Trembling aspen site index in relation to environmental measures of site quality at two spatial scales

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Abstract: To evaluate the variation in trembling aspen (*Populus tremuloides* Michx.) productivity at a large geographic scale, we examined the relationships between site index and environmental factors from 142 even-aged, fully stocked stands located on a variety of sites across interior British Columbia. Site index was derived from stem analysis and the environmental measures included climate surrogates (latitude, longitude, and elevation), biogeoclimatic zone, slope–aspect, actual soil moisture regime (SMR), and soil nutrient regime (SNR). The spatial gradients (latitude, longitude, and elevation), slope–aspect, SMR, and SNR affected aspen site index, but their relationships greatly varied with biogeoclimatic zone. At the provincial scale, these relationships were weaker than on the zonal scale. Among the models developed for predicting aspen site index, we recommend the zone-specific all-factor model for application, which explained 82% of the variation of site index and provided unbiased and precise predictions.

Résumé : Nous avons examiné les relations entre l'indice de station et les facteurs environnementaux dans 142 peuplements équiennes de densité relative adéquate situés sur une variété de sites dans toute la zone intérieure de la Colombie-Britannique afin d'évaluer la variation dans la productivité du peuplier faux-tremble (*Populus tremuloides* Michx.) sur une vaste échelle géographique. L'indice de station a été obtenu par l'analyse de tige et les mesures environnementales incluaient des variables représentatives du climat (latitude, longitude et altitude), la zone biogéoclimatique, l'orientation de la pente, le régime hydrique du sol et le régime nutritif du sol. Les gradients spatiaux (latitude, longitude et altitude), l'orientation de la pente, le régime hydrique du sol et le régime nutritif du sol influencent l'indice de station du peuplier, mais leurs relations varient grandement selon la zone biogéoclimatique. À l'échelle de la province, ces relations sont plus faibles qu'à l'échelle des zones. Parmi les modèles qui ont été développés pour prédire l'indice de station du peuplier, nous recommandons en pratique le modèle spécifique à chaque zone qui tient compte de tous les facteurs. Ce modèle explique 82% de la variation dans l'indice de station et génère des prédictions précises et non biaisées.

[Traduit par la Rédaction]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is one of the most common tree species in the boreal and temperate forests of North America. Aspen's high plasticity to many environmental factors is evident from its wide geographic distribution, range of climates and sites, and association with many different species. Aspen's distribution is curtailed to the south by dry climates and to the west by perhumid climate. Low growing season temperatures limit aspen's growth at the northern limit of its distribution; however, aspen grows far beyond the southern permafrost boundary, occurring on warmer slopes free of permafrost. In interior Alaska, aspen can grow in regions with winter minimum temperatures as low as –61°C and only 180 mm annual precipitation. Aspen tolerates these extremes through very low evapotranspiration rates in the cool summers of these regions (Strothmann and Zasada 1965; Perala 1990).

Topography affects aspen growth in different ways in northern and southern latitudes. In the subarctic and boreal climates of Alaska and Canada, the best growth occurs on warm-aspect slopes. In the western and central regions of the United States, and in the woodland–prairie ecotone of Canada, aspen growth is most vigorous on cool-aspect slopes (Shepperd 1986). The most productive aspen growth occurs on well drained and aerated, loamy, nutrient-rich soils, derived from base-rich parent materials. Soils with high clay content and growing-season water tables <60 cm deep are less productive for aspen growth (Graham et al. 1963; Perala 1977).

In British Columbia (B.C.), aspen is common throughout all submontane and montane, continental, forested biogeoclimatic zones including the Boreal White and Black Spruce (BWBS), Sub-Boreal Spruce (SBS), Interior Cedar–

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Hemlock (ICH), Montane Spruce (MS), and Interior Douglas-Fir (IDF) zones that were classified to differentiate biogeoclimatic variations of forest ecosystems (Krajina 1969; Meidinger and Pojar 1991). Although each of the zones covers a wide spatial range in terms of latitude, longitude, and elevation, environmental characteristics such as mean annual precipitation and temperature vary greatly among these zones (Table 1). These environmental variations within aspen’s native range in British Columbia may suggest a corresponding variation in the species’ productivity.

