

Site index, site quality, and foliar nutrients of trembling aspen: relationships and predictions

Han Y.H. Chen, Karel Klinka, and Richard D. Kabzems

Abstract: To examine the relationships between trembling aspen (*Populus tremuloides* Michx.) productivity, environmental attributes, and foliar nutrients and to make accurate predictions of trembling aspen productivity, we sampled 60 naturally established, fire-originated, and even-aged trembling aspen stands in northern British Columbia. Trembling aspen site index significantly varied with latitude, elevation, aspect, slope position, edatopes, some forest floor and mineral soil physical and chemical properties, and concentrations of some foliar nutrients. To predict site index, we developed multiple linear regression models using climatic variables, topographic properties, edatopes, soil physical and chemical properties, or foliar nutrients as predictors. Model accountability for variation of site index differed in decreasing order from soil model, climatic model, forest floor model, foliar nutrient model, edatope model, topographic model, to mineral soil model. Examined by the test data set, all models were unbiased, but they had different levels of precision in prediction in decreasing order from edatope model, soil model, forest floor model, mineral soil model, foliar nutrient model, climatic model, to topographic model. The soil and foliar nutrients models may provide insight into ecosystem processes, but the models using climatic variables and topographic properties or edatopes as predictors are recommended for predicting trembling aspen site index.

Résumé : Les auteurs ont échantillonné 60 peuplements équiennes de peuplier établis naturellement à la suite d'un feu dans le nord de la Colombie Britannique dans le but d'étudier les relations entre la productivité du peuplier faux-tremble (*Populus tremuloides* Michx.), les caractéristiques environnementales et les nutriments foliaires et de prédire avec précision la productivité du peuplier faux-tremble. L'indice de site du peuplier faux-tremble variait significativement selon la latitude, l'altitude, l'exposition, la position dans la pente, l'édatope, certaines propriétés chimiques et physiques du sol minéral et de la litière ainsi que la concentration de certains nutriments foliaires. Dans le but de prédire l'indice de site, les auteurs ont développé des modèles de régression linéaire multiple à l'aide des variables climatiques, des propriétés topographiques, des édatopes, des propriétés chimiques et physiques du sol et des nutriments foliaires comme variables indépendantes. La fiabilité des modèles pour la variation de l'indice de site allait en décroissant du modèle basé sur le sol, le climat, la litière, les nutriments foliaires, les édatopes, la topographie au modèle basé sur le sol minéral. Sur la base du groupe de données utilisées pour effectuer les tests, tous les modèles étaient non biaisés. Cependant, leur degré de précision allait en décroissant du modèle basé sur les édatopes, le sol, la litière, le sol minéral, les nutriments foliaires, le climat au modèle basé sur la topographie. Les modèles basés sur le sol et les nutriments foliaires peuvent procurer certaines connaissances des processus de l'écosystème mais ceux qui utilisent les variables climatiques et les propriétés topographiques ou les édatopes comme variables indépendantes sont recommandés pour prédire l'indice de site dans le cas du peuplier faux-tremble.

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Introduction

Forest productivity is determined by solar radiation, temperature, water, nutrients, soil aeration, and biotic interactions — the factors directly affecting growth of vascu-

lar plants (Spurr and Barnes 1980). For various forest ecosystems, identifying environmental attributes of forest productivity and developing models for predicting forest productivity continue to be a major impetus (Fralish 1994; Raich et al. 1997; Reich et al. 1997). Site index, the top height of dominant and codominant trees at a reference age, has been widely used to measure potential forest productivity for a given species under the condition that height growth is not affected by nonsite factors, such as suppression and damage due to diseases or insects (Spurr and Barnes 1980; Nigh 1996, 1997; Chen et al. 1998a). Accurate predictions of site index for timber species are essential in forest management, especially in site- and species-specific decision making (SPWG 1997). Empirical species-specific models provide simple and efficient tools for estimating site index using height growth models for mature stands or using growth intercept models for young stands with free-growing trees (Nigh 1996; Chen et al. 1998a). These models, however,

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H.Y.H. Chen¹ and K. Klinka. Forest Sciences, University of British Columbia, 3rd Floor, Forest Sciences Center, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

R.D. Kabzems. Ministry of Forests, Forest Resources and Practices, 8808-72nd Street, Fort St. John, BC V1J 6M2, Canada.

¹Author to whom all correspondence should be addressed. Present address: Ontario Ministry of Natural Resources, Northeast Science and Technology, Highway 101 East, P.O. Bag 3020, South Porcupine, ON P0N 1H0, Canada. e-mail: chenh@gov.on.ca

Table 1. Summary of trembling aspen stand and site characteristics used for model construction and validation.

	Model plots ($n = 40$)		Validation plots ($n = 20$)	
	Mean	Range	Mean	Range
Latitude ($^{\circ}$ N)	56.63	55.42–58.60	56.31	55.42–58.60
Longitude ($^{\circ}$ W)	121.76	120.04–122.60	121.77	120.04–122.60
Elevation (m)	664	450–750	669	450–750
Slope (%)	5.4	0.0–35.0	9.0	0.0–40.0
Rooting depth (cm)	49	20–90	53	25–85
Stocking (stems/ha)	1890	550–4150	1940	450–3600
Basal area (m ² /ha)	15.2	4.7–36.3	17.4	4.6–36.3
Top height (m)	17.1	6.8–26.4	17.4	7.4–23.8
Age at breast height (years)	51.0	36.3–70.3	52.2	38.3–69.7
Diameter at breast height (cm)	14.9	8.1–26.1	15.8	6.6–29.5
Site index (m)	17.2	6.7–27.9	17.2	6.8–24.7

Note: Top height, age, and diameter are the means of the three selected dominant trees from each stand.

are not applicable where crop stands or free-growing trees are absent (Monserud et al. 1990; Wang 1995; Chen et al. 1998a).

An alternative method for predicting site index is based on relationships between site index and environmental variables or foliar nutrients (Fralish 1994; Wang 1995). As most direct environmental factors vary greatly in time, indirect measures of environmental variables have been widely applied to examine the relationships between site index and site quality, which is defined as the sum of all environmental factors affecting the biotic community of an ecosystem (Daniel et al. 1979; Spurr and Barnes 1980). To predict site index, for instance, longitude, latitude, and elevation have been used as indirect measures of regional climate (Monserud et al. 1990; Klinka et al. 1996), slope position, slope gradient, and aspect have been used as measures of local climates and available soil moisture and nutrients (Fralish and Loucks 1975; Fralish 1994; Wang 1995), and units of various vegetation, soil, or ecological classifications have been used as measures of overall site quality (Kabzems and Klinka 1987; Klinka and Carter 1990; Vanclay 1992; Klinka et al. 1994; Wang and Klinka 1996; Kayahara et al. 1997; Chen et al. 1998b). Direct measures of forest floor and mineral soil physical and chemical properties (Fralish and Loucks 1975; Brown and Loewenstein 1978; Monserud et al. 1990; Edmonds and Chappell 1994; Klinka et al. 1994; Kayahara et al. 1995; Wang 1995) or foliar nutrients (Radwan and Harrington 1986; Kayahara et al. 1995; Wang 1995) have also been related to site index to elucidate the relationships between soil and foliar nutrients and site productivity. However, these predictive models have rarely been validated, and it remains uncertain how different measures of site quality account for variation of site index and how effective in prediction the models are.

