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Estimating trembling aspen productivity in the boreal transition ecoregion of Saskatchewan using site and soil variables

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Short Title: Site productivity of trembling aspen

ABSTRACT

Productivity of trembling aspen as expressed by site quality index (SQI) in natural stands growing on three different soil parent material types (fluvial, lacustrine and glacial till) in the boreal transition ecoregion of Saskatchewan was evaluated by using soil and site variables. The soil and site variables used were either general categorical variables such as parent material and ecosite, or continuous variables such as soil texture (percent sand or clay), pH, carbon, nitrogen, C:N ratios, and elemental composition. It was not possible to reliably estimate SQI using only categorical site variables or continuous soil variables when all plots were grouped together. However, when plots were grouped by parent material type, over 45% of the variability in trembling aspen productivity was explained using the common soil measurements of texture and pH. In estimating SQI, there was an interaction between both pH and soil texture with parent material. On fluvial and lacustrine parent material increased clay content was positively correlated to SQI but was negatively correlated to SQI on till, while pH was positively correlated with SQI on fluvial parent material but negatively on lacustrine. Including more sophisticated measures of soil nutrient availability in the forest floor and BC horizons did not improve the SQI prediction. This study indicates that it is possible to estimate trembling aspen productivity using simple site and soil variables, provided that differences in soil properties within parent material groupings are considered in the analysis.

Keywords: site quality index, parent material, soil texture, tree productivity.

Trembling aspen (*Populus tremuloides*) is the dominant tree species in the boreal transition ecoregion of Saskatchewan, a transitional area between forest to the north and prairie to the south, where it grows on a wide variety of soil types. It is an important tree species both economically, in terms of timber harvest, and ecologically, for providing ecosystem services such as wildlife habitat (Burns and Honkala 1990). Developing a better understanding of the soil properties regulating trembling aspen growth in this region will allow for more site specific management practices. This is particularly important in the context of adaptation to climate change because the boreal transition is one region which has suffered dieback as it is prone to water stress and associated insect defoliation events (Allen et al. 2010).

Previous studies have shown the importance of landscape scale differences in climate (often expressed as degree-days or climate moisture index) on the productivity of trembling aspen and other tree species (e.g. Ung et al. 2001; Hogg et al. 2005). However, within a given region with minimal differences in climate, tree productivity is likely controlled by soil physical and chemical properties (Grigal 2009). The two main resources that trees derive from the soil are water and nutrients so the soil and site variables that optimize their availability will likely enhance trembling aspen productivity.

Soil water availability is a function of soil texture, topographical position, and organic matter with increased clay content, lower topographic position, and increased organic matter associated with increased soil water (Gómez-Plaza et al. 2001; Greminger et al. 1985; Nyberg 1999; Qiu et al. 2001). Soil parent material, which is closely associated with soil texture, may therefore be a good proxy for soil water availability with fine textured lacustrine soils having a greater capacity to hold water than coarse textured fluvial soils. Soil water holding capacity and water availability, expressed as soil texture and topographical position, were shown to positively impact aspen growth in the Upper Great Lakes Region and Manitoba (Gustafson et al. 2003; Martin and Gower 2006). On the other hand, water availability (or a proxy such as soil texture) did not influence aspen productivity in Quebec (Pinno et al. 2009) or British Columbia (Chen et al. 2002).