Relationships between environmental factors and site index have been and continue to be examined in many studies (e.g., Monserud 1984; Monserud et al. 1990; Wang 1995; Chen et al. 1998*b*). Most of these studies have had limited success in accounting for the variation in site index over a large geographic area. Efforts to understand the influence of site on aspen growth have increased in the province during the last decade, partly because of the species’ potential as a fibre source and partly the increasing role of hardwoods in silvicultural management. Several previous studies addressed aspen productivity, including height growth modeling (Chen et al. 1998*a*), local prediction of site index from environmental factors (Chen et al. 1998*b*), and characterization of humus forms in aspen ecosystems (Fons et al. 1998).

This study presented an opportunity to examine the variation in site index at a large spatial scale, as our database covered the entire interior British Columbia. The objectives of our study were (*i*) to examine the effect of environmental factors on aspen site index at different spatial scales, i.e., provincial and zone scales, and (*ii*) to develop predictive site index models from easily measurable environmental factors.

Materials and methods

Study area and sampling methods

Study stands were deliberately selected to capture the widest range of climate, soil moisture, and soil nutrients possible for supporting aspen growth throughout the BWBS, ICH, IDF, MS, and sub-boreal (SB) zones, a group combining the SBS and SBPS zones (Fig. 1, Table 1). Aspen can tolerate minimum temperatures down to –58.9°C (Smith River, BWBS zone), and maximum temperatures up to 43.3°C (Greenwood, DF zone). Annual precipitation extremes tolerated by aspen range from 276 mm (Alexis Creek, IDF zone), to 1419 mm (Mica Dam, ICH zone). Within the study zones, the ICH zone has the highest mean annual precipitation (795 mm), and the IDF zone has the lowest (442 mm).

Frequent forest fires maintain a large portion of the landscape in early and mid-seral stages. Depending on the zone and local site conditions, shade-intolerant aspen frequently associates with black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *Picea glauca*), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The soils typically associated with aspen stands include Brunisols, Luvisols, and Podzols (rarely Gleysols or organic soils) developed from a variety of parent materials. Associated humus forms

Table 1. Summary of trembling aspen study plots by biogeoclimatic zones with ranges in elevation, latitude, longitude, and climatic characteristics.

Biogeoclimatic (BEC) zone	No. of plots	Elevation range (m)	Latitude (N)	Longitude (W)	Mean annual precipitation (mm)[a]	Mean annual temperature (°C)[a]	Site index (m)[b]
Boreal White and Black Spruce (BWBS)	59	525–980	55°42′–59°35′	120°26′–133°10′	446 (46)	0.6 (84)	13.7 (5.5–25.1)
Interior Cedar–Hemlock (ICH)	19	380–1025	49°02′–55°28′	116°11′–128°31′	795 (60)	5.5 (60)	21.7 (13.0–30.7)
Interior Douglas-Fir (IDF)	23	960–1285	49°22′–52°11′	119°05′–123°31′	442 (90)	5.1 (73)	16.2 (8.7–24.6)
Montane Spruce (MS)	18	980–1285	49°01′–49°31′	115°30′–119°35′	598 (13)	3.1 (12)	22.8 (12.6–29.6)
Sub–boreal (SB)	23	790–1040	52°08′–54°35′	121°21′–124°32′	620 (92)	2.2 (129)	17.0 (10.5–23.7)
Total or range	142	380–1285	49°01′–59°35′	115°30′–133°10′	276–1916	–3.2 to 9.7	5.5–30.7

[a]Values in parentheses are numbers of climatic stations.
[b]Values in parentheses are ranges.

Fig. 1. Trembling aspen sample plot locations in British Columbia.

are mormoders, moders, mullmoders, or mulls (Fons et al. 1998).

