

Relationships between ecological site quality and site index of lodgepole pine and white spruce in Northern British Columbia

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Abstract To establish a link between ecological site quality and forest productivity in the 'sub-boreal' portion of the Prince Rupert Forest Region, site index and site quality data from 93 lodgepole pine stands and 77 white spruce stands were obtained and analyzed. The study stands were distributed across two climatic regimes (biogeoclimatic subzones), eight soil moisture regimes, and five soil nutrient regimes. These regimes were used as categorical variables in stratification of the stands and regression analysis. Site index of lodgepole pine and white spruce changed with soil moisture and nutrient regimes but not with climate. The pattern of change in relation to soil moisture was similar for both species but different in relation to soil nitrogen. Compared to lodgepole pine, site index of white spruce was lower on water-deficient, water-surplus, and nitrogen-deficient (very poor, poor, and medium) sites but the same or higher within the slightly dry to very moist and rich to very rich edatopic region. Of the five types of regression models developed, the edatope model showed strong relationships between site index and soil moisture and nutrient regimes [$R^2 > 0.80$, SEE (standard error of estimates) < 1.6 m] for both lodgepole pine and white spruce. This model was used to construe site index isolines which were superimposed onto edatopic grids. It was concluded that the categorical measures of soil moisture and soil nutrients are good predictors of lodgepole pine and white spruce site index over a large area.

Key words Lodgepole pine, White spruce, Ecological site quality, Soil moisture regime, Soil nutrient regime, Site index, Forest productivity.

【摘要】 不列颠·哥伦比亚省北部小杆松及白云杉立地指数与生态立地质量的关系。王庆礼(中国科学院沈阳应用生态研究所, 沈阳 110015), 王高峰, K. Klinka(不列颠·哥伦比亚大学林学系, 温哥华 V6T 1Z4, 加拿大)。-应用生态学报, 1994, 5(1): 1-15。

为在 Prince Rupert 林区的“亚北方”部分建立生态立地质量与森林生产力的联系, 对从 93 个小杆松林分 and 77 个白云杉林分获得的数据进行了分析。所研究的林分处于两个气候状况、8 个土壤水分状况以及 5 个土壤养分状况。这些气候、土壤水分和养分状况被视为等级变量用于林地分类和回归分析。小杆松和白云杉的立地指数随土壤水分和养分状况变化而变化, 但不依赖于气候变化。与土壤水分相关的变化格局对两个种来说很相似, 但与土壤养分相关的变化格局则全然不同。在所建立的 5 类回归模型中, 土壤小区模型对于两个种都显示出立地指数与土壤水分和养分状况具有很强的相互关系($R^2 > 0.80$, $SEE \leq 1.6$ m)。可以认为土壤水分和养分的等级度量在大范围内可作为小杆松和白云杉立地指数的预测预报因子。

关键词 小杆松 白云杉 生态立地质量 土壤水分状况 土壤养分状况 立地指数 森林生产力 回归模型

1 Introduction

Rational silvicultural decision-making must be based on the knowledge of (a) ecological characteristics of forest sites and (b) growth of forest trees on different sites. This is necessary because each tree species is adapted to a certain range of ecological conditions, and in consequence, it will grow and behave in ways that depend on the ecosystems or sites in which it grows (Klinka and Feller 1984).

In British Columbia, biogeoclimatic ecosystem classification is widely used to recognize different types of forest ecosystems according to ecological quality of their sites (Pojar et al. 1987, Meidinger and Pojar 1991). With the classification system in place, silvicultural management has been given a solid ecological foundation; however, relationships between forest growth and ecological site quality has not yet been fully developed. The purpose of this study was to determine how site conditions within the 'sub-boreal' portion of the Prince Rupert Forest Region affect the growth of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*).

Forest productivity (i.e., the growth performance of a given tree species on a site) has always been an essential consideration in stand management. Site index (SI) has been the most widely used measure of forest productivity, as well as site quality or site productivity (i.e., the inherent capacity of a site to support the growth of a given tree species) (e.g., Jones 1969). We adopted site index as a species-specific measure of forest productivity, recognizing that it only indicates height growth performance at a selected point in time.

Q. Wang (1992) discussed a conceptual problem of relating site index to site-quality as the latter term is used ambiguously for denoting both forest productivity and ecological site quality. Firstly, two different species growing on the same site may have different site index; secondly, the same tree species may have the same site index on two ecologically different sites. Therefore, site index is the measure of productivity relative to a given species and cannot be a true measure of ecological quality of the site, and ecological site quality cannot be a true measure of forest productivity. The current usage contradicts the ecological perspective that defines site quality as the sum of all the many environmental factors affecting the biotic community of an ecosystem (Daniel et al. 1979). Therefore, it is more appropriate to use the term ecological site quality than site quality when describing ecological characteristics of a forest site.

When relating forest productivity to ecological site quality, the question at once arises as to what basis site data are to be evaluated in order to clarify the relationships. The biogeoclimatic ecosystem classification considers site to be the physical environment (climate, topography, and soil) of a geographically circumscribed ecosystem, and organizes ecosystems into environmentally characterized site units with the aid of vegetation (Pojar et al. 1987). This implies recognizing different kinds of sites, each with different ecological conditions or quality for plant growth.

While it is fairly easy to work with individual environmental factors, it is very difficult to determine their integrated effect on plants. Because of compensating effects, sites with different combinations

of individual environmental factors can have similar ecological quality (Bakuzis 1969, Assmann 1970, Damman 1979, Klinka and Carter 1990). To circumvent this problem, the biogeoclimatic ecosystem classification uses the primary factors that have direct and major influence on plant establishment, survival, and growth: climate (light and temperature), soil moisture, soil nutrients, and soil aeration (e.g., Hills 1952, Krajina 1969, Grier et al. 1989). The diagnosis of ecological quality of a site then means to determine the expression or value of these primary factors on the site.

