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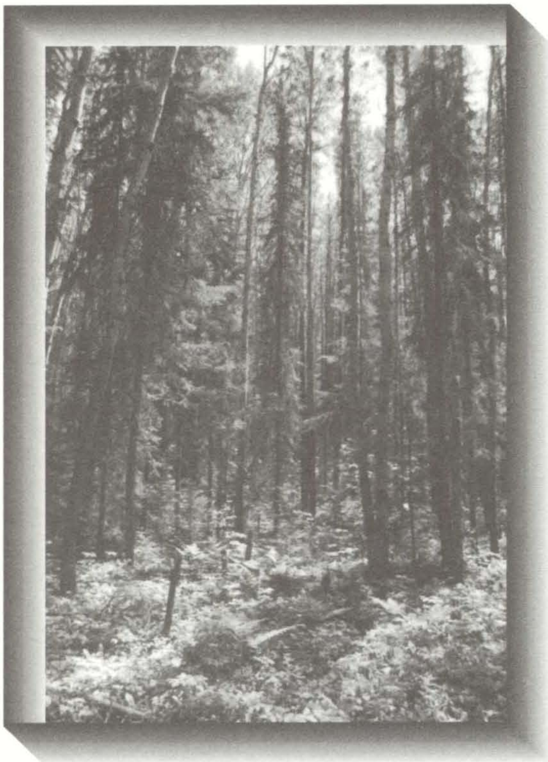

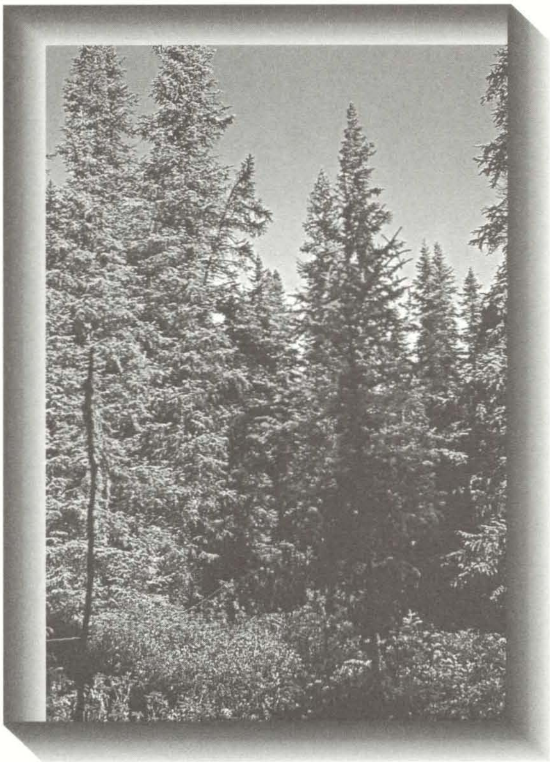

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Natural Resources Canada
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Guy R. Larocque, W. John Parton[1]
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Natural Resources Canada
Canadian Forest Service - Laurentian Forestry Centre
Sainte-Foy, Quebec

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ABSTRACT

Polymorphic site productivity functions were derived for black spruce (*Picea mariana* [Mill.] B.S.P.) in the Clay Belt region of Northern Ontario using data from permanent sample plots. The main intent was to relate different height growth patterns to the characteristics of the operational groups of the forest ecosystem classification implemented for Ontario's Clay Belt. Five models based on the logistic, Chapman-Richards and Weibull functions were tested. Dummy variables were incorporated into the models to represent the influence of different operational groups on site productivity. The integration of basic ecological information and polymorphic site productivity functions provided a good explanation of the growth patterns within each operational group. Thus, although some operational groups had very close site index values at age 50, they were characterized by different patterns of long-term height development. Of the various models tested, the Weibull and Chapman-Richards functions, constrained to satisfy the condition that top height equals site index at age 50, produced the best fit.