Sample plots were established in naturally established, unmanaged, fully stocked, even-aged aspen stands older than 50 years at breast height (1.3 m) without a history of suppression or damage. Most of the selected stands originated after wildfire, and each stand had a uniform, single, aspen-dominated canopy layer. The developmental stage of study stands ranged from the stem exclusion to understory reinitiation stages (Oliver and Larson 1996). The stands were also relatively uniform in understory vegetation, humus form, and soil characteristics. Within each stand a 20 × 20 m sample plot relatively uniform in stand and environmental characteristics was established.

Determination of environmental factors

Biogeoclimatic maps (B.C. Ministry of Forests 1988) were used to identify the zone in which each plot was located. Climatic records (based on 1200 weather stations) of mean annual, summer, and winter precipitation; mean annual temperature; maximum and minimum temperatures; and mean sum degree-days >5°C were obtained from the B.C. Ministry of Forests to characterize the climate in each study zone (Table 1). Topographic maps were used to determine the latitude and longitude of each plot, elevation was measured with a Thommen pocket altimeter, and aspect was measured with a Suunto pocket compass. Topography was described according to Luttmerding et al. (1990), and soils and vegetation were described in accordance with the site diagnosis procedure developed by Green and Klinka (1994). Soil moisture regime (SMR) and soil nutrient regime (SNR) of each plot were estimated in the field using a combination of topographic and soil morphological properties and indicator plants (if present) as described in Klinka et al. (1989) and Green and Klinka (1994).

Stem analysis and site index determination

Within each plot the three largest dominant trees (by DBH), with no visible evidence of growth abnormalities or damage, were felled for stem analysis. Total tree heights were measured in the field after felling. Stem discs were then cut at 30 cm above the root collar, and at 1-m intervals to the top of the tree. Stunted trees had stem disks cut at 30 cm above the root collar, and at 50-cm intervals to the top of the tree. In the laboratory, each disc was split and a razor was used to expose two, clear radial sections, from pith to bark. Where necessary, zinc oxide powder was applied to make the rings clearly visible. Rings were counted in the two directions with the aid of a binocular microscope. Particular attention was paid to abrupt changes in radial increment indicating possible suppression or damages.

Raw stem analysis data were adjusted using Carmean's (1972) algorithm to calculate tree height corresponding to the age at each sectioned disk (Dyer and Bailey 1987; Huang 1994; Chen and Klinka 2000). The height versus age curves for the three sampled trees per plot were examined for uniformity and the presence of suppression or damage. All sampled trees within each plot showed a similar height growth pattern up to the age of 70 years. This is not very surprising since trembling aspen is a very shade-intolerant species. A linear interpolation method was used to develop an average curve for each sample plot using Carmean's correction (Nigh 1996; Chen and Klinka 2000); height–age data were averaged by plot in 5-year intervals in age up to the youngest sampled tree in the plot. The site index (SI) for each plot is calculated as the mean height of the sampled trees at breast-height age 50 years.

Data analysis

The effects of zone, spatial gradients (LAT, latitude; LON, longitude; and ELE, elevation), and local site factors such as slope–aspect (RG, ridge; E, slope >3% and azimuth 45–135°; S, slope >3% and azimuth 135–225°; W, slope >3% and azimuth 225–315°; N, slope >3% and azimuth 315–45°; and FL, flat), SMR (VD, very dry; MD, moderately dry; SD, slightly dry; F, fresh; M, moist; and VM, very moist), and SNR (VP, very poor; P, poor; M, medium; R, rich; and VR, very rich) were examined using the general linear model procedure (Neter et al. 1996; SPSS, Inc. 1997). The effects of zone and slope–aspect, SMR, or SNR on site index were tested by

$$[1] \qquad \mathrm{SI} = \mu + Z_i + S_j + Z \times S_{ij} + \varepsilon_{k(ij)}$$

where SI is site index; Z_i is the effect of zone; S_j is the effect of slope–aspect, SMR, or SNR; $Z \times S_{ij}$ is the interaction between zone and slope–aspect, SMR, or SNR; and $\varepsilon_{k(ij)}$ is the error term.