Relationships between site index and ecological site quality have been the focus of recent research efforts in British Columbia. Kabzems and Klinka (1987a, b), Courtin et al. (1988), Green et al. (1989), Carter and Klinka (1990, 1991), Klinka and Carter (1990), Kayahara (1992), and Q. Wang (1992) used categorical measures of ecological site quality to explain the variation in site index of coastal tree species. This study expands these efforts to lodgepole pine and white spruce. All these studies are parts of an coordinated effort aiming to establish a stronger link between biogeoclimatic ecosystem classification and growth and yield studies. They also address the plea of Grier et al. (1989) for regional surveys of site productivity and for examining the relation between the various extrinsic and intrinsic site factors and forest productivity. If the biogeoclimatic ecosystem classification is an appropriate ecological classification system, then it should yield useful measures of ecological site quality for explaining the variation in productivity of different tree species on different forest sites.

2 Materials and Methods

One hundred and thirty - three sample plots were located in naturally established, unmanaged, even - aged stands with a relatively wide range in age and stocking, and without a history of damage (Table 1). In addition, data from 18 lodgepole pine plots (Q. Wang 1992) and 15 white spruce plots (G. Wang 1993) were included. The study stands were on average 75 years old, uniformly stocked (60 to 90% tree layer cover), and situated north and south of Smithers, Telkwa, Houston, and Burns Lake. Each study stand had a more or less uniform, single tree layer, which featured dominants of one or two (exceptionally three) study species.

Table 1 General characteristics of lodgepole pine and white spruce study stands

Characteristic	Minimum	Mean	Maximum
Latitude	53°55'N	54°20'N	55°05'N
Longitude	126°30'W	127°45'W	128°25'W
Elevation (m)	505	760	940
Lodgepole pine (n=93)			
Stand age (@bh)	25	71	154
Site index (m/50 yr)	8.9	18.0	24.8
White spruce (n=77)			
Stand age (@bh)	34	78	140
Site index (m/50 yr)	4.3	17.2	25.4

The study stands were located in two geographically adjacent subzones of the Sub - boreal Spruce (SBS) zone, each representing a distinct segment of montane boreal climate: dry and cool (SBSdk) and moist and cold (SBSmc) (Table 2). A more complete climatic, vegetation, and soil description of the subzones was given by Pojar et al. (1984). In each stand, a 0.04 ha plot was located to represent an in-

dividual ecosystem relatively uniform in soil, understory vegetation, and stand characteristics. The sample plots were deliberately located to represent the widest possible gradient of ecological site quality for each of the study tree species (Verbyla and Fischer 1989).

Table 2 Means of selected climatic characteristics for the dry cool (dk) and Moist Cold (mc) sub-boreal spruce (SBS) subzones

Subzone	SBSdk	SBSmc
Climatic station *	Telkwa	Fort Babine
Elevation (m)	683	716
Mean annual precipitation (mm)	468.3	600.5
Mean precipitation May - Sept. (mm)	212.7	247.6
Mean precipitation of the driest summer month (mm)	27.9	36.5
Mean precipitation of the wettest winter	49.8	66.3
Mean annual temperature (°C)	2.9	1.2
Mean temperature of the warmest month (°C)	14.3	13.0
Mean temperature of the coldest month (°C)	-11.3	-14.3
Potential evapotranspiration (E_{max} mm/year)	247.1	231.0
Actual evapotranspiration (E_t mm/year) on zonal sites	210.6	222.6
E_t/E_{max} on zonal sites	0.85	0.96
Water deficit (mm/year) on zonal sites	36.5	8.4
Index of continentality	33.0	36.9

* Environment Canada (1982).

Site, soil, and vegetation of each plot were described using the abbreviated procedure employed by the Ecological Program Staff of the B. C. Forest Service (Luttmerding et al. 1990). The climate (represented by biogeoclimatic subzone) of each plot was identified from the map of Pojar et al. (1988) according to its location. Soil moisture regimes (SMR_s) and soil nutrient regimes (SNR_s) were estimated in the field using a combination of topographic and soil morphological properties and the methods described by Klinka et al. (1989).

Each regional climate has a unique regional soil moisture gradient that relatively ranges from 0 to 8. The relatively driest soil in any climate is designated always very xeric (0) and the relatively wettest is designated always hydric (8) (Klinka et al. 1984, Pojar et al. 1987, Klinka et al. 1989). In consequence, the same relative SMR, do not signify the same amount of soil water available for evapotranspiration by vascular plants, particularly in the upper half of the scale (0 to 4). For example, a very xeric soil (0) in a very dry and warm climate will likely have a high growing - season water deficit, while in a very wet and cool climate the same soil will likely have low or no water deficit.

The study of vegetation - environment relationships and interpretation of ecosystems across a wide range of climates requires knowledge of actual soil moisture conditions, i. e., the integration of many regional soil moisture gradients and the development of quantitatively characterized actual SMR, each describing the average amount of soil water actually available for plants. When actual SMR, are defined and characterized, the actual SMR of a site is determined by estimating its relative SMR and converting it to an actual SMR, on the basis of established correlations between relative and actual SMR, for a given biogeoclimatic unit (Table 3).

This study adopted the criteria proposed by Klinka et al. (1989), and used the energy/soil limited model of Spittelhouse and Black (1981) for calculation of potential evapotranspiration (E_{max}), actual evapotranspiration (E_t), and water deficit for each of the 18 SBSmc lodgepole pine plots established by Q. Wang (1992) and the 15 SBSdk white spruce plots established by G. Wang (1993). Each of

these plots was then assigned an appropriate actual SMR either according to E_t/E_{max} ratio or the depth of growing - season water table or gleyed soil horizon (Table 3). The actual SMR for the remaining 85

sample plots was determined by conversion of their field estimated relative SMR, on the basis of the relationship between relative and actual SMR, established for the 33 intensively studied sample plots.