Trembling aspen (*Populus tremuloides* Michx.), the most widely distributed tree species in North America (Perala 1990), occurs in all interior forested biogeoclimatic zones of British Columbia, especially in the Boreal White and Black Spruce (BWBS) zone (Meidinger and Pojar 1991). Managing this species for sustainable production requires a good understanding of its productivity attributes and an accurate prediction of its productivity. In this study, we addressed the following questions. (i) How is trembling aspen site index related to different measures of site quality and foliar nutri-

ents? (ii) Do the predictive models based on different measures of site quality or foliar nutrients as predictors differ in their ability to explain the variation of site index? (iii) Do the models differ in their ability to predict site index?

Materials and methods

Study area and stands

A total of 60 stands were located in the Moist and Warm Boreal White and Black Spruce (BWBSmw) subzone near Dawson Creek, Fort St. John, and Fort Nelson, British Columbia, in the early summer of 1995 (Table 1). This subzone represents the core of the natural distribution of trembling aspen in British Columbia (Meidinger and Pojar 1991). Data (means for a period of 30 years, 1951–1980) from the four closest climatic stations (Dawson Creek, Dawson Creek A, Fort St. John, and Fort Nelson) indicate that the mean annual precipitation ranges from 445 to 504 mm, mean annual temperature is -1.4 to 1.3° C, mean temperature of the warmest month ranges from 14.9 to 16.6° C, and mean frost free period ranges from 78 to 115 days (Environment Canada 1982). The soils in the study area are primarily fine-textured Gray Luvisols with some Brunisols, Gleysols, and Regosols (Green and Lord 1978). Lamimoder and Mormoders are the most common humus forms in the trembling aspen ecosystems (Fons et al. 1998). The study stands were naturally established, fire originated, fully stocked, even aged, without a history of damage, and dominated by trembling aspen with occasional components of balsam poplar (*Populus balsamifera* L.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia* Engelm.). The stands were deliberately selected to capture the widest range of available soil moisture and nutrient conditions that support trembling aspen growth. In each stand, a 0.04-ha rectangular plot, relatively uniform in topography, soil, understory vegetation, and stand characteristics, was randomly located to represent the stand.

Measurements of site quality and foliar nutrients

For each study plot, latitude, longitude, and altitude were identified according to the plot location on topographic maps. Topographic properties were assessed according to Luttmerding et al. (1990). Slope position was described as crest, upper slope, middle slope, lower slope, or level (flat). Slope shape was described as concave, convex, or straight. Aspect (degrees) and slope gradient (percent) were measured with a compass and a clinometer, respectively. Soil moisture regime (SMR) and soil nutrient regime (SNR) were identified in the field using a combination of topographic properties and soil morphological properties (Green and Klinka

Table 2. Forest floor and mineral soil (0–30 cm) physical and chemical properties and foliar nutrients in all sampled plots ($n = 60$).

	Forest floor		Mineral soil		Foliage	
	Mean	Range	Mean	Range	Mean	Range
Depth (cm)	5.77	1.7–13.8	na		na	
Bulk density (g/cm ³)	0.07	0.03–0.17	1.31	0.84–1.67	na	
pH	5.38	3.90–6.30	4.83	3.60–7.10	na	
tC (%)	38.95	27.0–46.0	1.45	0.50–7.50	na	
tN (%)	1.37	0.79–1.77	0.09	0.04–0.38	2.258	1.57–2.89
min-N (mg/g)	0.545	0.10–1.02	0.016	0.002–0.08	na	
Available P (mg/g)	0.147	0.07–0.24	0.087	0.001–0.36	2.7	2.00–4.40
Extractable K (mg/g)	1.292	0.64–1.75	0.076	0.03–0.33	11.2	8.3–21.7
Extractable Ca (mg/g)	11.6	5.1–15.9	1.01	0.09–8.00	0.94	5.1–15.5
Extractable Mg (mg/g)	1.32	0.49–2.89	0.14	0.03–0.68	1.83	1.12–3.90
Extractable S (mg/kg)	na		3.61	0.60–18.9	na	
Extractable Mn (mg/g)	na		na		0.32	0.07–0.66
Extractable Zn (mg/kg)	na		na		120.8	52–232
Extractable B (mg/kg)	na		na		23.8	4.0–53.0
Extractable Al (mg/kg)	na		na		55.0	31–118
Extractable Fe (mg/kg)	na		na		443.5	31–79

Note: Foliar nutrients are totals. na, not applicable or not measured.

1994). A particular combination of SMR and SNR was referred to as an edatope (Pojar et al. 1987).

Forest floor (LFH horizons) and mineral soil (0–30 cm in depth) were sampled and analyzed for physical and chemical properties (Table 2). The depth of the forest floor was measured in the field from 15 random locations within each sampled plot. Bulk density (grams per cubic centimetre) of the forest floor and mineral soil (0–30 cm) was determined from cores taken at five locations. Forest floor and mineral samples taken from the five locations were composited into one sample of each. Forest floor samples were dried at 70°C for 24 h and ground in a Wiley mill. Mineral soil samples were air-dried and passed through a 2-mm sieve to remove coarse fragments.

Forest floor samples were analyzed to determine pH using a pH meter with a 1:5 suspension in water and total carbon (tC, percent) by loss on ignition at 500°C (induction furnace) using a LECO carbon analyzer, total nitrogen (tN, percent) with a Technicon autoanalyzer following micro-Kjehldal digestion (Carter 1993), mineralizable nitrogen (min-N, milligrams per gram) by an anaerobic incubation procedure (Powers 1980), available phosphorus (P, milligrams per gram) using the ascorbic acid reductant method on Bray P-1 (dilute acid ammonium fluoride) extract, and extractable (exchangeable by Morgan's) potassium (K, milligrams per gram), calcium (Ca, milligrams per gram), and magnesium (Mg, milligrams per gram) by extraction with Morgan's solution of sodium acetate at pH 4.8 and absorption spectrophotometry with an acetylene–air flame (Price 1978). Mineral soil samples were analyzed to determine pH using a pH meter with a 1:1 suspension in water and concentrations of tC, tN, min-N, P, K, Ca, and Mg using the same methods as for the forest floor samples. Extractable sulphur (SO₄-S, milligrams per kilogram) was also determined for mineral soil samples using an inductively coupled plasma (ICP) spectrophotometer on a 0.01 M CaCl₂ extract (Price 1978).

Foliar samples were taken from five dominant trees in August 1995 following the procedure given by Ballard and Carter (1986). On each tree, a minimum of two branches from the uppermost half to quarter of the live crown were sampled. The samples were dried at 70°C for 24 h, ground, and analyzed for total N, P, K, Ca, manganese (Mn, milligrams per kilogram), zinc (Zn, milligrams per kilogram), aluminum (Al, milligrams per kilogram), and iron (Fe, milligrams per kilogram) by the method of Parkinson and Allan

(1975) and boron (B, milligrams per kilogram) by the azomethine H method (Gaines and Mitchell 1979). All concentrations of nutrients were expressed on the basis of sample dry mass.