Multiple regression models were developed to predict site index. Site index – environment relationships were examined for linearity and homogenous variance on continuous variables including latitude, longitude, and elevation. Categorical factors were converted into dummy variables in the multiple regression analysis. The backward stepwise procedure was used in selecting independent variables at a significance level of $P < 0.05$. Models using only climatic, topographic, or edaphic variables alone were not sufficient for predicting site index as reported by Chen et al. (1998*b*). Similar results were found in this study. Consequently, only the model using all environmental measurements at the provincial scale and the zone-specific model (all-factor model) are presented in this paper. Residuals from model fittings were examined for precision and bias. The precision was examined using mean squared prediction error (Neter et al. 1996). If a model is unbiased, a fitted regression of predicted versus measured site indices should not be different from the regression $y = x$ (Neter et al. 1996; Chen and Klinka 2000).

Table 2. Effect of biogeoclimatic zone, elevation, longitude, and latitude on trembling aspen site index.

Source	SS	df	MS	*F*	*P*
Zone (Z)	48.64	4	12.16	0.88	0.480
Elevation (E)	17.51	1	17.51	1.26	0.264
Longitude (LON)	26.81	1	26.81	1.93	0.167
Latitude (LAT)	0.01	1	0.01	0.00	0.983
Z × E	143.42	4	35.86	2.58	0.040
Z × LON	112.91	4	28.23	2.03	0.094
Z × LAT	100.69	4	25.17	1.81	0.130
Error	1692.83	122	13.88		

Results

Effect of spatial, topographic, and edaphic gradients

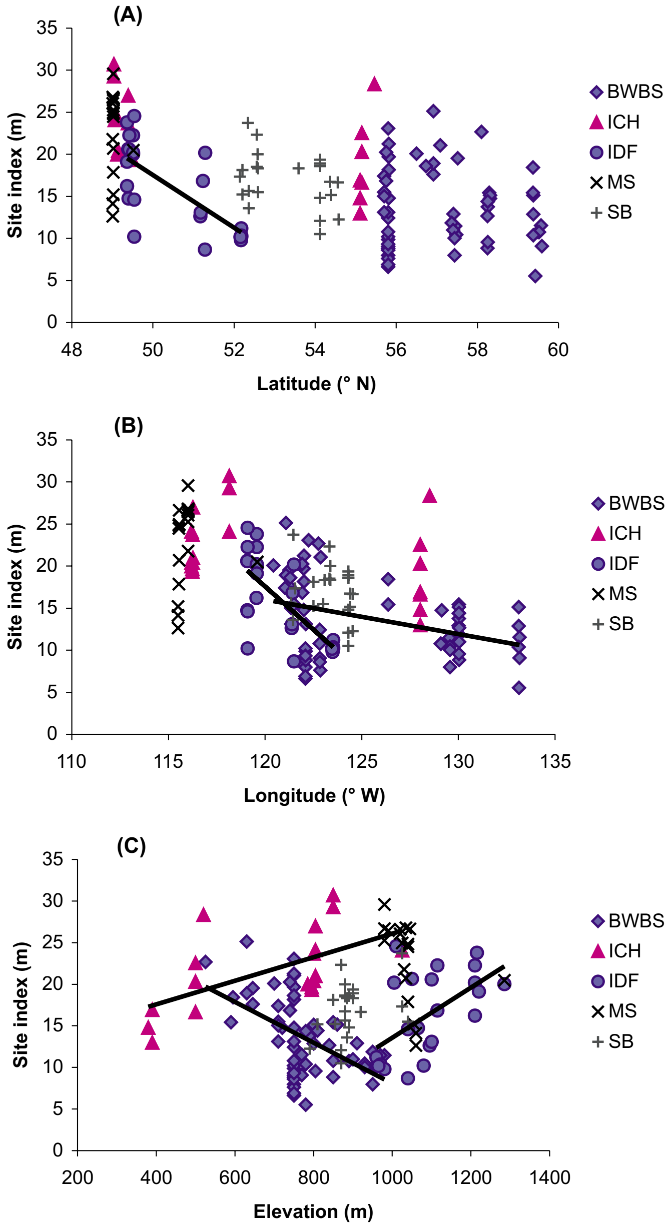
Mean aspen site index varied among zones (Table 1). It further varied greatly within each zone because of the variation of local site conditions. For the 142 plots, it ranged from a minimum of 5.5 m, on a moderately dry, nutrient-poor site on a ridge crest in the BWBS zone, to a maximum of 30.7 m, on a moist, nutrient very rich site on a flat in the ICH zone.