In terms of soil fertility, nitrogen (N) is generally considered to be the nutrient most limiting tree growth in boreal and temperate environments (Reich et al. 1997; Turkington et al. 1998) so any increases in soil N availability may lead to increases in tree growth. There is some evidence, however, that the growth of *Populus* trees in the boreal transition ecoregion can also be limited by low phosphorus (P) availability (Liang and Chang 2004; Pinno and Bélanger 2009; Pinno et al. 2010). Base cations, and in particular calcium (Ca), have also been shown to be positively correlated to trembling aspen and *Populus* growth in both field and greenhouse settings (Bowersox and Ward 1977; Lu and Sucoff 2001; Paré et al. 2001). The forest floor and A horizons are known to contain the largest fraction of fine roots in boreal forests (Strong and La Roi 1983; Steele et al. 1997) and thereby provide a reasonable estimate of nutrient availability for the trees (e.g. Hamel et al. 2004). However, the bulk elemental composition of the parent C horizon was shown to be more indicative of nutrient limitations than forest floor or surface soil available nutrient concentrations in temperate and boreal forests. For example, Bailey et al. (2004) also showed that sugar maple foliar Ca and magnesium (Mg) status and mortality were more strongly linked to B horizons compared to forest floor Ca and Mg chemistry. Kobe (1996) and van Breemen et al. (1997) suggested that the parent C elemental composition may be a reliable predictor of sugar maple mortality as well as Ca and Mg nutrition. Finally, tThiffault et al. (2006) showed that the signal of very low Ca and Mg availability was weak in the forest floor and A horizons, probably because the chemical signature of these horizons are controlled by litterfall which exhibits well balanced nutrient ratios, whereas it was very high in the deeper mineral soil. With P, the composition of the parent material also serves as a good indicator of primary mineral P, whereas a large fraction of P in the forest floor is biological (Cross and Schlesinger 1995). In this respect, the parent C material may give a good indication of long-term nutrient reserves for these sites.

Ecosites are ecological units that develop under similar nutrient and moisture regimes (Beckingham et al. 1996) and therefore may be related to trembling aspen productivity (Carmean 1996a; Stadt et al. 2007). The presence of earthworms may also indicate higher site fertility due to litter incorporation in the mineral soil and the increased decomposition rates associated with earthworms (Bohlen and Edwards 1995; Haimi and Einbork 1992).

The influence of these soil and site variables are generally marginal compared to landscape scale climate variables in studies which cover a large geographic range (Chen et al. 2002; Hamel et al. 2004). The goal of this study was to identify the soil and site variables related to trembling aspen productivity within the boreal transition ecoregion of Saskatchewan. Our approach is fundamentally similar to other recent aspen productivity studies in Minnesota (Grigal 2009) and Québec (Pinno et al. 2009) except we focus on field measurements of the soil and site variables as well as aspen productivity, whereas most other studies have used soil information available from maps and physical properties databases. Given the relatively dry climate of this ecoregion, we expect that soil and site properties which represent increased water availability will be associated with increased trembling aspen productivity. Specifically, we hypothesize that aspen productivity will be greatest on lacustrine parent material followed by till and then fluvial deposits, and that trembling aspen productivity will increase positively with increasing clay content. As for the effect of topography, we expect lower slopes to be more productive than level or upper slopes as the trees in the lower slopes should benefit from wetter conditions. Soil nutrients are expected to play a secondary role in determining trembling aspen productivity in this region because soils in the boreal transition ecoregion are generally nutrient-rich. We do expect, however, that the richer ecosites will be more productive than the mesic ecosites and that soil nutrient levels will be positively related to productivity.

MATERIAL AND METHODS

Study Area and Field Sampling

We worked in the boreal transition ecoregion of northeast Saskatchewan within a radius of approximately 75 km of the town of Tisdale (52º 51’N, 104º 03’W) (see Bélanger and Pinno (2008) for more details). The size of the study area was restricted in order to limit the climatic influence on tree growth between sites and emphasize differences due to edaphic factors. The climate is characterized by average temperatures ranging from -18.5ºC in January to 17.4ºC in July with an annual precipitation of 400 mm. Climate simulations from the BIOSIM hydroclimatic model (Régnière and St-Amant 2007) for 12 locations covering the whole study area predicted mean degree-days of growth greater than 5°C at 1616 with a coefficient of variation (CV) of 3.5%, and a mean Thornthwaite potential evapotranspiration at 1478 mm with a CV of 2.7%. The low variability in climate predictions between sampling points confirms that climate is not likely responsible for significant differences in soil development and tree growth within the sampling area.

The dominant tree species in the area are trembling aspen along with white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*). Forested areas are normally islands of trees ranging from 1 ha to 100s ha in size and surrounded by agricultural land. The soils in this area are classified mainly as Dark Gray Chernozems and Gray Luvisols (Soil Classification Working Group 1998) developed on glacial till, lacustrine and fluvial parent materials. Some Eutric Brunisols developed on fluvial parent material. The topography for the area is relatively flat with slopes greater than 10% only occurring in the till areas.