Table 3 Differentiating characteristics for actual soil moisture regimes (SMR_a) and their relationship to relative SMR, in the SBSdk and SBSmc subzones (after Q. Wang 1992)

Soil moisture regime	Actual SMR	Relative SMR	
		SBSdk	SBSmc
1a. Prolonged water deficit occurs			
2a. $E_t/E_{max} > 0.40$ but ≤ 0.60	Very dry (VD)	0	0
2b. $E_t/E_{max} > 0.60$ but < 0.90	Moderately dry (MD)	1-2	1-2
2c. $E_t/E_{max} \geq 0.90$	Slightly dry (SD)	3-4	3
1b. Prolonged water deficit does not occur			
3a. Utilization of soil - stored water occurs and growing - season soil water table or gleyed horizons absent	Fresh (F)	5	4
3b. No utilization occurs or growing - season water table or gleyed horizons present			
4a. Growing - season soil water table or gleyed horizon ≥ 60 cm deep	Moist (M)	6	5
4b. Growing - season soil water table or gleyed horizon > 30 cm but < 60 cm	Very moist (VM)	6	6
4c. Growing - season soil water table or gleyed horizon > 30 cm deep but > 0 cm	Wet (W)	7	7
4d. Growing season water table at or above the ground surface	Very wet (VW)	8	8

* E_t/E_{max} - Actual evapotranspiration/potential evapotranspiration ratio.

As for soil moisture, the study of vegetation - environment relationships and ecosystem interpretations across a range of climates requires knowledge of actual soil nutrient conditions for plant growth, that is integration of many regional soil nutrient gradients and the development of quantitatively characterized actual SNR_a. This, in turn, requires identification of quantitative criteria which can then be used to divide a soil nutrient gradient into ecologically meaningful SNR_a. This study adopted the criteria identified for the SBS zone by Q. Wang (1992) who characterized field - estimated, five traditionally used SNR, by selected soil chemical properties and the frequency of nitrophytic plants (Table 4). In consequence of the developed correlations between qualitative and quantitative criteria, it was possible to assign each

study plot into an appropriate, quantitatively characterized SNR on soil morphological properties and understory vegetation of the plot.

Knowing the regional climate (biogeoclimatic subzone), actual SMR, and actual SNR for each sampleplot, study stands were stratified according to (a) climate, (b) actual SMR, (c) actual SNR, and (d) actual SMR and SNR combinations or edatopes, and assigned into (e) site series recognized by the Ecological Program Staff of the B. C. Forest Service in the SBSdk and SBSmc subzones.

In each sample plot, five tallest and largest (dominant) trees for each study species which had no obvious evidence of growth abnormalities and damage were measured for breast height age (bha), using an increment borer, and top height, using a Suunto clinometer. Site

Table 4 Means and standard deviations (in parentheses) of the forest floor and mineral soil properties and frequency of nitrophytic plants (F_{NITR3}) used to characterize soil nutrient regimes in the sub-boreal pine-spruce (SBPS) and SBS zones

Property	Soil nutrient regime				
	Very poor	Poor	Medium	Rich	Very rich
	(VP) (n=6)	(P) (n=15)	(M) (n=21)	(R) (n=20)	(VR) (n=10)
SBPS and SBS zones					
Forest floor	4.3	4.3	4.4	5.3	5.9
pH	(0.2)	(0.4)	(0.7)	(0.8)	(0.5)
C/N	63	50	39	39	29
	(9.6)	(12)	(6.5)	(6.6)	(3.8)
Total P(kg · ha ⁻¹)	15	33	67	94	302
	(8)	(13)	(51)	(45)	(203)
Total S(kg · ha ⁻¹)	21	39	58	118	474
	(11)	(23)	(57)	(83)	(479)
Mineral soil					
pH	5.9	5.5	5.1	6.1	6.1
	(0.3)	(0.4)	(0.7)	(0.9)	(0.5)
C/N	95	65	35	39	33
	(32)	(17)	(15)	(12)	(15)
Forest floor and mineral soil					
Mineralizable - N (kg · ha ⁻¹)	2.7	9.7	30	38	130
	(0.9)	(3.1)	(13)	(13)	(79)
Exchangeable Ca, Mg, K (kg · ha ⁻¹)	1203	1040	1376	3960	8278
	(291)	(789)	(1641)	(1875)	(3627)
Frequency of nitrophytic plants					
F_{NITR3}	1.5	3.7	9.3	25.2	38.2
	(0.8)	(2.9)	(14.7)	(19.4)	(21.1)

index was taken from height growth tables of Goudie (1984) for lodgepole pine and Goudie and Mitchell (1986) for white spruce.

Biogeoclimatic subzone, actual SMR, and actual SNR data were used as independent categorical variables in stratification, analysis of variance, and regression analysis for each study species. Site index was investigated for normality using a graphical analysis (probability plot) (Chambers et al. 1983, Wilkinson 1990). One way analysis of variance (ANOVA) and Tukey's test (Zar 1974) were conducted to detect differences in site index among groups of plots stratified according to categorical variables.

In order to specify appropriate models, the relationships between site index and dependent variables were checked for nonlinearity using a graphical display (Chambers et al. 1983, Wilkinson 1990).

Simple and multiple regressions employing dummy (qualitative or indicator) variables (Chatterjee and Price 1977) were used to examine relationships between site index and ecological site quality. The relationships examined are specified in Table 5.