Stem analysis and determination of site index

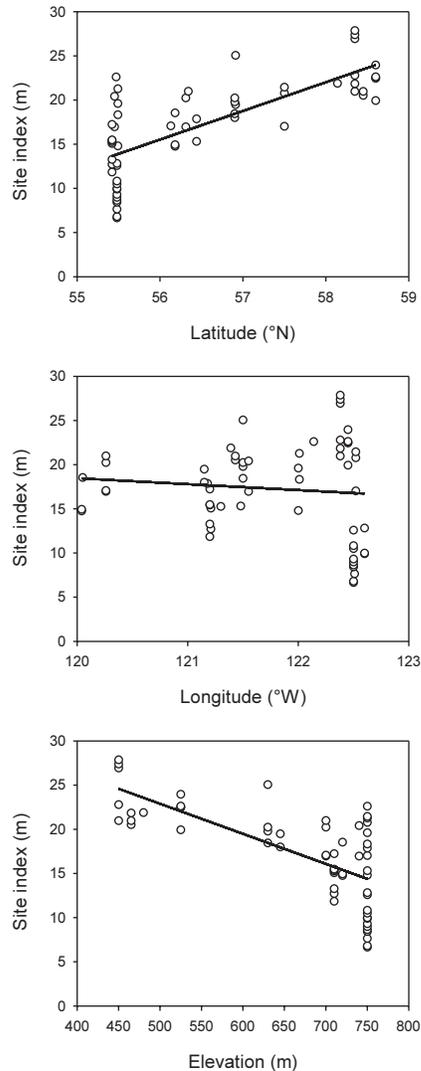
In each plot, three dominant trees were felled for stem analysis. After total height of each felled tree was measured in the field, stem discs were cut at 0.3, 0.8, and 1.3 m above the ground surface and then at 1-m intervals between 1.3 m to the top of each tree. In the laboratory, each disc was transversely cut with a sharp knife and zinc oxide powder was added to make the rings clearly visible. With a microscope, rings were counted in two directions until the same count was obtained.

Raw data from stem analysis were adjusted using Carmean's algorithm to calculate true tree height corresponding to the age at each cross-cut (Dyer and Bailey 1987). Plots of height versus age were graphically examined for each site tree to examine normality of height growth. No obvious suppression or damage was found in the 180 (three trees per plot) sampled trees. An average height growth curve was computed from three sampled trees for each study plot using Richards' three-parameters equation (Monserud 1984; Wang and Klinka 1996; Chen et al. 1998a). The equation was fitted by a nonlinear least square procedure (Neter et al. 1996). For each plot, an actual site index at the reference age 50 years at breast height was then calculated from the fitted equation.

Data analysis

Relationships between site index and the measures of site quality and foliar nutrients were examined for linearity and homogenous variances using all data (model and validation plots) (Table 1). With the exception of a quadratic relationship between site index and aspect, all other relationships were linear. A transformation on aspect was applied accordingly. Linear regression analysis was used to examine the relationships between site index and latitude (degrees north), longitude (degrees west), elevation (metres), slope gradient (percent), and aspect (degrees). One-way analysis of variance was used to examine the relationships between site index and slope positions, types of slope shape, and edatopes (combinations of SMR and SNR). Pearson's correlation analysis was used to examine relationships between site index and each of the measures of forest floor and mineral soil properties and foliar nutrients.

Fig. 1. Site index (SI) in relation to indirect climatic variables (latitude, longitude, and elevation). The regression relationships ($n = 60$) are $SI = -166.3 + 3.242(\text{latitude})$, $R_a^2 = 0.54$, $P < 0.001$; $SI = 98.86 - 0.67(\text{longitude})$, $R_a^2 = 0.01$, $P = 0.45$; and $SI = 39.88 - 0.34(\text{elevation})$, $R_a^2 = 0.47$, $P < 0.001$.

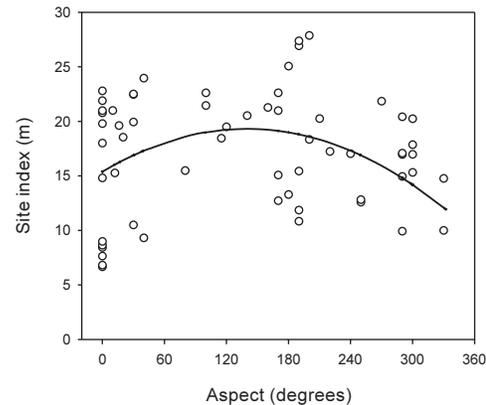


Correlation analysis was also performed to examine relationships among continuous measures of site quality and foliar nutrients.

We developed multiple regression models to predict site index. Before model development, data were randomly split into two sets, one set for model construction ($n = 40$) and one set for model validation ($n = 20$) (Table 1). Models were constructed using solely regional climatic variables (longitude, latitude, and elevation), topographic properties (slope, aspect, slope position, and slope shape), edatopes (combinations of SMR and SNR; Pojar et al. 1987), soil (forest floor and mineral soil) physical and chemical properties, or foliar nutrients as predictors. We also developed models that combined regional climatic variables with foliar nutrients or the measures of local site quality (all measured environmental factors except regional climatic variables) as predictors to determine whether adding regional climatic variables to the models using local site quality or foliar nutrients as predictors can improve model accountability for variation of site index and model prediction.

To limit the number of predictors, the backward stepwise procedure was used in selecting independent variables at a significance level of $P < 0.05$ (SYSTAT 1997). Multiple linear regression anal-

Fig. 2. Site index (SI) in relation to aspect. The regression relationship is $SI = 15.39 + 0.056(\text{aspect}) - 0.0002(\text{aspect})^2$, $R_a^2 = 0.082$, $P = 0.03$.



ysis was used for continuous independent variables. General linear model analysis was applied when models contained categorical variables. The categorical variables were coded as dummy variables after the predictors were determined.

Model comparisons were made in two steps. First, as models are unbiased when a linear least square procedure is applied in regression fitting (i.e., sum of errors is equal to zero) (Rawlings 1988; Neter et al. 1996), we compared model accountability for variation of site index by examining residual variances (Sokal and Rohlf 1981; Nigh and Sit 1996; Chen et al. 1998a). Bartlett's test was applied to test the equality of residual variances from different models (Walpole 1982; Zar 1984). We then used the test data set to compare the predictability of models by examining (i) the bias of each individual model through testing if the differences in predicted minus measured site index differed significantly from zero and (ii) the level of precision of different models by calculating the mean square of the prediction error (MSPR) (Neter et al. 1996) and testing the equality of variance of the prediction error (i.e., predicted minus measured site index of the test data) (Walpole 1982; Zar 1984).

Results

Site index in relation to measures of site quality and foliar nutrients

Site index was significantly related to the indirect measures of regional climate (Fig. 1). It increased with latitude and decreased with elevation ($P < 0.05$, Fig. 1). Longitude significantly influenced site index only when latitude was presented in multiple regression analysis (Table 3). Latitude was also negatively correlated with elevation ($r = -0.89$, $P < 0.001$).

In relation to topography, site index was higher for southerly than northerly slopes ($P < 0.05$, Fig. 2). With change in slope position, site index decreased from the lower slope, middle slope, upper slope, to crest ($P < 0.001$, Fig. 3), and the site index for the level slope (flat sites) was in between the lower and middle slope positions ($P < 0.001$, Fig. 3). Site index, however, was not significantly related to slope gradient (percent) ($R^2 = 0.01$, $P = 0.45$) or slope shape (i.e., concave, convex, and straight) ($P = 0.06$).