Within this region, fifty temporary sampling locations were delineated in naturally established, nearly pure (>80%) trembling aspen stands showing no evidence of cattle grazing, timber harvesting or other disturbance. No more than two plots were allowed in a single stand and then they were at least 100 m apart. Stand ages ranged from 20 to 75 years old and canopy heights from 11 to 22 m. A stratified design was used so that all three parent materials were almost equally represented with 16 plots located on lacustrine parent material and 17 plots on both of fluvial and till parent materials.

Plot centers were randomly located within selected stands and the three closest canopy trees (dominant and co-dominant) were measured for height and diameter. These three trees were cored at breast height (1.3 m) with the cores then put in plastic straws and taken back to the lab for ring counting. Plot sizes varied slightly depending on the location of the canopy trees but were on average about 25 m^2 and never exceeded 50 m^2. This approach differs slightly from other larger scale approaches at the stand level which select the three tallest trees per hectare (Carmean 1975; Perron et al. 2009). The benefit of our approach is that it enabled a microsite scale analysis of the soil and site factors related to trembling aspen productivity.

Two soil pits were therefore dug in each plot within 1.5 m of the three canopy tree stems. The depth of the forest floor and Ah horizons were recorded and then averaged to obtain a plot value. Soil samples were taken from the forest floor, Ah and upper B horizons as well as the horizon corresponding to the 50 cm depth, designated as a BC horizon. Categorical site variables that were recorded included soil drainage class, ecosite, topographic position, presence of earthworms, parent material, and textural class of the Ah, upper B and BC horizons. Soil drainage was grouped into five categories (rapid, well, moderately-well, imperfect, and poor) representing increasingly poorer soil drainage (Beckingham et al. 1996). Topographic position was grouped into three categories of upper slope, lower slope, and level. Due to elevation changes in the till areas, elevation (m) was recorded with a GPS unit and used as a continuous variable to estimate tree growth. Ecosite was determined based on understory vegetation, drainage, and soil type (Beckingham et al. 1996) with "d" ecosites considered mesic while ecosites "e" and "f" considered progressively richer sites.

Soil Analyses

Soil samples were air-dried and then sieved with a 2 mm mesh to remove coarse fragments before being bulked by volume, resulting in one sample per plot for each soil horizon. Particle size distribution was determined for the Ah and BC horizons using the Horiba Partica LA-950 Laser Particle Analyzer. Sodium hexametaphosphate and sonication were used on the samples to disperse particles before measurement. The Ah samples were also treated with NaOCl to remove organic matter and disperse mineral aggregates. The soil textural class determined in the field was corrected using the laboratory data.

Total carbon (C) and N of the forest floor and Ah horizons were determined by dry combustion and infrared detection using a Leco CNS-2000 Analyzer at 1100ºC. Electrical conductivity and pH of the forest floor and Ah horizons were measured in water. Mineralizable N was determined with incubations for eight weeks at 22ºC of 2.5 g of the forest floor and 10 g of Ah horizon material. Samples were rinsed twice with deionized water prior to the incubation to remove soluble forms of N. Throughout the incubation, samples were watered twice per week to keep the samples moist. After the incubation, NH_4 and NO_3 were extracted with a 2 *M* KCl solution and analyzed colourimetrically with a Technicon Auto-Analyzer.

The bulk elemental composition of the forest floor and C horizon was determined from fused beads prepared from a 1:5 soil / lithium tetraborate mixture which were then finely ground (M4 Fluxer, Corporation Scientifique Claisse, Quebec City, Canada). Two grams of the finely ground beads were then digested in 15 ml of HCl and 5 ml of HNO_3 at 100ºC for six hours in Teflon beakers covered with a watch glass. Calcium, Mg, potassium (K), sodium (Na), aluminum (Al) and iron (Fe) were analyzed using atomic absorption/emission (SpectraAA 220, Varian Analytical Instruments). Phosphorous was analyzed colourimetrically (molybdenum blue) from the same digests with a Technicon Auto-Analyzer (Pulse Instrumentation, Saskatoon, Canada).