Effect of spatial gradients on site index differed among biogeoclimatic zones. There was a significant interaction between zone and elevation and a marginally significant interaction between zone and latitude (Table 2). Site index decreased with increasing latitude in the IDF zone, but no effect was found in other zones (Fig. 2A; $P < 0.05$). Site index also decreased with increasing longitude in both the BWBS and the IDF zones, but longitude had no effect on site index in ICH, MS, and SB zones (Fig. 2B; $P < 0.05$). Site index decreased with increasing elevation in the BWBS zone but increased in the ICH and the IDF zones (Fig. 2C; $P < 0.05$). The lack of effect of latitude, longitude, and elevation on site index in the MS zone and SB climate may be attributed to insufficient data as the spread on the x variable was very narrow.

Effect of slope–aspect on site index varied between zones (Fig. 3; $P < 0.05$). Site index on ridges was lower than on other slope–aspects because of limited soil moisture and nutrient availability. In the coldest zone (i.e., the BWBS zone), site index was higher on the warm-aspect (southeast and south aspects) slopes, and in the relatively warmer climates, represented by the IDF, ICH, and MS zones, site index was greater on the cool-aspect (north, northeast, and northwest) slopes. However, effect of slope–aspect on site index in the SB zones was not conclusive (Fig. 3; $P > 0.05$).

The effect of SMR and SNR on site index did not significantly change with zones, although for a given SMR or SNR, site index could vary significantly between zones (Fig. 4). Site index increased with increasing soil moisture up to moist SMR, but further increase in SMR resulted in a lower site index (Fig. 4A; $P < 0.05$). With increasing SNR

Fig. 2. Effect of latitude, longitude, and elevation on site index in relation to biogeoclimatic zone. Fitted regression lines are significant ($P < 0.05$). Abbreviations for zones are given in Table 1.



from very poor to very rich, site index increased (Fig. 4B; $P < 0.05$). Insufficient number of sample plots, however, limited the opportunity to determine possibly subtle differences in site index between neighbouring SNRs or SMRs.

Fig. 3. Mean aspen site index in relation to slope–aspect stratified by biogeoclimatic zones for all study plots. Abbreviations for zones are given in Table 1; abbreviations for slope–aspects are as follows: RG, ridge; E, east aspect; S, south aspect; W, west aspect; N, north aspect; and FL, flat.