When study sites were identified according to SMR and SNR, site index significantly differed among edatopes ($P < 0.05$, Fig. 4). Site index increased with increasing nutrient

Table 3. Models of predicting site index (SI) from only climatic variables ([1]), topographic properties ([2]), edatopes ([3]), forest floor properties ([4a]), mineral soil (0–30 cm) properties ([4b]), soil (forest floor and mineral soil) properties ([4c]), and foliar nutrients ([5]) ($n = 40$ for all models).

No.	Constituent	Model	R_a^2	SEE (m)
[1]	Climatic variables	$SI = 23.649 + 4.018(LAT) - 1.922(LONG)$	0.734	2.771
[2]	Topographic properties	$SI = 6.837 + 0.0804(ASP) - 0.0002(ASP)^2 + 2.51(UPP) + 6.255(MID) + 9.745(LOW) + 10.895(LEV)$	0.598	3.407
[3]	Edatopes	$SI = 7.927 + 3.781(P_MD) + 7.711(P_SD) + 11.163(M_SD) + 15.519(R_FM)$	0.632	3.260
[4a]	Forest floor properties	$SI = -10.075 + 1.423(D_{ff}) + 3.346(pH_{ff}) - 0.733(tN_{ff}) + 8.578(K_{ff})$	0.730	2.790
[4b]	Mineral soil properties	$SI = 17.437 + 2.656(tN_{ms}) - 30.368(P_{ms})$	0.565	3.542
[4c]	Soil properties	$SI = 9.249 + 1.37(D_{ff}) - 0.039(tC_{ff}) + 11.856(K_{ff}) + 16.988(Mg_{ms}) - 30.373(P_{ms})$	0.793	2.441
[5]	Foliar nutrients	$SI = 1.038 + 1.4112(N_f) - 5.208(P_f) + 0.04(Zn_f) - 19.262(Mn_f)$	0.668	3.097

Note: All independent variables are significant ($P < 0.05$) and models are significant ($P < 0.001$). R_a^2 , adjusted R^2 ; SEE, standard error of the estimate. All variable units are the same as in Table 2. Climatic variables: LONG, longitude; LAT, latitude; ASP, aspect. Topographic dummy variables: UPP, upper slope; MID, middle slope; LOW, lower slope; LEV, level slope. Edatope dummy variables: P_MD, poor and moderately dry; P_SD, poor and slightly dry; M_SD, medium and slightly dry; R_FM, rich and fresh to moist. Forest floor variables: D_{ff} , depth; pH_{ff} , pH value; tN_{ff} , total N; K_{ff} , extractable K; tC_{ff} , total C. Mineral soil variables: tN_{ms} , total N; P_{ms} , available P; Mg_{ms} , extractable Mg. Foliar nutrient variables: N_f , total N; P_f , total P; Zn_f , total Zn; Mn_f , total Mn.

Fig. 3. Site index (SI) in relation to slope position. Error bars are 1 SE of the means.

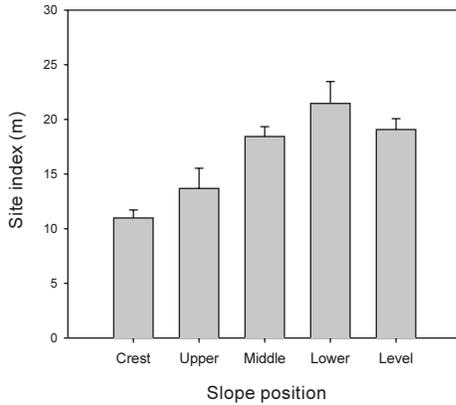
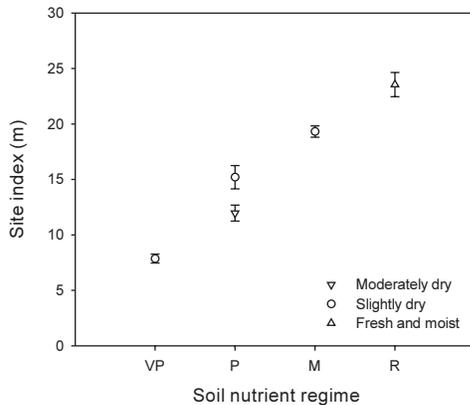


Fig. 4. Site index (SI) in relation to edatopes, combinations of soil moisture regime (moderately dry, slightly dry, fresh and moist) and soil nutrient regime (VP, very poor; P, poor; M, medium; R, rich). Error bars are 1SE of the means.



availability on slightly dry sites and with increasing available soil moisture on poor sites ($P < 0.05$, Fig. 4). The highest site index was on fresh and moist and rich sites; the

Table 4. Pearson’s correlation coefficient (r) between site index and forest floor and mineral soil (0–30 cm) physical and chemical properties and foliar nutrients.

	Forest floor	Mineral soil	Foliage
Depth (cm)	0.657	na	na
Bulk density (g/cm^3)	-0.451	-0.282	na
pH	0.698	0.493	na
tC (%)	0.355	0.503	na
tN (%)	0.573	0.536	0.519
min-N (mg/g)	0.202	0.427	na
Available P (mg/g)	0.217	-0.667	-0.016
Extractable K (mg/g)	0.494	0.364	0.238
Extractable Ca (mg/g)	0.657	0.531	0.243
Extractable Mg (mg/g)	0.627	0.580	0.244
Extractable S (mg/kg)	na	0.507	na
Extractable Mn (mg/g)	na	na	-0.436
Extractable Zn (mg/kg)	na	na	0.325
Extractable B (mg/kg)	na	na	0.548
Extractable Al (mg/kg)	na	na	-0.346
Extractable Fe (mg/kg)	na	na	0.118

Note: Boldface indicates a significant correlation ($n = 60$, Bonferroni $P < 0.05$). Foliar nutrients are totals. na, not applicable or not measured.

lowest site index occurred on moderately dry and very poor sites (Fig. 4).

Site index was significantly correlated with several forest floor properties (Table 4). It was positively correlated, in decreasing order of significance, with pH, depth, and concentrations of Ca, Mg, tN, and K and negatively correlated with bulk density (Table 4). No significant correlation existed between site index and concentration of min-N or P (Table 4).

Site index was also significantly correlated with several mineral soil physical and chemical properties (Table 4). In decreasing order of significance, site index was positively correlated with concentrations of Mg, tN, Ca, S, and tC, pH, and concentration of min-N and negatively correlated with concentration of P (Table 4). There was no significant correlation between site index and bulk density or concentration of K (Table 4).

In relation to concentrations of foliar nutrients, site index

Table 5. Bartlett's statistics (*b*) to test the equality of residual variances from the models in Tables 3 and 6.