SQI Determination and Data Analysis

Tree cores were dried, sanded with progressively finer grits until the annual growth rings were clearly visible under a dissecting microscope, and then aged. Breast height age was combined with individual tree height to determine site quality index (SQI) at an age of 50 years using the formula for trembling aspen developed in northwest Ontario (Carmean 1996b):

$$SQI_{BH50} = 25.7149 + 0.7182(H - 1.3) + 6.2483[\ln(H - 1.3)] - 4.5453[\ln(BHAge)] \\ - 1.2334[\ln(BHAge)^2] - 6.5116(\frac{H - 1.3}{BHAge}) + 0.01186[\ln(H - 1.3)]BHAge$$

where *H* is height (m) and *BHAge* is the age at breast height (1.3 m). Site quality index was averaged for each plot.

ANOVA was used to compare SQI between different groupings of the categorical site variables (e.g. parent material, ecosite, drainage and soil textural classes). These categorical variables encompass a series of physical and chemical characteristics that can potentially act simultaneously to influence forest stand productivity and could potentially provide a simple relationship for estimating aspen productivity. Therefore, ANCOVA was used as a means to conduct multiple regressions using the categorical site variables to estimate aspen SQI. Examining the continuous variables, on the other hand, allow to better link aspen productivity to soil and ecosystem processes. Correlation analysis was first used to determine the suite of continuous variables (e.g. soil texture, soil chemical properties and elevation) most closely related to SQI for all fifty plots and then SQI variability was analyzed with these same variables using stepwise multiple regression analysis. To determine the potential links between the categorical and continuous variables, correlation and multiple regression analyses were repeated for the continuous variables after grouping by the different categorical site variables. The maximum number of variables selected in the multiple regression analysis was set at three in order to keep the relationships practical while maximizing predictive capability. Non-linear relationships to SQI were also examined using both single and multiple regressions. However, none of the non-linearmodels had a greater predictive capability than linear models. For this reason, only the linear models are presented and discussed. Normality of residuals and equality of variances was confirmed for all models presented. Statistics were conducted using JMP 7 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Site quality index values ranged from 12.0 to 23.1 (average values shown in Table 1) and were not significantly different among the groupings of parent material ($p=0.283$), ecosite ($p=0.884$), slope position ($p=0.614$), soil drainage ($p=0.492$), presence of earthworms ($p=0.340$), and Ah horizon textural class ($p=0.336$). For the continuous variables (average values shown in Table 1), correlation analysis for all fifty plots combined showed that only forest floor C and N concentrations as well as Ah horizon sand content were significantly (negatively) correlated to SQI (Table 2).

Our hypothesis that categorical site variables would be important predictors of aspen productivity was not upheld. The ANCOVA based multiple regression analysis, derived from the categorical site variables alone or in combination with continuous soil variables, was unsuccessful in identifying the most productive growing sites for trembling aspen in the boreal transition ($R^2<0.1$, $p>0.05$, results not shown).

A significant multiple regression equation derived from the continuous variables included forest floor C concentration, BC horizon silt content and Ah horizon sand content (Table 3). However, the measured versus predicted SQI graph (Figure 1a) shows that this equation overestimates at lower SQI values and underestimates at higher SQI values. After grouping by categorical variables, the only one of these groupings which improved site index prediction was parent material type:

(1) For the fluvial sites, SQI was positively correlated to Ah horizon pH and negatively correlated to Ah sand content (Table 2). The most robust multiple regression equation included Ah horizon pH and BC horizon clay content (Table 3);

(2) For lacustrine sites, SQI was positively correlated to BC horizon clay content and marginally positively correlated to total N concentration in the Ah horizon (Table 2). The strongest multiple regression equation included BC horizon clay content and depth of the Ah horizon (Table 3);

(3) For till sites, SQI was negatively correlated to Ah horizon clay content (Table 2). Soil texture was also related to slope position and soil drainage in the till sites with lower slope positions having significantly higher Ah horizon clay content compared to level and upper slope positions ($p=0.026$, 18.7% vs 11.7% respectively). Imperfectly and poorly drained sites had higher Ah horizon clay content than the moderately, well, and rapidly drained sites on till parent material ($p=0.034$, 23.2% vs 12.7% respectively). The multiple

regression equation that explained the most SQI variability for till plots included Ah horizon clay content and BC horizon sand content (Table 3).