Means and standard deviations of site index in relation to categorical variable were shown in categorical plots (Wilkinson 1990). A distance weighted least square (DWLS) smoothing method (McLain 1974, Wilkinson 1990) was used to superimposed the isolines of site index onto edatopic grids. All data were summarized and analyzed using the SYSTAT and SYGRAPH statistical packages (Wilkinson 1990).

3 Results

3.1 Relationships between site index and climate

Table 5 Synopsis of the regression models used to test the relationships between site index (SI, m @ 50 yr of bha) and selected categorical variables[1] and [6] $SI = f(BGCS_s)$

where BGCSs (biogeoclimatic subzones) are dummy variables representing SBSdk and SBSmc subzones.

[2] and [7] $SI = f(SMR_s)$ where SMR_s are dummy variables representing actual soil moisture regimes from VD through VW; VD = very dry, MD = moderately dry, SD = slightly dry, F = fresh, M = moist, VM = very moist, W = wet, and VW = very wet.[3] and [8] $SI = f(SNR_s)$ where SNR_s are dummy variables representing actual soil nutrient regimes from VP through VR; VP = very poor, P = poor, M = medium, R = rich, and VR = very rich.[4] and [9] $SI = f(SMR_s, SNR_s)$ where SMR_s and SNR_s are dummy variables defined above.[5] and [10] $SI = f(BGCS, SMR_s, SNR_s)$ where BGCS, SMR_s, and SNR_s dummy variables defined above.

Stratification of all lodgepole pine and white spruce study stands according to biogeoclimatic subzones did not indicate any significant change of site index with climate. Comparing only lodgepole pine stands on zonal sites (slightly dry and medium in the SBSdk subzone, fresh and medium in the SBSmc subzone), the mean site index increased from 18.9 m in the SBSdk subzone to 20.2 m in the SBSmc subzone. A similar comparison of site index for spruce showed a slight decrease from 17.8 m in the SBSdk subzone to 17.4 m in the SBSmc subzone for the stands on zonal sites.

3.2 Relationships between site index and soil moisture

There were similar, strong, and curvilinear relationships between site index of lodgepole pine and white spruce and actual SMR_s (Figures 1 and 2). Mean site index of both species increased from very dry to fresh sites, reached a plateau on fresh and moist sites (approximately 20 m) — the region of the most productive growth for both species — and decreased from moist to very wet sites. On very dry, wet, and very wet sites, spruce site index was considerably lower than that of lodgepole pine. ANOVA and Tukey's test indicated for both species the presence of a weak productivity gradient

coinciding with the assumed soil moisture gradient ($P \leq 0.05$).

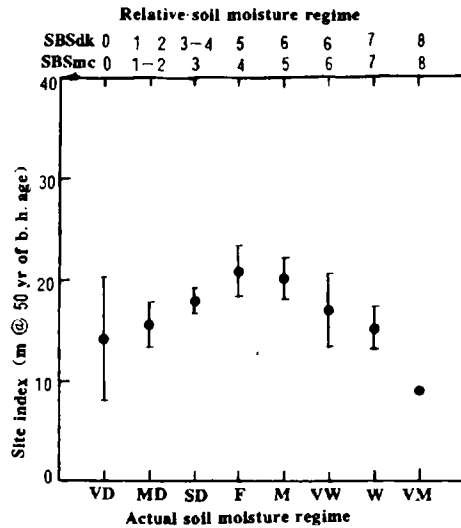


Fig. 1 Categorical plot of lodgepole pine site index in relation to actual and relative soil moisture regimes (SMR_s). Symbols for the actual SMR_s are defined in Table 3. Vertical bars represent standard deviation.

3.3 Relationships between site index and soil nitrogen

Stratification of study stands according to SNR_s showed a different relationship for each species (Figures 3 and 4). Mean lodgepole pine site index increased from very poor to rich sites with the rate of increasing nitrogen availability, and reached a plateau (approximately 20m) on rich and very rich sites. There was no significant difference in site index between

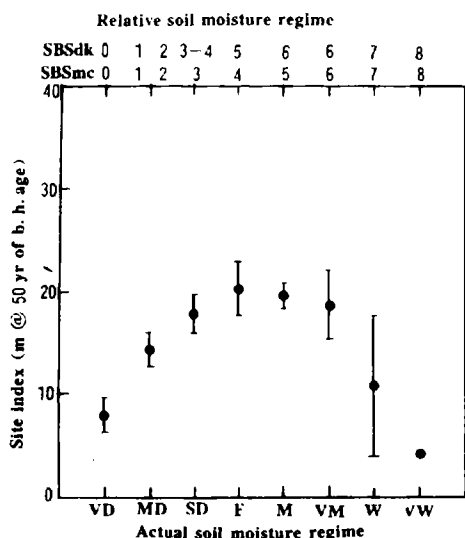


Fig. 2 Categorical plot of white spruce site index in relation to actual and relative soil moisture regimes (SMR_s). Symbols for the actual SMR_s are defined in Table 3. Vertical bars represent standard deviation.

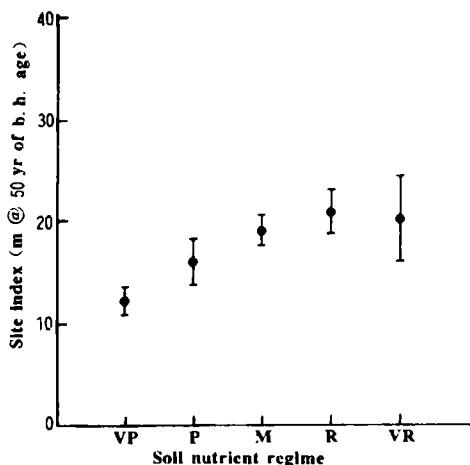


Fig. 3 Categorical plot of lodgepole pine site index in relation to soil nutrient regimes (SNR_s). Symbols for SNR_s are defined in Table 3. Vertical bars represent standard deviation.

medium, rich and very rich sites — the region of the most productive growth. In comparison to lodgepole pine, mean white spruce site index increased consistently from very poor through to very rich sites on which it reached the value of nearly 23m. ANOVA and Tukey's test indicated

that the relationship between productivity and assumed nitrogen gradients was weak for lodgepole pine ($P \leq 0.05$) but strong for spruce ($P \leq 0.05$).