Model	Model											
	[2]	[3]	[4a]	[4b]	[4c]	[5]	[6]	[7]	[8a]	[8b]	[8c]	[9]
[1]	0.989	0.991	0.999	0.971	0.986	0.997	0.971	0.852	0.833	0.941	0.760	0.919
[2]		0.999	0.986	0.995	0.951	0.998	0.927	0.782	0.762	0.886	0.686	0.859
[3]			0.988	0.994	0.956	0.999	0.932	0.789	0.769	0.891	0.693	0.865
[4a]				0.966	0.989	0.995	0.975	0.861	0.843	0.947	0.771	0.926
[4b]					0.920	0.987	0.890	0.734	0.714	0.844	0.638	0.815
[4c]						0.969	0.997	0.920	0.905	0.983	0.841	0.970
[5]							0.948	0.813	0.794	0.911	0.719	0.887
[6]								0.946	0.933	0.994	0.875	0.986
[7]									0.999	0.975	0.982	0.987
[8a]										0.965	0.989	0.979
[8b]											0.918	0.998
[8c]												0.939

Note: Boldface indicates that residual variances are significantly different between models ($b < b_{k=2(\alpha=0.05; n=40)} = 0.951$).

Table 6. Models of predicting site index (SI) from combinations of climatic variable(s) and topographic properties ([6]), edatopes ([7]), forest floor properties ([8a]), mineral soil (0–30 cm) properties ([8b]), soil (forest floor and mineral soil) properties ([8c]), and foliar nutrients ([9]) ($n = 40$ for all models).

No.	Constituent	Model	R_a^2	SEE (m)
[6]	Climate and topographic properties	SI = 24.15 + 2.898(LAT) – 1.438(LONG) + 0.0348(ASP) – 0.0001(ASP) ² + 0.58(UPP) + 2.44(MID) + 5.64(LOW) + 4.04(LEV)	0.806	2.368
[7]	Climate and edatopes	SI = –144.41 – 2.746(LAT) + 3.891(P_MD) + 5.377(P_SD) + 6.50(M_SD) + 11.46(R_FM)	0.910	1.616
[8a]	Climate and forest floor properties	SI = – 177.708 + 3.356(LAT) + 0.564(D_{ff}) + 1.148(tN_{ff}) – 0.037(tC_{ff})	0.919	1.529
[8b]	Climate and mineral soil properties	SI = – 149.533 + 2.873(LAT) + 4.815(tN_{ms}) – 0.401(tC_{ms}) + 3.564(Ca_{ms}) – 0.585(S_{ms})	0.857	2.029
[8c]	Climate and soil properties	SI = – 165.121 + 3.088(LAT) + 1.052(tN_{ff}) – 0.0203(tC_{ff}) – 5.946(P_{ms}) + 1.664(Ca_{ms})	0.938	1.333
[9]	Climate and foliar nutrients	SI = – 136.172 – 2.549(LAT) + 0.733(N_f) – 0.525 (K_f) – 9.603(Mn_f) + 0.064(B_f)	0.874	1.905

Note: All independent variables are significant ($P < 0.05$) and models are significant ($P < 0.001$). R_a^2 , adjusted R^2 ; SEE, standard error of the estimate. Mineral soil variables: tC_{ms} , total C; Ca_{ms} , extractable Ca; S_{ms} , extractable S. Foliar nutrient variables: K_f , total K; B_f , total B. Other symbols are as in Table 3.

was significantly positively correlated with concentrations of tN and B and negatively with Mn (Table 4). However, other measured nutrients were not correlated with site index.

Model comparisons

Multiple regression models using different measures of site quality or foliar nutrients as predictors had different levels of accountability for variation of site index ($n = 40$) (Tables 3 and 5). The descriptive measures (i.e., adjusted R^2 (R_a^2) and standard error of the estimate (SEE)) of model performance indicated that soil model [4c] was the best, followed by climatic model [1], forest floor model [4a], foliar nutrient model [5], edatope model [3], topographic model [2], and mineral soil model [4b] (Table 3). Only soil model [4c], however, had significantly better accountability for site index than mineral soil model [4b] ($P < 0.05$, Table 5).

Adding climatic variables to the measures of local site quality (topography, edatopes, and soil properties) or foliar nutrients improved model accountability for site index ($P <$

0.05, Tables 3, 5, and 6). Topographic model [6] accounted for 81% of the variation of site index and was better than model [2] ($P < 0.05$, Table 3). Similarly, models [7], [8a], [8b], [8c], and [9] were better than models [3], [4a], [4b], [4c], and [5], respectively, as well as model [1] ($P < 0.05$, Tables 3, 5, and 6). Among the models using the measures of local site quality or foliar nutrients together with climatic variables as predictors (Table 6), soil model [8c] had the highest accountability for site index ($R_a^2 = 0.938$, SEE = 1.333 m). The model was better than models [6], [8b], and [9] and had a similar accountability as models [7] and [8a] (Tables 5 and 6).

When tested with an independent data set ($n = 20$), all models presented in Tables 3 and 6 were unbiased in predicting site index (Table 7). Models, however, had different levels of precision in prediction (Fig. 5; Tables 7 and 8). Comparisons among the models using only climatic variables, measures of local site quality, or foliar nutrients as predictors indicated that edatope model [3] had the smallest

Table 7. Predictability of the models in Tables 3 and 6 validated by the validation data set ($n = 20$).

	Model												
	[1]	[2]	[3]	[4a]	[4b]	[4c]	[5]	[6]	[7]	[8a]	[8b]	[8c]	[9]
Mean error	-1.30	1.98	-0.01	-0.19	0.05	0.02	0.24	-0.57	-0.89	-1.27	-0.27	-0.30	-0.75
t	-1.27	2.02	-0.01	-0.28	0.06	0.32	0.26	-1.04	-1.52	-1.78	-0.24	-0.34	-0.95
P	0.21	0.06	0.99	0.79	0.95	0.97	0.80	0.31	0.14	0.09	0.82	0.74	0.36
MSPR	20.9	19.1	7.9	9.1	14.6	8.6	18.0	6.1	6.8	10.2	25.8	14.8	12.6

Note: Mean error, mean of residuals (predicted – actual site index (m)); t , Student's t statistic; P , probability of mean error equal to zero; MSPR, mean square of prediction error.

Table 8. Bartlett's statistics (b) to compare the levels of precision of the models from Tables 3 and 6 in predicting validation data.

Model	Model												
	[2]	[3]	[4a]	[4b]	[4c]	[5]	[6]	[7]	[8a]	[8b]	[8c]	[9]	
[1]	0.999	0.893	0.920	0.984	0.909	0.997	0.837	0.861	0.938	0.994	0.986	0.969	
[2]		0.910	0.936	0.991	0.925	0.999	0.857	0.880	0.952	0.989	0.992	0.979	
[3]			0.997	0.955	0.999	0.922	0.991	0.997	0.992	0.848	0.953	0.974	
[4a]				0.973	0.999	0.946	0.980	0.989	0.999	0.879	0.971	0.987	
[4b]					0.966	0.995	0.912	0.932	0.984	0.961	0.999	0.997	
[4c]						0.936	0.986	0.993	0.997	0.866	0.964	0.982	
[5]							0.870	0.893	0.961	0.984	0.995	0.984	
[6]								0.998	0.968	0.787	0.909	0.938	
[7]									0.980	0.813	0.929	0.955	
[8a]										0.900	0.982	0.994	
[8b]											0.963	0.939	
[8c]												0.997	

Note: Boldface indicates that levels of precision are significantly different between models ($b < b_{\alpha=0.05; n=20} = 0.902$).

MSPR, followed by soil model [4c], forest floor model [4a], mineral soil model [4b], topographic model [2], and climatic model [1] (Table 7). Only edatope model [3], however, was significantly more precise than climatic model [1] (Fig. 5; Table 8).