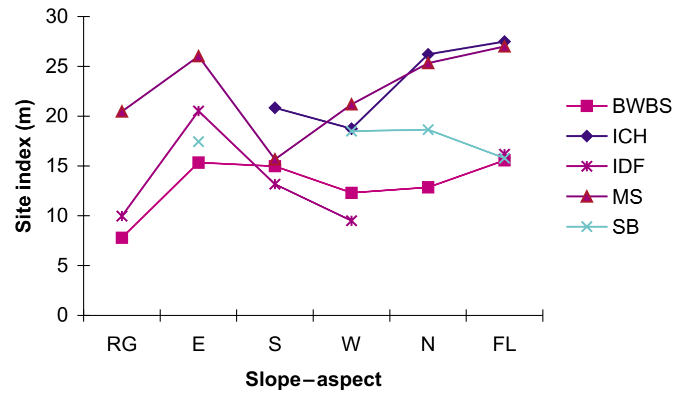
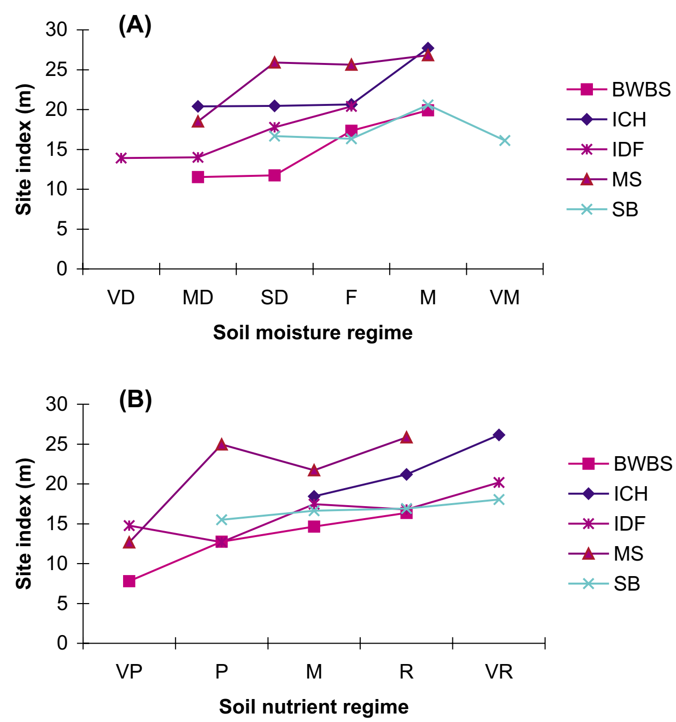


Fig. 4. Mean site index of aspen in relation to (A) soil moisture regime (SMR) and (B) soil nutrient regime (SNR) according to biogeoclimatic zones. Abbreviations for zones are given in Table 1. Abbreviations for SMR are as follows: VD, very dry; MD, moderately dry; SD, slightly dry; F, fresh; M, moist; and VM, very moist; abbreviations for SNR are as follows: VP, very poor; P, poor; M, medium; R, rich; and VR, very rich.



Site index predictions

At the provincial level, the model 1 developed using all environmental variables accounted for 61% of the variation in site index (Table 3). When zone was introduced in combination with all other variables, the zone-specific model 2 (zone, all factor) accounted for 82% of the variation in site index (Table 3), which is much higher than that of model 1. However, the predictors in the zone-specific model varied among zones.

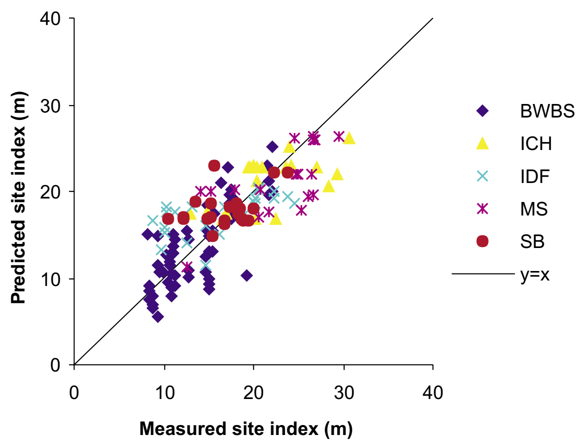
Residual analysis revealed that model 1 had a mean squared prediction error of 10.9, whereas model 2 had a mean squared prediction error of 4.9. When the predicted versus measured site indices of the model 1 were plotted, the fitted regression line was significantly different from the line $y = x$ (Fig. 5A; $P < 0.05$), indicating that model 1 overestimated site indices at the lower range but underestimated site

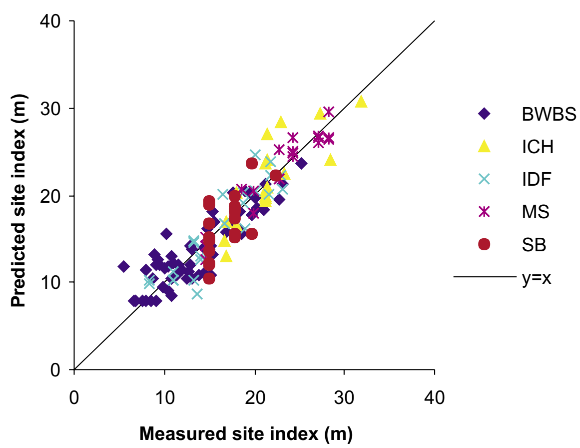
Table 3. Prediction models for aspen site index (SI) at the provincial scale (model 1) and zone-specific scale (model 2) (N = 142).