The measured versus predicted SQI plot for the three parent material regression equations (Figure 1b) indicates that trembling aspen SQI in the boreal transition can be effectively estimated using such an approach.

DISCUSSION

Simple Soil Attributes to Estimate SQI of Aspen

Overall, our results indicate that the relatively simple soil attributes of texture (percent sand or clay) and pH have the largest impact on aspen productivity in this region, although their impact differs as a function of parent material type. More complex soil variables such as elemental composition, mineralizable N, and categorical site variables such as ecosite are not as strongly related to aspen productivity. The predictive ability of the regression equations is comparable to equations developed for trembling aspen SQI in British Columbia (Chen et al. 2002) and Québec (Pinno et al. 2009). These basic soil properties are consistently important predictors of aspen and poplar productivity, but the specific relationship varies by location. For example, in the boreal shield of Quebec, pH of the forest floor was positively related to aspen SQI (Pinno et al. 2009) but the range of pH values was on average two units lower than that found in the current study. In another study relating soil properties to hybrid poplar productivity in Alberta, texture (% sand) showed a peaked distribution with maximum productivity associated with 70% sand content (Pinno et al. 2010) while in the current study this relationship to texture was linear and varied by parent material type. Therefore, it is important to determine the relationship between these basic soil characteristics and productivity at the local level where management decisions are made. Most other studies of trembling aspen SQI were conducted across large geographic areas where hydroclimatic variables were shown to be the best predictors of trembling aspen growth (e.g. Ung et al. 2001; Hogg et al. 2005), which is not at all useful locally.

Impacts of Soil Moisture and Nutrient Availability

The approach of grouping sites by parent material is similar to that taken for estimating trembling aspen productivity in the boreal shield of Quebec (Pinno et al. 2009) and Ontario (Carmean 1996b). When all plots were analyzed together, it was not possible to reasonably explain trembling aspen productivity. This is likely due to the interaction between soil texture and parent material. Our hypotheses that increasing soil moisture availability due to high clay content and lower topographic positions would increase trembling aspen productivity in Saskatchewan proved correct only for the fluvial and lacustrine soils. Similarly, Paré et al. (2001) in Quebec and Martin and Gower (2006) in Manitoba found that trembling aspen trees were taller on clay soils compared to coarser textured soils, presumably because of the greater water holding capacity of the clay soils. However, for till sites in our study, finer textures resulted in poorer growth because these are generally associated with depressional microsites and poorly drained soils, suggesting that trembling aspen growth responds positively to increasing soil moisture availability up until the point where the soil water becomes stagnant and poorly oxygenated. Carmean (1996b) also found this pattern in Ontario and suggested that trembling aspen grows best on well drained sites with clay subsoils to hold moisture. Therefore, even within a limited region such as our study area, it is not possible to generalize that a single resource, such as low water availability, is dominant in controlling tree productivity.

Nutrient availability is also a factor controlling tree growth on lacustrine sites with SQI of trembling aspen being correlated with total N in the Ah horizon. This relationship was expected since N was previously shown to be correlated with aspen and poplar growth (Haikio et al. 2007; Rennenberg et al. 2010). Other soil nutrients, however, were not correlated with trembling aspen productivity for this parent material type. For fluvial sites, pH of the Ah horizon may also reflect improved tree nutrition because optimal nutrient availability is often found at pH values between 6 and 7 (Havlin et al. 2003). The lower total Ca, Mg and K in the fluvial parent material compared to the other parent material types (Table 1) points to the larger role of an improved acid-base status of the soil (i.e. increased pH) on increased tree growth. On till sites, the effects of soil nutrient availability on aspen growth is overshadowed by other controlling factors, namely soil water availability. This is in accordance with the idea that non-optimal soil moisture often overrides soil nutrient availability in determining trembling aspen productivity (Carmean 1996b).