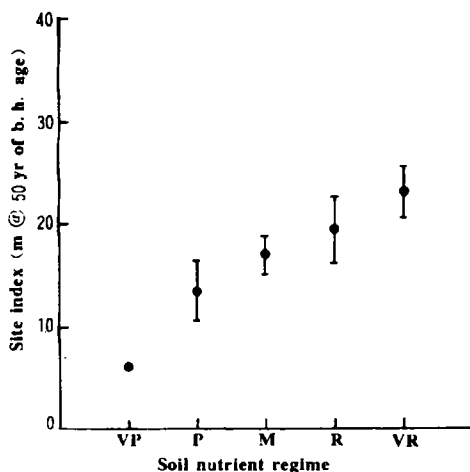


Fig. 4 Categorical plot of white spruce site index in relation to soil nutrient regimes (SNR_s). Symbols for SNR_s are defined in Table 3. Vertical bars represent standard deviation.

3.4 Regression analysis

Five regression models (Table 5) were developed to test relationships between site index and categorical measures of ecological site quality for lodgepole pine (equations [1] through [5], Table 6) and white spruce (equations [6] through [10], Table 7). All models were significant at $P \leq 0.05$, except for the climatic models (equations [1] and [6]).

The climatic models showed no relationships with site index and inclusion of biogeoclimatic subzone as a categorical variable into the edatopic models did not improve their performance (equations [5] and [10]). These results corroborate the earlier comparison, and suggest that the relationship between forest productivity and assumed climatic gradients is weak for both species.

The SMR and SNR models (equations [2] and [3], Table 6; equations [7] and [8], Table 7) each had moderate rela-

Table 6 Models for the regression of lodgepole pine site index (SI, m @ 50 yr of bha) on selected categorical variables (n=93)

- [1] $SI = 18.21 - 0.44(SBSdk) - 0.00(SBSmc)^*$
Adjusted $R^2 = 0.01$ SEE $^{**} = 3.2$ m
- [2] $SI = 8.90 + 5.25(VD) + 6.68(MD) + 9.04(SD) + 11.92(F) + 11.18(M) + 8.08(VM) + 6.30(W) + 0.00(VW)$
Adjusted $R^2 = 0.45$ SEE = 2.4 m
- [3] $SI = 20.23 - 7.98(VP) - 4.11(P) - 1.09(M) + 0.51(R) + 0.00(VR)$
Adjusted $R^2 = 0.60$ SEE = 2.0 m
- [4] $SI = 14.17 - 9.27(VP) - 5.27(P) - 3.11(M) - 1.72(R) - 0.00(VR) + 4.17(VD) + 6.85(MD) + 8.13(SD) + 9.33(F) + 8.48(M) + 6.97(VM) + 1.89(W) + 0.00(VW)$
Adjusted $R^2 = 0.82$ SEE = 1.4 m
- [5] $SI = 14.21 + 0.52(SBSdk) + 0.00(SBSmc) - 9.41(VP) - 5.31(P) - 3.06(M) - 1.61(R) - 0.00(VR) + 4.12(VD) + 6.52(MD) + 7.84(SD) + 8.98(F) + 8.26(M) + 6.76(VM) + 1.79(W) + 0.00(VW)$
Adjusted $R^2 = 0.82$ SEE = 1.4 m

Symbols used for dummy variables are explained in Table 5. * Model is not significant at $P \leq 0.05$. ** SEE - standard error of estimates.

tionships with site index, but the edatope models (equation [4], Table 7; equation [9], Table 7) accounted for the largest proportion of the variation in site index ($R^2 > 0.8$) and gave the lowest standard error (ranging from 1.4 to 1.6 m) for each species (Figures 5 and 6). Actual SMR and SNR were found to exhibit a

high collinearity. Consequently, the effect of changes in either of these categorical variables cannot be examined independently, and the use of the edatope model should be restricted to site and stand conditions representative of the sample population.

3.5 Relationships between site index

Table 7 Models for the regression of white spruce site index (SI, m/50 yr) on selected categorical variables (n = 77)

- [6] $SI = 17.01 + 1.17(SBSdk) + 0.00(SBSmc)^*$
Adjusted $R^2 = 0.01$ SEE = 4.2 m
- [7] $SI = 4.30 + 3.67(VD) + 10.08(MD) + 13.59(SD) + 16.05(F) + 15.38(M) + 14.45(VM) + 6.55(W) + 0.00(VW)$
Adjusted $R^2 = 0.65$ SEE = 2.5 m
- [8] $SI = 22.89 - 16.74(VP) - 9.43(P) - 6.03(M) - 3.58(R) - 0.00(VR)$
Adjusted $R^2 = 0.58$ SEE = 2.7 m
- [9] $SI = 7.13 - 10.09(VP) - 7.17(P) - 5.05(M) - 2.83(R) - 0.00(VR) + 9.25(VD) + 13.01(MD) + 15.37(SD) + 16.10(F) + 15.58(M) + 14.97(VM) + 10.58(W) + 0.00(VW)$
Adjusted $R^2 = 0.85$ SEE = 1.6 m
- [10] $SI = 6.90 + 8.36(VD) + 11.81(MD) + 13.90(SD) + 15.02(F) + 15.62(M) + 14.10(VM) + 10.08(W) + 0.00(VW) - 11.87(VP) - 6.80(P) - 5.10(M) - 2.56(R) - 0.00(VR) + 1.80(SBSdk) + 0.00(SBSmc)$
Adjusted $R^2 = 0.89$ SEE = 1.4 m