Model No.	Predictor	Model
1	Spatial gradients, SMR, and SNR	SI = 97.1 – 0.0053(ELE) – 0.53(LAT) – 0.377(LON) – 1.84(MD_SMR) + 4.19(M_SMR) – 8.74(VP) – 2.47(P)
		Adjusted R^2 = 0.61, SEE = 3.57, P < 0.0001
2	Zone; all predictors	SI = BWBS × (29.5 – 0.019(ELE) – 2.12(P) + 3.12(F_SMR) + 6.21(M_SMR) – 7.36(RG) – 3.56(N) – 2.67(W)) + SB × (17.85 – 2.8(FL) + 4.6(M_SMR)) + IDF × (340.95 – 2.694(LON) + 2.89(SD_SMR) – 6.95(S)) + MS × (24.3 – 4.32(MD_SMR) + 3.94(R) + 2.74(N) – 5.29(S)) + ICH × (12.6 + 0.011(ELE) + 4.61(M_SMR) + 5.37(FL))
		Adjusted R^2 = 0.82, SEE = 2.42, P < 0.0001

Note: All independent variables are significant (P < 0.05). SEE, standard error of the estimate. Abbreviations for zones are given in Table 1; ELE, elevation; LAT, latitude; LON, longitude. Soil moisture regime: MD_SMR, moderately dry; SD_SMR, slightly dry; F_SMR, fresh; and M_SMR, moist. Soil nutrient regime: VP, very poor and P, poor. Slope–aspect: RG, ridge; E, east; S, south; W, west; N, north; and FL, flat.

Fig. 5. Measured site index versus predicted site index by (A) model 1 and (B) model 2 in Table 3. Solid lines are linear regression lines using measured site index as the independent variable and predicted site index as the dependent variable.





indices at the high range. When the predicted versus measured site indices of the model 2 were examined, the fitted regression line was not different from the line $y = x$ (Fig. 5B; P = 0.8).

Discussion

The major finding of this study was that the relationship between forest productivity and environmental factors may vary at different spatial scales or at different geographical locations. Therefore, the pivotal points of this discussion are (*i*) how aspen productivity changes along environmental gradients and (*ii*) how aspen productivity can be best predicted from measured environmental factors at two different scales.

Influence of spatial, topographic, and edaphic gradients on forest productivity

Spatial gradients (latitude, longitude, and elevation) had different effects on aspen site index in different zones. The negative relationship between site index and longitude and elevation in the BWBS zone may be explained by the effect of a lower temperature east of the Rocky Mountains and a higher elevation. Cooler temperatures may be a limiting factor constraining growth under favorable soil moisture conditions. Chen et al. (1998*b*) also reported that aspen site index decreases with increasing elevation in the same portion of the BWBS zone. The IDF is the warmest and driest zone of all five zones in this study. The less productive growth of aspen in the eastern part of the IDF zone may be related to a weak influence of the Pacific Ocean causing more frequent growing-season droughts (Meidinger and Pojar 1991). At lower elevations in the IDF and ICH zones, higher temperatures probably cause higher evapotranspiration, resulting in water deficits. At higher elevations, evapotranspiration likely decreases because of a decrease in mean annual temperature from 9°C at low-elevation sites to 2°C at high-elevation sites.