Neither the forest floor C and N levels (including mineralizable N and C:N ratios) nor the forest floor and BC horizon bulk elemental composition were related to trembling aspen productivity. Combined with the lack of difference in trembling aspen SQI between parent material types, these results suggest that trembling aspen is capable of growing reasonably well on soils with a wide range of nutrient availabilities (Burns and Honkala 1990). It is also interesting that these more thorough laboratory analyses did not produce soil variables that were better related to aspen productivity relative to simple soil variables such as texture and pH. In this respect, it may be relatively easy to perform soil mapping that is appropriate for trembling aspen growth. This has recently been done in Minnesota (Grigal 2009) where an aspen productivity index (APX) was developed based on soil and forest productivity maps and databases. This index grouped soil properties into three categories influencing aspen growth: water availability, nutrient availability, and other growth factors in an approach fundamentally similar to our study. The APX is now being used to compare forest productivity among all soil mapping units in Minnesota (Grigal 2009), thereby demonstrating the practical application of site quality studies in natural resource management.

Categorical Site Variables

None of the categorical site variables studied were useful in estimating trembling aspen productivity, indicating that a more sophisticated approach is necessary in this region. Parent material type provides a general indicator of soil texture, but SQI was not significantly different among parent material types due to the large SQI ranges within each parent material type. For example, on sandy fluvial parent material, SQI ranged from 12 to 21. This lack of difference in aspen growth between parent material types is similar to what was found in Québec (Pinno et al. 2009) and Sweden (Johansson 2002). However, others found differences in tree growth among parent material types. For example, black spruce growth in Québec (Hamel et al. 2004), lodgepople pine growth in Alberta (Dumanski et al. 1973), and trembling aspen growth in Québec (Paré et al. 2001) were all greater on relatively finer textured parent materials than on coarser textured parent material groupings. Although SQI was not different among parent material types in our study, it is interesting that it was the best grouping variable for modeling SQI with site and soil variables. This indicates that the important factors controlling site specific trembling aspen productivity are due to specific differences in soil properties within parent material groupings rather than being due to general differences between parent material types.

Ecosite provides a general measure of site moisture and fertility but was not related to aspen productivity. This may be because the soil and site variables (e.g. soil texture and understory vegetation) used in ecosite description may not be the same variables that are important in determining tree productivity. For example, some of the supposedly richest "f" ecosites on till parent material were found in lower slope areas which supported rich understory growth but poor tree growth. Similar relationships have been found in northern Ontario for black spruce, jack pine, and trembling aspen (Carmean 1996a) where it was argued that the soil descriptions used in forest ecosite classification are not taking into account the soil variables most related to tree productivity. However, Stadt et al. (2007) found that stratification by ecosite helped improve the performance of models that used competition and light estimation indices to predict diameter growth of five species of mature trees from natural boreal mixed forests. They suggested that the species have different niche characteristics and that competitive interactions change across ecosites due to the changing site conditions. This is somewhat similar to our models developed from parent material groupings, except that the dominant variables within an ecosite are aboveground variables such as competition intensity and light availability. Ecosite may therefore be a stratification that is well suited for light competition, whereas parent material may be better suited for stratifying based on belowground resources.

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Table 1: Soil physical and chemical properties as well as elevation for the three parent material groupings. Values are averages and standard deviation.