Symbols employed for dummy variables are explained in Table 5. * Models are not significant at $P \leq 0.05$. and site series

Stratification of study stands according to SBSdk and SBSmc2 site series recognized by the Ecological Program Staff of the B. C. Forest Service in the SBSdk and SBSmc subzones showed weak and very generalized relationships to site index (Table 8). The earlier described

trends of change in mean site index with climate, soil moisture, and soil nitrogen were detectable but obscured. Site index did not vary between species and climate, i. e., between edaphically comparable SBSdk and SBSmc2 site series. Within each biogeoclimatic unit, two groups of site series could be recognized: (a) a low site

index group ($SI < 18$ m) related apparently to very poor and poor SNR_s , and (b) a

high site index group ($SI \geq 18$ m) related

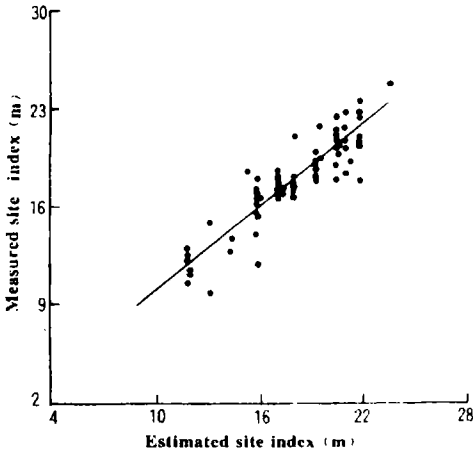


Fig. 5 Plot of estimated (edatope model, equation [4], Table 6) against measured lodgepole pine site index (SI , m @50 yr of bha).

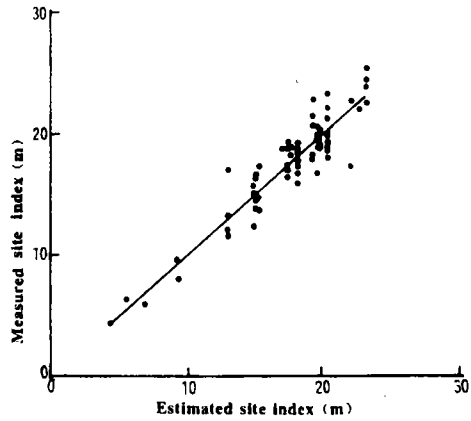


Fig. 6 Plot of estimated (edatope model, equation [9], Table 7) against measured white spruce site index (SI , m @50 yr of bha).

Table 8 Range of relative and actual soil moisture regimes (SMR_s), soil nutrient regimes (SNR_s), number of study stands (N), and means (M) and standard deviation (S) of site index (SI , m @ 50 yr of bha) for studied SBSdk and SBSmc2 site series

Site series	SMR		SNR	Lodgepole pine			White spruce		
	Relative *	Actual		N	M	S	N	M	S
SBSdk subzone									
01 Sxw - Spruce - Purple peavine	3-5	SD-F	P-R	19	19.7	2.1	24	19.1	2.1
02 Pl - Juniper - Ricegrass	0-1	VD-MD	VP-P	8	14.6	2.0	2	15.1	na
03 Pl - Feathermoss - Cladina	2	MD	VP-M	11	15.4	2.1	7	15.3	1.4
05 Sxw - Spiraea - Feathermoss	3-4	SD	VP-M	11	17.8	1.3	8	17.3	1.4
06 Sxw - Twinberry - Coltsfoot	4-5	SD-F	M-VR	15	21.0	1.9	25	20.2	2.6
07 Sxw - Horsetail	5-6	F-VM	M-VR	11	21.5	2.0	19	21.4	2.3
09 Sb - Creep snowberry - Sphag.	6-8	VM-VW	VP-P	3	14.8	3.5	2	10.5	na
10 Sb - Soft sedge - Sphagnum	6-8	VM-VWM	VR	1	18.1	na	4	21.5	2.0
SBSmc2 variant									
01 Sxw - Huckleberry	3-4	SD-F	P-R	24	19.1	2.0	12	18.0	1.8
02 Pl - Huckleberry - Cladina	0-2	VD-MD	VP-M	7	15.9	2.5	4	12.8	1.2
03 SbPl - Feathermoss	3-5	SD-M	VP-P	7	17.1	0.7	1	13.6	na
05 Sxw - Twinberry - Coltsfoot	4-5	F-M	M-R	19	20.7	1.5	16	18.7	1.1
06 Sxw - Oak fern	4-5	F-M	R-VR	11	21.1	1.4	12	19.9	1.6
07 Sxw - Scrubbirch - Feather-moss	5-6	M-VM	VP-P	3	13.1	2.5	1	12.3	na
09 Sxw - Devil'sclub	6-7	M-VM	R-VR	11	20.6	1.4	10	19.5	1.5
10 Sxw - Horsetail	6-7	M-W	P-VR	16	19.6	2.7	14	18.6	2.4
12 SbSxw - Scrub birch Sedge	7-8	W-VW	P-VR	3	13.1	3.9	2	8.1	na

* Relative SMR_s , very xeric (0) corresponding to very dry (VD) actual SMR and hydric (8) corresponding to very wet (VW) actual SMR , have not been used in differentiating SBSdk and SBSmc2 site series. The study stands for which these regimes were recognized were assigned to the relatively driest or the relatively wettest site series in each biogeoclimatic unit. Symbols for SMR_s and SNR_s are explained in Table 3 and 4, respectively.

apparently to medium, rich and very rich SNR_s. These results suggest that site series are poor predictors of lodgepole pine and white spruce site index.

