western hemlock. *For. Sci.* 26(2):283-90.
- Spurr, S.H. and B.V. Barnes. 1980. *Forest ecology*. John Wiley & Sons, New York, N.Y. 687 pp.
- Swan, H.S.D. 1960. The mineral nutrition of Canadian pulpwood species: I. The influence of nitrogen, phosphorus, potassium and magnesium deficiencies on the growth and development of white spruce, black spruce, jack pine and western hemlock seedlings grown in a controlled environment. *Pulp Paper Res. Inst. Can. Woodlands Res. Index* No. 116.
- Taylor, R.F. 1935. Available nitrogen as a factor influencing the occurrence of Sitka spruce and western hemlock seedlings in the forests of southern Alaska. *Ecology* 16(4):580-602.
- Tesch, S.D. 1981. The evolution of forest yield determination and site classification. *For. Ecol. Manage.* 3:169-82.
- Trewartha, G.T. and L.H. Horn. 1980. *An introduction to climate*. 5th ed. McGraw-Hill Inc., New York, N.Y. 416 pp.
- Turner, D.P. and E.H. Franz. 1985. The influence of western hemlock and western redcedar on microbial numbers, nitrogen mineralization, and nitrification. *Plant and Soil* 88:259-67.
- Valentine, K.W.G., P.N. Sprout, T.E. Baker, and L.M. Lavkulich (editors). 1981. *The soil landscapes of British Columbia*. Queen's Printer, Victoria, B.C. 197 pp.
- Van den Driessche, R. 1971. Response of conifer seedlings to nitrate and ammonium sources of nitrogen. *Plant and Soil* 34:421-39.

- Viets, F.G. 1965. The plant's need and use of nitrogen. In Soil nitrogen. W.V. Bartholomew and F.E. Clark (editors.). Am. Soc. Agron. Madison, Wis., pp. 503–49.
- Wang, G.G. 1995. White spruce site index in relation to soil, understory vegetation and soil nutrients. Can. J. For. Res. 25:29–38.
- Wang, G.G., P.L. Marshall, and K. Klinka. 1994. Height growth pattern of white spruce in relation to site quality. For. Ecol. Manage. 68:137–47.
- Wang, Q. 1992. Ecological and height growth analysis of some sub-boreal immature lodgepole pine stands in central British Columbia. Ph.D. thesis. Fac. For., Univ. B.C., Vancouver, B.C. 207 pp.
- Wang, Q., G.G. Wang, K.D. Coates, and K. Klinka. 1994a. Use of site factors to predict lodgepole pine and interior spruce site index in the Sub-Boreal Spruce zone. B.C. Min. For., Res. Branch, Victoria, B.C. Res. Note No. 114.
- Wang, Q., G.G. Wang, K. Klinka, and K.D. Coates. 1994b. Relationships between ecological site quality and site index of lodgepole pine and white spruce in Northern British Columbia. Chinese J. Appl. Ecol. 5(1):1–15.
- Wiley, K.N. 1978. Site index tables for western hemlock in the Pacific Northwest. Weyerhaeuser Co., For. Resour. Cent., For. Pap. No. 17. 28 pp.
- Wooldridge, D.D. 1961. Environmental factors related to growth and management of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Ph.D. thesis. Univ. Wash., Seattle, Wash. 211 pp.