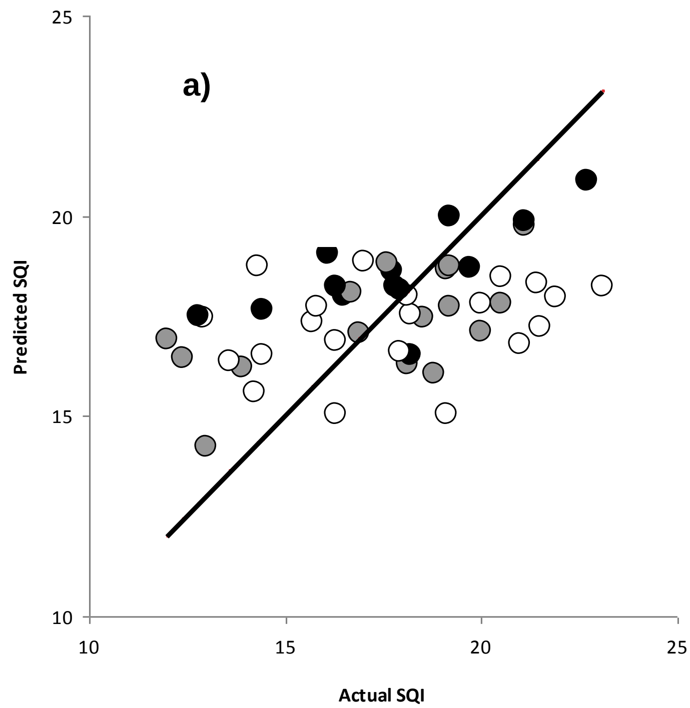
	Units	Fluvial	Lacustrine	Till
SQI		17.6 (3.0)	18.5 (2.9)	16.9 (2.6)
Forest Floor				
pH		6.7 (0.4)	6.9 (0.3)	6.9 (0.3)
C	mg g^{-1}	289.5 (77.5)	263.9 (65.3)	301.2 (58.4)
N	mg g^{-1}	17.1 (4.7)	17.1 (1.6)	17.8 (1.8)
C:N		17.1 (1.1)	17.1 (1.6)	17.8 (1.8)
NO_3^-	mg g^{-1}	3.9 (3.1)	5.1 (3.0)	5.4 (3.5)
Ca	mg g^{-1}	21.5 (9.0)	22.7 (3.8)	23.4 (5.5)
Mg	mg g^{-1}	2.6 (1.0)	4.2 (1.4)	3.9 (1.4)
K	mg g^{-1}	1.2 (0.2)	1.8 (0.9)	1.3 (0.2)
PO_4	mg g^{-1}	0.4 (0.3)	0.6 (0.3)	0.4 (0.1)
C:P		90.7 (48.4)	65.5 (56.2)	93.5 (50.6)
N:P		5.3 (2.9)	3.8 (3.1)	5.3 (3.2)
Ca:Mg		8.3 (2.2)	5.9 (1.8)	6.4 (1.4)
Ah horizon				
Depth	cm	11.4 (7.5)	14.0 (6.8)	8.1 (5.6)
pH		6.5 (0.7)	6.8 (0.5)	6.6 (0.4)
C	mg g^{-1}	47.8 (6.3)	40.0 (14.7)	77.6 (7.1)
N	mg g^{-1}	3.1 (4.0)	3.1 (1.3)	5.5 (4.6)
C:N		14.1 (7.2)	10.9 (1.4)	13.5 (2.0)
NO_3^-	mg g^{-1}	3.6 (3.4)	3.4 (2.8)	6.0 (7.6)
Sand	%	58.6 (20.3)	19.4 (16.6)	36.3 (14.4)
Clay	%	12.4 (9.1)	41.2 (18.8)	14.1 (6.3)
BC horizon				
Ca	mg g^{-1}	11.9 (12.8)	19.7 (20.6)	31.2 (31.7)
Mg	mg g^{-1}	5.6 (3.7)	16.2 (10.2)	13.1 (8.5)
K	mg g^{-1}	16.8 (2.0)	21.3 (2.4)	17.9 (2.4)
PO_4	mg g^{-1}	0.07 (0.06)	0.14 (0.07)	0.13 (0.11)
N:P		5.7 (7.8)	4.2 (6.0)	5.1 (6.3)
Ca:Mg		2.1 (1.2)	1.1 (0.5)	2.0 (1.1)
Sand	%	56.5 (25.8)	8.9 (10.7)	18.7 (16.6)
Clay	%	6.6 (6.2)	49.5 (14.0)	27.8 (12.5)
Elevation	m	474 (57)	416 (68)	519 (75)

Table 2: Correlation coefficients between continuous soil variables, elevation and SQI for all plots combined and each parent material individually. Bold values are statistically significant at *P≤0.10, **P<0.05, ***P<0.01.