4 Discussion

Equal representation of stands according to biogeoclimatic subzones, SMR_s, and SNR_s would be the most desirable situation for the study of relationships between site index and ecological site quality. This situation, however, is nearly impossible to fulfill, as certain climatic, soil moisture, and soil nutrient combinations may not occur or occur very rarely in the landscape. The usual sequence of sites in a topographically diversified landscape proceeds in a diagonal direction, i. e. , from water - deficient and poor sites to water - surplus and rich sites. Such a diagonal sequence was present and sampled in the study area.

In relation to SMR_s, both lodgepole pine and white spruce study stands were poorly represented on very dry, wet, and very wet sites; in relation to SNR_s, a poor representation occurred for lodgepole pine stands on very rich sites, and for spruce stands on very poor sites. In consequence, our analysis of site index - ecological site quality relationships suffered from missing values and the bias introduced by sampling when the study stands were stratified according to SMR_s and SNR_s. Therefore, the reader should evaluate the site index trends and predictions presented in this study with this bias in mind.

Despite a limited representation of climates and poor representation of certain combinations of SMR_s and SNR_s, the large amount of variation explained by the edatope models revealed the presence of strong relationships between lodgepole pine and white spruce site indices and categorical measures of ecological site quality.

The results obtained conform well with those reported for Douglas - fir in the Coastal Western Hemlock zone by Carter and Klinka (1990) and Klinka and Carter (1990), lodgepole pine in the SBS zone by Q. Wang (1992), and white spruce in the SBS zone by G. Wang (1993).

The strength of relationships between site index and site series will depend on (1) appropriate number of well distributed stands for each tree species and site series and (2) the edatopic range and/or overlap of site series. The wider and/or overlapping edatopic range, the weaker relationships between site index and site series. An occasionally poor representation of species and site series and overlapping SMR and/or SNR ranging in nearly all site series are the factors which in this study prevented site series to be more effective in predicting site index. However, a poor site index - site series relationship is inconsequential as it by no means detracts from the strong relationships between site index, SMR_s, and SNR_s quantified by the edatope models (equations [4], Table 6; equation [8], Table 7).

Both lodgepole pine and white spruce have a wide ecological amplitude in relation to climate, soil moisture, and soil nutrient gradients (e. g. , Krajina 1969, Nienstaedt and Zasada 1990). Growth of these species increases with increasing potential evapotranspiration from cool to warm climates. Within the SBS zone, site index will also increase from relatively cooler to warmer climates, presumably reflected by biogeoclimatic subzones. Insignificant differences in site index for both lodgepole pine and white spruce between zonal sites found in this study indicate that the SBSdk and SBSmc subzones are climatically akin. A similar situation was suggested by Laing and McCulloch (1988) for the SBSmc subzone and ICHm-

c2 variant.

It may be that the differences in precipitation and temperature between the study subzones do not exert a significant influence on forest growth via actual evapotranspiration. This is likely due to compensating effects between precipitation and temperature. Due to a higher temperature in the SBSdk subzone, there is a greater potential (based on potential evapotranspiration) for vascular plant activity in the SBSdk subzone than in the SBSmc subzone (Table 2). However, this potential is not likely realized due to a lower precipitation in the SBSdk subzone. Higher precipitation (and lower water deficit) in the SBSmc subzone is responsible for a slightly higher actual evapotranspiration relative to the SBSdk subzone. Thus, due to the presence of a weak climatic (actual evapotranspiration) gradient between the SBSdk and SBSmc subzones, examination of site index – ecological site quality relationships in the study stands can be justified without considering a climatic factor.

In relation to SNR_s, white spruce site index was lower than that of lodgepole pine on all but rich and very rich sites, suggesting that lodgepole pine is relatively less demanding for nitrogen to maintain the growth level within given soil moisture conditions than spruce. Assuming the presence of fresh or moist sites, the most productive growth of lodgepole pine occurred within the medium and rich segment of a soil nitrogen gradient, with the maximum site index of nearly 25 m on fresh and very rich sites. The most productive growth of spruce was also confined to fresh and very rich sites, with the maximum site index of 24 m. Our characterization of the edatopes supporting for the most productive growth of each species is in agreement with Krajina (1969).

Krajina (1969) stated that the most productive growth of lodgepole pine occurs on fresh to moist and rich sites, and that very rich sites do not support the growth of the species. It is suggested that this discrepancy is due to the difference in characterizing the soil nutrient gradient and SNR_s. He considered very rich sites to have not only a very high available – nitrogen level but also to be calcium – rich, with pH > 6 in the surface soil horizons. Indeed, lodgepole pine is rare on circum-neutral soils and absent on alkaline soil (Krajina 1969, Cochran 1985).

Compared to white spruce, little is known about lodgepole pine nutrient relationships (e. g. , Krajina 1969, Lotan and Perry 1983, Cochran 1985). Some studies have shown none or weak relationships between soil nutrient levels and growth (e. g. , Duffy 1964), while others claimed significant response to nitrogen fertilization (e. g. , Etter 1969). On the basis of this study and considering the studies of Q. Wang (1992) and Yole et al. (1991), it is suggested that lodgepole pine is nitrogen less – demanding than white spruce and that its growth response to nitrogen additions will likely be inconsequential, except on very poor and poor sites. If our interpretation of site index – SNR relationships is correct then a significant growth response of spruce to nitrogen additions should occur on very poor through to rich sites. This has been, in fact, found by Brockley (pers. comm.) in recently established spruce fertilizer trials.