In contrast with the comparisons of model accountability for variation of site index, the models using climatic variables together with the measures of local site quality or foliar nutrients as predictors (models [7], [8a], [8b], [8c], and [9]) did not significantly improve the precision in prediction compared with models [3], [4a], [4b], [4c], and [5], respectively (Fig. 5; Tables 7 and 8). Only topographic model [6] was more precise than topographic model [2] ($P < 0.05$, Table 8).

Among the models using climatic variables together with the measures of local site quality or foliar nutrients as predictors, topographic model [6] was the best in prediction, followed by edatope model [7], forest floor model [8a], foliar nutrient model [9], soil model [8c], and mineral soil model [8b] (Fig. 5; Table 7). Model [8b], which overestimated site index in one case by more than 15 m, was significantly less precise in prediction than models [6], [7], and [8a] (Fig. 5; Table 8).

Discussion

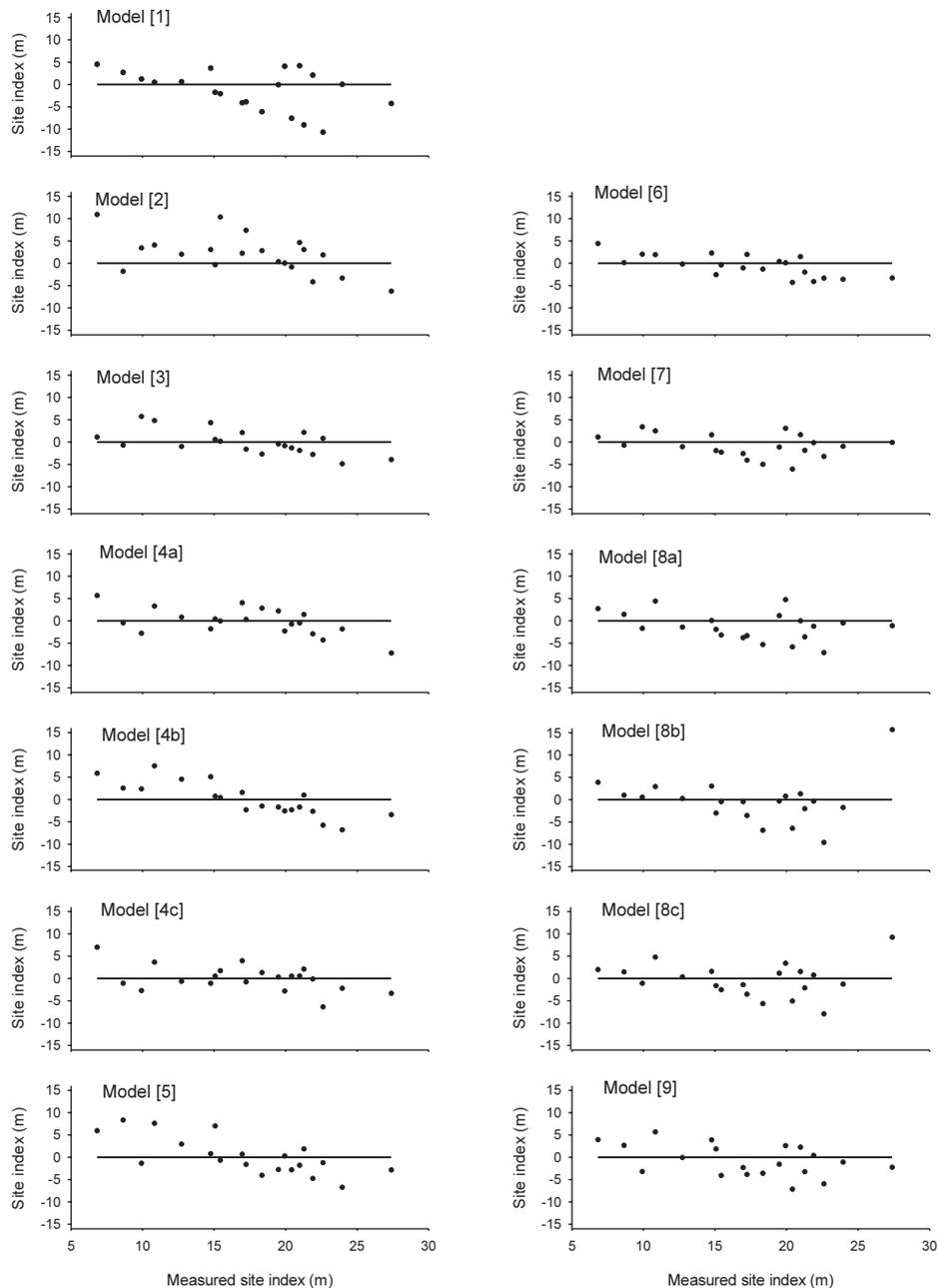
Conceptually, productivity of any vascular plant decreases when an environmental factor is outside the optimum range for growth of the plant (Odum 1971). In natural ecosystems, the multiple dimensions of environmental variables and in-

teractions among the variables, their temporal and spatial variability, and vegetation feedback often impose uncertainty in examining cause–effect relationships between productivity and environmental variables (Monserud et al. 1990; Raich et al. 1997; Reich et al. 1997; Wang 1997). Further, the impact of environmental factors on tree growth may vary greatly with scale, ecosystem type, and tree species (Odum 1971; Schneider 1994; Reich et al. 1997). For example, climate may be very important in determining forest productivity when it varies greatly within a study area from optimum to threshold levels approaching the tolerance limit for tree species, such as in studies covering a large geographic area and (or) a large variation in elevations (e.g., Monserud et al. 1990; Klinka et al. 1996; Raich et al. 1997; Chen et al. 1998b). Climate may not be as important, however, as a predictor when it is more or less at its optimum conditions for a species throughout the study area (e.g., Klinka and Carter 1990) or when a study occurs within a narrow range in climate (e.g., Wang and Klinka 1996). In consequence, relationships between forest productivity and site quality are often examined on a species-specific and ecosystem-specific basis if quantitative predictions are set to be objectives.

Relationships between site index, site quality, and foliar nutrients

In this study, trembling aspen site index increased with latitude and decreased with elevation. As the frost-free period and precipitation during the growing season increase with latitude and decrease with elevation from Dawson

Fig. 5. Prediction error of the models in Tables 3 and 6 in relation to measured site index ($n = 20$). The lines are $Y = 0$.



Creek to Fort St. John to Fort Nelson on the northeastern plateau of British Columbia (Environment Canada 1982), the longer and wetter growing season may contribute to a higher productivity of the stands in higher latitudes and lower elevations. Many other studies have reported that forest productivity decreases with increasing elevation as temperature decreases (Spurr and Barnes 1980; Monserud et al. 1990; Klinka et al. 1996; Raich et al. 1997). On a grand scale, however, site index decreases with latitude for subalpine fir (*Abies lasiocapa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the continental subalpine forest of British Columbia (Klinka et al. 1996; Chen et al. 1998b) and for interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) over a large geographic area (Monserud et al. 1990). In both studies, latitude

and elevation were more independent. That longitude was the least significant factor in determining trembling aspen site index among the three indirect climatic variables in this study may be attributed to (i) a small longitudinal variation among the study stands and (ii) its least influence on temperature and precipitation among the three indirect climatic variables in the study area (Meidinger and Pojar 1991; Klinka et al. 1996).