	All	Fluvial	Lacustrine	Till
Forest Floor				
pH	-0.059	0.313	-0.413	-0.273
C	**-0.315****	-0.357	-0.355	-0.070
N	**-0.306****	-0.371	-0.333	-0.111
C:N	0.043	0.086	0.044	0.143
NO_3^-	-0.010	0.127	-0.075	-0.349
Ca	0.081	0.307	0.076	-0.281
Mg	0.159	0.285	0.350	-0.143
K	-0.012	-0.167	-0.185	0.188
PO_4	0.013	-0.112	-0.145	0.200
C:P	-0.109	-0.270	0.246	-0.162
N:P	-0.121	-0.283	0.243	-0.163
Ca:Mg	-0.093	-0.098	-0.257	-0.142
Ah horizon				
Depth	0.076	0.080	0.063	-0.213
pH	0.136	**0.570****	**-0.442***	-0.078
C	0.066	0.129	0.402	0.123
N	0.055	0.055	**0.479***	0.076
C:N	0.088	0.225	-0.115	0.261
NO_3^-	0.118	0.171	0.248	0.191
Sand	**-0.238***	**-0.540****	-0.258	0.299
Clay	0.194	0.352	0.158	**-0.616*****
BC horizon				
Ca	-0.075	0.078	-0.363	0.122
Mg	0.021	0.036	-0.247	0.222
K	0.198	0.026	0.275	0.038
PO_4	0.065	-0.464	0.285	0.226
N:P	0.053	0.443	-0.040	-0.250
Ca:Mg	-0.040	0.298	-0.139	-0.144
Sand	0.024	0.144	**-0.480***	**0.435***
Clay	0.180	-0.109	**0.617****	-0.247
Elevation	-0.225	0.106	-0.025	**-0.420***

Table 3: Multiple regression models for predicting trembling aspen productivity using continuous soil and site variables for all plots combined and for each parent material grouping. SEE is the standard error of the estimate, VAR# is the variable number as it appears in the equation and SS is the sum of squares for each individual regression variable.

Equation	R^2	p	SEE	Var 1 SS	Var 2 SS	Var 3 SS
Continuous Variables for all Parent Materials Combined						
23.91 - 0.11(Forest Floor % C) - .05(BC horizon % Silt) - 0.03(Ah horizon % sand)	0.158	0.012	2.63	40.00	23.83	20.67
Fluvial						
-2.08 + 3.21(Ah horizon pH) - 0.19(BC horizon % clay)	0.454	0.015	2.39	47.42	18.87	
Lacustrine						
11.61 + 0.21(BC horizon % clay) - 0.27(Ah Depth)	0.536	0.003	1.97	47.69	27.25	
Till						
19.17 - 0.22(Ah horizon % Clay) + 0.04(BC horizon % Sand)	0.451	0.015	2.09	42.07	7.93	



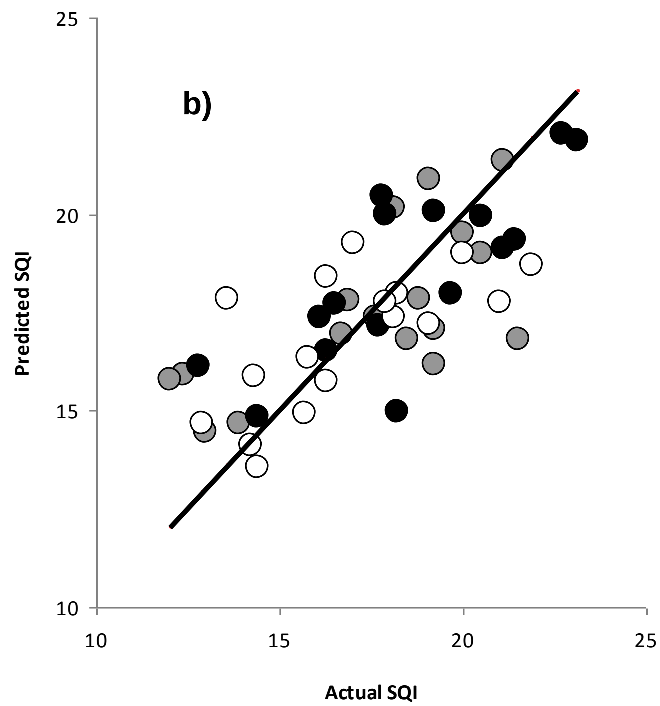


Figure 1: Actual versus predicted site quality index modeled using continuous soil variables for (a) all plots grouped together and (b) grouped by parent material. Black circles represent lacustrine plots, grey circles represent fluvial plots, and white circles represent till plots. The solid line is the ideal 1:1 line.