Although the effect of changes in either of SMR or SNR cannot be examined independently, and despite a biased edatopic representation of the study stands, it appears for both lodgepole and white spruce that the variation in site index along a soil moisture gradient was higher than that along a soil nitrogen gradient,

which show that site index isolines for lodgepole pine and spruce are akin, with spruce being more sensitive to extremes in water deficit or water surplus and supply of available soil nitrogen than lodgepole pine. Spruce site index appears to be equal to or surpasses (by approximately 2m) lodgepole pine site index only in the slightly dry to very moist and rich to very rich edatopic region. On all other sites, lodgepole pine site index appears to be higher than that of spruce, with the difference in favour of lodgepole pine increasing (up to approximately a maximum of 2 m) with decreasing supply of available nitrogen and increasing water deficit or water surplus.

for the purpose of timber production, white spruce should always be considered a major crop species in the slightly dry to very moist and rich to very rich (most productive) edatopic region in the SBSdk and SBSmc subzones, with lodgepole pine playing a role of a major or minor species. On the remainder of the sites, lodgepole pine should be considered as a major crop species and spruce a minor crop species with its presence decreasing with decreasing supply of available nitrogen and increasing water deficit or water surplus. When making final tree species selection decisions, this interpretation should take into account (a) possible differences in

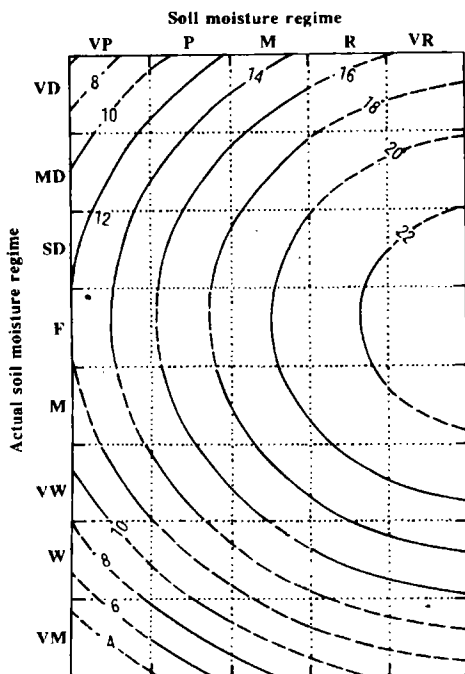


Fig. 7 An edatopic grid showing lodgepole pine site index isolines for both SBSdk and SBSmc subzones calculated from equation [4] (edatope model) and fitted using quadratic smoothing algorithm. Dashed isolines are beyond the range of SMR - SNR combinations of the study stands. Symbols for SMR_s and SNR_s are explained in Table 3 and 4, respectively.

Thus, on the basis of site index and

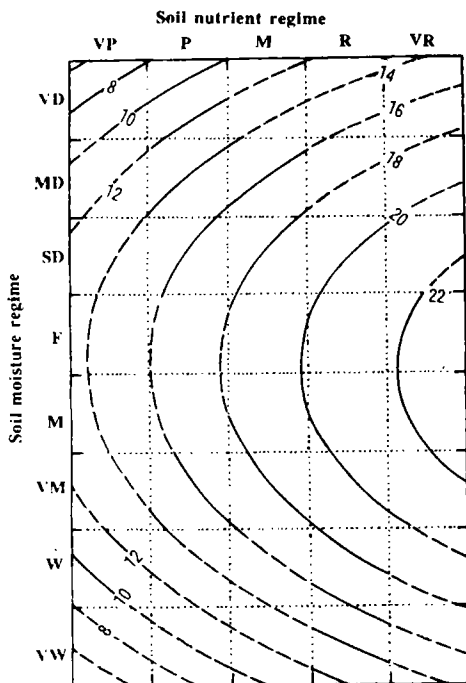


Fig. 8 An edatopic grid showing white spruce site index isolines for both SBSdk and SBSmc subzones calculated from equation [8] (edatope model) and fitted using quadratic smoothing algorithm. Dashed isolines are beyond the range of SMR - SNR combinations of the study stands. Symbols for SMR_s and SNR_s are explained in Table 3 and 4, respectively.

volume and/or value of timber crops pro-

duced in relation to rotation, (b) crop reliability, (c) silvicultural feasibility, and (d) ecosystem biodiversity of different tree species combination options (Klinka and Feller 1984).

With biogeoclimatic classification in use, and relationships between site index and ecological site quality analyzed, it is appropriate to develop operational tools for estimating site index of potential crop species for any given forest site. Considering (a) the wide usage of edatopic grids, (b) necessity to identify biogeoclimatic subzone, SMR, and SNR for identification of site associations or site series, (c) the usefulness of the categorical measures of soil moisture and soil nutrients in estimating their direct measures, and (d) performance of the regression models developed, it is proposed that site index isolines construed by the edatope models and superimposed onto edatopic grids is the most efficient means for field forestry personnel (Krajina 1972) (Figures 7 and 8).

5 Conclusions

Strong and meaningful relationships were obtained when using categorical measures of ecological site quality as independent variables in describing their relationships with lodgepole pine and white spruce site index in the SBSdk and SBSmc subzones. The most useful variables were soil moisture regime and soil nutrient regime. Biogeoclimatic subzone did not improve performance of the edatope models, probably due to climatic affinities between the subzones. The mode of variation in site index of both species conformed well with trends proposed by Krajina (1969). In order to estimate lodgepole pine and spruce site index in situa-

tions where direct estimates of site index are inappropriate, the use of isolines construed by the edatope model is recommended following testing of the model on an independent data set.

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