Among topographic properties examined in this study, aspect and slope position were the most significant factors in determining trembling aspen site index. A higher trembling aspen productivity on warm-aspect sites was also observed in Alaska (Viereck et al. 1983; Perala 1990). In the southwestern United States, however, more productive trembling aspen sites are more typically found on northerly slopes than

on southerly slopes as a result of moister and cooler conditions on northerly slopes (Perala 1990). In high latitudes where moisture is not a limiting factor, the greater productivity on warm-aspect slopes may be attributed to higher temperature and more adequate solar radiation during the growing season (Viereck et al. 1983). A greater forest productivity on lower slopes was expected, as lower slopes usually have a greater availability of soil moisture and nutrients (Fralish 1994). Edatope, a combination of SMR and SNR that is used as the basic indirect measure of site quality in the biogeoclimatic ecosystem classification (Pojar et al. 1987), was a useful predictor of site index in this and several other studies (Klinka and Carter 1990; Wang and Klinka 1996; Kayahara et al. 1997).

As in many other studies, forest productivity was correlated with the forest floor and mineral soil physical and chemical properties and foliar nutrients (Fralish and Loucks 1975; Radwan and Harrington 1986; Monserud et al. 1990; Klinka et al. 1994; Kayahara et al. 1995; Wang 1995; Raich et al. 1997; Reich et al. 1997). The strong correlation between site index and the depth of the forest floor may indicate that a site with a higher productivity has a greater litterfall (Reich et al. 1997). The significant positive correlation between site index and pH values of the forest floor and mineral soil suggests that trembling aspen stands have a higher productivity in less acid soils.

It is notable that site index was positively correlated with tN concentrations in the forest floor, mineral soil, and foliage. Thus, it is evident that N is an important growth-limiting factor in some of the trembling aspen stands, as in many other forest stands (Radwan and Harrington 1986; Klinka et al. 1994; Kayahara et al. 1995; Wang 1995; Reich et al. 1997; Chen et al. 1998b). The concentration of min-N in mineral soil was also significantly correlated with trembling aspen site index as well as the concentration of tN in mineral soil (Appendix). In contrast with the finding that min-N (anaerobic incubation), a measure of potential N mineralization rather than actual N mineralization in situ, was the best measure of available soil N (Powers 1980; Klinka and Carter 1990; Klinka et al. 1994), the significance of correlation between site index and the tN concentration in this study was greater than that between site index and the min-N concentration in both the forest floor and mineral soil. A similar result has been reported in a study of relationships between white spruce (*Picea glauca* (Moench) Voss) site index and soil in a sub-boreal montane climate (Wang 1995).

Besides N, concentrations of available P and extractable S, K, Ca, and Mg in the forest floor and (or) mineral soil were also correlated with trembling aspen site index. As reported in many other forest ecosystems (Klinka et al. 1994; Kayahara et al. 1995; Raich et al. 1997; Chen et al. 1998b), available P in mineral soil was negatively correlated with forest productivity. Kayahara et al. (1995) suggested that such a pattern may be the result of luxury consumption of P on N-poor, low-productivity sites. The relationship between site index and available P is likely questionable, as the techniques used to determine the true quantity of plant-available P in mineral soil are problematic (Carter 1993; Klinka et al. 1994; Cade-Menun and Lavkulich 1997). The significant positive correlation between mineral soil S and site index

may indicate that low productivity in some stands may be also attributed to S deficiency (Wang 1995). Extractable K, Ca, and Mg were positively correlated with site index as well as tN in the forest floor and mineral soil (Appendix). A similar pattern was found for the boreal coniferous forest (Klinka et al. 1994) and the high-elevation coniferous forest (Chen et al. 1998b). It is uncertain, however, if such relationships can be globally generalized, and it is unclear how these nutrients interact with N.

Besides N, among all measured foliar nutrients, only B and Mn were correlated with site index. Boron, an important element for formation of cell walls and tissue differentiation (Marschner 1986), was positively correlated with site index in this study. A similar finding has been reported in western redcedar (*Thuja plicata* Donn ex D. Don) (Radwan and Harrington 1986). This may indicate that B is also a growth-limiting factor in some of the trembling aspen stands (Ballard and Carter 1986). Foliar Mn was significantly negatively correlated with site index and concentrations of tN, Ca, and Mg in mineral soil (Appendix). In some of the study stands, it was significantly higher than in western redcedar (Radwan and Harrington 1986) and exceeded the toxicity levels for some agriculture plants (Marschner 1986). It is not clear, however, how Mn interacts with other nutrients and what are the possible mechanisms that affect trembling aspen height growth.

Model comparisons and implications

Among the multiple regression models using different measures of site quality or foliar nutrients alone as predictors (Table 3), soil model [4c] was the best, while mineral soil model [4b] was the worst in explaining the variation of trembling aspen site index. Edatope model [3], however, had the highest precision in predicting site index (Fig. 5; Tables 3 and 7). Units of various ecological site classifications have been reported as good predictors for site index (e.g., Monserud 1984; Klinka and Carter 1990; Rayner 1992; Vanclay 1992; Wang and Klinka 1996; Kayahara et al. 1997). Studies on coastal Douglas-fir (*Pseudotsuga menziesii* Mirb.(Franco)) (Klinka and Carter 1990) and white spruce (Wang 1995; Wang and Klinka 1996) indicate that edatopes are more useful explanatory variables for site index than measured soil nutrients. Mineral soil nutrients were poor predictors of site index in many studies (e.g., Monserud et al. 1990; Wang 1995). Soil nutrients measured at a given point in time may not precisely reflect actual nutrient availability for tree growth over a long period of time (≥ 50 years) due to great temporal variability of soil nutrients (Wang 1997).

With the addition of climatic variables to the measures of local site quality or foliar nutrients as predictors, the models increased their accountability for trembling aspen site index, but only the topographic model significantly improved the precision in prediction. The insignificant increases or decreases in predictability by adding climatic variables to the models using only forest floor and mineral properties, edatopes, and foliar nutrients as predictors may indicate that climatic influences on site index are partially reflected in forest floor and mineral soil properties, edatopes, and foliar nutrients, as they are a function of climate (Buol et al. 1989; Klinka and Carter 1990; Wang and Klinka 1996). Indeed, in

this study, some of the measured forest floor and mineral soil properties and foliar nutrients were significantly correlated with longitude, latitude, or elevation. The climatic effect may also be partially reflected in edatopes, as they were inferred from a number of forest floor and mineral soil morphological properties (Pojar et al. 1987; Klinka et al. 1994).

Among the models using climatic variables and different measures of local site quality or foliar nutrients as predictors, the best model for explaining the variation of site index was soil model [8c], followed by forest floor model [8a], edatope model [7], foliar nutrient model [9], mineral soil model [8b], and topographic model [6]. The topographic model, however, had the highest precision in prediction, followed by the edatope model, forest floor model, foliar nutrient model, soil model, and mineral soil model. The soil model, forest floor model, and foliar nutrient model may have great importance in understanding ecosystem processes and causes of productivity. Practically, these models may also be used to predict potential productivity (site index) for stands recovering from suppression or damage when height growth models are not applicable. Considering the ease and consistency in measuring environmental variables and effectiveness in prediction, the models using climatic variables and topographic properties or edatopes as predictors are recommended for predicting trembling aspen site index. These models are capable of predicting site index with or without presence of crop stand or free-growing trees on a site. Such predictions may be conducive to use for growth and yield projections and forest management planning over large areas within a geographic information system (GIS) in northern British Columbia.