Throughout North America, aspen occurs at lower elevations in the northern, and at higher elevations in the southern, portions of its range. In certain areas of the United States, aspen grows in similar climatic conditions to those studied in British Columbia. In Colorado, aspen occupies an elevation belt from 2100 to 3350 m, in the Intermountain region from 900 to 3350 m, and in southern California from 1850 to 3250 m (Maini and Cayford 1968; Shepperd 1986; Shepperd and Engelby 1983; Strothman and Zasada 1965; DeByle and Winokur 1985; Perala 1990). Precipitation within the natural range of aspen always exceeds evapotranspiration, and the southern border of aspen's range coincides with the isopleth of 2.5 cm average surface water runoff (Perala 1990). This pattern in aspen distribution implies that a water deficit is the most important limiting factor for aspen growth in warmer southern regions, and low temperature is the most important limiting factor in cooler northern regions or at high elevations.

Alaska studies have reported optimal aspen growth on warm-aspect (south or southwest) slopes, while studies based in the North American Southwest and Canadian Prairie Provinces reported optimal growing conditions for aspen on cool-aspect (north) slopes (DeByle and Winokur 1985; Shepperd 1986; Shepperd and Engelby 1983; Strothmann and Zasada 1965). The relationships between site index and slope–aspect in British Columbia were consistent with those of other studies in Canada and the United States. Warm-aspect slopes in the BWBS zone had higher site indices than cool-aspect slopes. South-facing slopes in the BWBS zone compensate for the attenuated angle of solar incidence, providing increased heat in an area where cool temperatures limit forest growth. The opposite is true for the drier and warmer zones, where a cool-aspect slope is critical in prolonging snowmelt and ameliorating evaporative water loss.

Several studies examining site index and site quality relationships have indicated the two key elements of the biogeoclimatic ecosystem classification, i.e., SNR and SMR, as important predictors of potential site productivity (Klinka and Carter 1990; Wang and Klinka 1996; Kayahara et al. 1997; Chen et al. 1998*c*). In general, site index increases with available soil moisture up to the point where excessive moisture may reduce soil aeration. For most species, site index increases consistently with increasing levels of available nutrients, particularly nitrogen. These studies also confirmed these relationships in several different climates.

Predictability of site index

Predicting site index from environmental factors has achieved various levels of success. Climatic influence on site index has been reported in several studies for site index prediction (Monserud 1984; Klinka et al. 1994; Chen et al. 1998*b*, 1998*c*). Local soil conditions such as soil nutrient measurements or field-identified SMRs and SNRs have been useful predictors in many studies (e.g., Fralish and Loucks 1975; Monserud et al. 1990; Klinka et al. 1994; Kayahara et al. 1995; Wang 1995, 1997; Wang and Klinka 1996; Chen et al. 1998*b*, 1998*c*). Models using the combination of climatic variables and local soil conditions as predictors are better than models using only climate variables or local site factors if models were developed for a large geographic area. However, many studies have failed to examine precision and bias in the models.

Two models are presented in this paper; an all-factor model at the provincial scale and a zone-specific all-factor model. The zone-specific model accounted for a considerably greater variation in site index than the all-factor model at the provincial scale. More importantly, the latter is not only less precise, i.e., a greater mean squared prediction error, but also biased. In comparison with other published site index prediction models, the zone-specific model is unbiased and has a reasonable precision in the prediction of site index. This model is recommended for predicting aspen site index in British Columbia.

Conclusions

Aspen growth in British Columbia generally increased with decreasing latitude and longitude, but the relationship between aspen growth and elevation varied with biogeoclimatic zones. Improved growth was also observed with increasing soil moisture and nutrients but growth declined on water-surplus sites. The most productive growth occurred at lower elevations and warm-aspect slopes in the boreal BWBS zone, at higher elevation and north-aspect slopes in the IDF and ICH zones, and at lower elevation and north-aspect slopes in the subalpine MS zone. High-elevation, north-aspect slopes appeared to compensate for relatively warm climates at low latitudes, while low-elevation, south-aspect slopes compensated for relatively cool climates at high latitudes. Relationships between aspen site index and SMR or SNR were consistent with those of other species studied in British Columbia. The zone-specific all-factor model explained 82% of the variation in site index and provided a precise and unbiased prediction. It is recommended for aspen site index prediction in British Columbia.

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