Conclusions

Within the northern boreal region in British Columbia, trembling aspen site index significantly varied with indirect measures of regional climate, i.e., latitude and elevation. With changes in aspect, site index was greater on warm-aspect than on cool-aspect slopes. Slope position was an important determinant for trembling aspen site index. Site index also varied with field-estimated available soil moisture and nutrient conditions. It was correlated with several measured soil physical and chemical properties as well as foliar nutrients. Nitrogen was the most important nutrient to trembling aspen height growth, as site index was highly related to tN concentration in the forest floor, mineral soil, and foliage. More productive sites had a thicker forest floor and a less acid forest floor and mineral soil. Site index was also correlated with several other measured nutrients in the forest floor, mineral soil, and foliage.

Multiple regression models developed accounted for different levels of the variation of site index and precision in prediction, depending on the variables used as predictors. Model accountability for variation of site index differed in decreasing order from the soil model, climatic model, forest floor model, foliar nutrient model, edatope model, topographic model, to mineral soil model. With the addition of the climatic variables to measures of local site quality or foliar nutrients, all models had significantly improved their accountability for the variation of site index. In predicting site index, all models were unbiased but had different levels of

precision in decreasing order from the edatope model, soil model, forest floor model, mineral soil model, foliar nutrient model, climatic model, to topographic model. With addition of climatic variables to the measures of local site quality or foliar nutrients, only the topographic model had significantly improved its precision in prediction. The soil and foliar nutrient models may provide insight into ecosystem processes, but the models using climatic variables and topographic properties or edatopes as predictors were the best in predicting trembling aspen site index.

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Appendix

Table A. Pearson's correlation coefficients (r) between measured nutrients in the forest floor, mineral soil, and foliage.

	tC _{ff}	tN _{ff}	min-N _{ff}	P _{ff}	K _{ff}	Ca _{ff}	Mg _{ff}	tC _{ms}	tN _{ms}	min-N _{ms}	P _{ms}	K _{ms}
tN _{ff}	0.67											
min-N _{ff}	0.36	0.37										
P _{ff}	0.17	0.31	0.13									
K _{ff}	0.40	0.40	0.50	0.52								
Ca _{ff}	0.29	0.60	0.24	0.06	0.37							
Mg _{ff}	0.41	0.63	0.02	0.11	0.26	0.60						
tC _{ms}	0.19	0.36	-0.16	-0.11	-0.24	0.38	0.49					
tN _{ms}	0.24	0.42	-0.18	0.04	-0.15	0.39	0.55	0.96				
min-N _{ms}	0.23	0.41	0.16	-0.31	-0.09	0.40	0.21	0.65	0.55			
P _{ms}	-0.03	-0.32	0.04	-0.19	-0.41	-0.55	-0.55	-0.23	-0.31	-0.13		
K _{ms}	0.11	0.34	-0.35	0.41	0.05	0.25	0.46	0.57	0.70	0.13	-0.34	
Ca _{ms}	0.08	0.34	-0.07	-0.20	-0.13	0.56	0.40	0.78	0.71	0.75	-0.34	0.43
Mg _{ms}	0.17	0.39	-0.19	0.02	-0.04	0.46	0.67	0.88	0.89	0.48	-0.45	0.69
S _{ms}	0.19	0.40	-0.03	0.02	-0.03	0.34	0.44	0.81	0.75	0.52	-0.30	0.43
N _f	0.10	0.39	0.15	0.19	0.27	0.40	0.28	0.28	0.29	0.27	-0.36	0.15
P _f	0.05	0.10	-0.07	0.30	-0.08	-0.07	-0.12	0.03	0.04	0.01	0.14	0.09
K _f	-0.08	-0.37	-0.06	-0.10	-0.15	-0.32	-0.33	-0.08	-0.13	-0.07	0.42	-0.17
Ca _f	-0.02	0.23	-0.09	0.17	0.24	0.49	0.19	0.01	0.05	0.23	-0.38	0.25
Mg _f	0.18	0.21	-0.09	0.12	0.13	0.27	0.64	0.23	0.26	0.08	-0.31	0.23
Mn _f	-0.04	-0.20	0.26	0.10	0.19	-0.44	-0.45	-0.58	-0.58	-0.31	0.35	-0.40
Zn _f	0.16	0.34	-0.07	0.34	0.10	0.13	0.12	0.20	0.24	0.24	-0.14	0.31
Cu _f	0.06	-0.08	-0.01	-0.15	-0.02	0.01	-0.19	0.07	0.02	0.14	0.20	-0.08
B _f	0.30	0.49	-0.19	0.23	0.22	0.46	0.69	0.50	0.61	0.20	-0.62	0.74
Al _f	0.01	-0.24	-0.18	-0.22	-0.22	-0.29	-0.04	-0.13	-0.13	-0.22	0.32	-0.10
Fe _f	0.09	-0.07	-0.01	-0.14	-0.05	-0.18	0.19	0.02	0.02	-0.18	0.13	-0.05

Note: Boldface indicates that the correlation is significant at $\alpha = 0.05$. Forest floor nutrients: tC_{ff}, total C; tN_{ff}, total N; min-N_{ff}, mineralizable N; P_{ff}, extractable P; K_{ff}, extractable K; Ca_{ff}, extractable Ca; Mg_{ff}, extractable Mg. Mineral soil nutrients: tC_{ms}, total C; tN_{ms}, total N; min-N_{ms}, mineralizable N; P_{ms}, extractable P; K_{ms}, extractable K; Ca_{ms}, extractable Ca; Mg_{ms}, extractable Mg; S_{ms}, extractable S. Foliar nutrients: N_f, total N; P_f, total P; K_f, total K; Ca_f, total Ca; Mg_f, total Mg; Mn_f, total Mn; Zn_f, total Zn; Cu_f, total Cu; B_f, total B; Al_f, total Al; Fe_f, total Fe.

Table A (concluded).

Ca _{ms}	Mg _{ms}	S _{ms}	N _f	P _f	K _f	Ca _f	Mg _f	Mn _f	Zn _f	Cu _f	B _f	Al _f
0.78												
0.55	0.70											
0.21	0.20	0.36										
-0.09	-0.11	0.11	0.48									
-0.18	-0.21	-0.07	0.22	0.45								
0.23	0.14	0.03	0.33	0.11	-0.19							
0.16	0.39	0.23	0.25	0.06	-0.02	0.37						
-0.58	-0.61	-0.34	0.06	0.13	0.32	0.02	-0.18					
0.10	0.08	0.24	0.25	0.34	-0.10	0.36	0.10	-0.12				
0.07	-0.11	0.04	0.18	0.22	0.38	0.03	-0.12	0.10	0.24			
0.42	0.71	0.42	0.22	-0.01	-0.41	0.40	0.45	-0.42	0.28	-0.15		
-0.16	-0.09	-0.20	-0.13	0.02	0.38	-0.12	0.20	0.23	-0.30	-0.05	-0.12	
-0.14	0.07	0.00	0.12	0.06	0.38	-0.08	0.32	0.28	-0.15	0.12	0.05	0.62