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RÉSUMÉ

Des fonctions polymorphes de productivité de site ont été développées pour l'épinette noire (*Picea mariana* [Mill.] B.S.P.) dans la Zone argileuse du nord de l'Ontario à partir de données de parcelles-échantillons permanentes. L'intention première fut de relier différentes tendances de croissance en hauteur aux caractéristiques des groupes opérationnels du système de classification écologique des forêts développé pour la Zone argileuse de l'Ontario. Cinq modèles basés sur les fonctions logistique, de Chapman-Richards et de Weibull ont été testés. Des variables factices ont été incorporées dans les modèles afin de représenter l'influence des différents groupes opérationnels sur la productivité des sites. L'intégration d'information écologique de base et de fonctions polymorphes d'indice de site a permis d'expliquer adéquatement les tendances de croissance à l'intérieur de chaque groupe opérationnel. Ainsi, même si certains groupes opérationnels avaient des indices de site très similaires à 50 ans, ils étaient caractérisés par différentes tendances de croissance en hauteur à long terme. Parmi les divers modèles testés, la fonction de Weibull et la fonction de Chapman-Richards, modifiées pour minimiser le biais à l'âge de référence, ont mieux représenté les données.

INTRODUCTION

Site index, despite its limitations, remains the most frequently applied method of evaluating site productivity in North America. Common practice has consisted in developing anamorphic site index curves because they could be derived easily from temporary sample plot data. Anamorphic site index curves are widely applied in wood supply analysis. Recent examples can be found in Gordon *et al.* 1989, Phillips 1992, Williams *et al.* 1990, Hacker and Bilan 1991, and Gilmore *et al.* 1993. However, major shortcomings have been associated with anamorphic curves (Carmean 1968, 1972, 1975; Monserud 1984a, 1985; Dolph 1991), among them the proportionality assumption across different sites (Carmean 1968, 1972; Graney and Burkhart 1973; Hann and Scrivani 1987). As polymorphic site index curves are considered more representative of the variability in height growth patterns across different sites (Daniel *et al.* 1979; Monserud 1984a; Smith 1984), they have been the subject of many studies in the last few decades. However, their derivation is more difficult and expensive than that of anamorphic site index curves because remeasurement data from permanent sample plots or stem analyses are required. Recent examples are the studies of Borders *et al.* (1984), Biging (1985), Dolph (1987, 1991), Alemdag (1988, 1991), Newnham (1988), Cieszewski and Bella (1989), Curtis *et al.* (1990), Quenet and Manning (1990), Cao and Durand (1991), Ker and Bowling (1991), Goelz and Burk (1992), and Newton (1992).

In the last three decades, efforts have focused on (i) using and improving nonlinear models mostly based on Richards' function (1959), (ii) applying stem analysis techniques to obtain remeasurement data from individual trees, (iii) associating site index with environmental factors and (iv) developing base age-invariant formulations (e.g., Bailey and Clutter 1974; Cieszewski and Bella 1989; Goelz and Burk 1992; Newton 1992; Cao 1993; Payandeh and Wang 1994). The advent of high-speed computers has facilitated parameter estimation of nonlinear models and the examination of complex relationships between environmental factors and tree growth. Regarding the integration of environmental factors, a popular approach has consisted in relating site index values to site factors such as (i) soil nutrient content or drainage conditions (e.g., Payandeh 1986; Brown and Marquard 1988; Walters *et al.* 1990; Klinka and Carter 1990; Monserud *et al.* 1990; Gale *et al.* 1991; Tamminen 1993), (ii) ecological classes derived from ecological classification systems (e.g., Green *et al.* 1989), (iii) the presence of understorey species (e.g., Corns and Pluth 1984; Strong *et al.* 1991; Nieppola 1993), and (iv) major soil groups (e.g., Steinbrenner 1979; Schmoldt *et al.* 1985; Rayner 1991).

This approach has aimed at providing a means of estimating the potential productivity of a species on a specific site. The development of relationships between site index and environmental factors has not been successful, except for some cases (e.g., Wang, Q. *et al.* 1994). Gale *et al.* (1991) mentioned as symptomatic the presence of collinearity between edaphic variables, insufficient samples, and the inadequacy of models to represent the complex interactions among various soil processes. The poor relationships obtained and the numerous ecological factors that must be sampled have thus far limited its usefulness in operational planning.

Another environmental-type approach is based on deriving site index curves for different habitat types or soil groups (e.g., Zahner 1962; Golden *et al.* 1981; Monserud 1984b, 1985; Amateis and Burkhart 1985; Payandeh 1991b; Stansfield *et al.* 1991; Huang 1994; Wang, G.G. *et al.* 1994). This approach presupposes that different habitat types or soil groups adequately integrate the various site factors affecting the long-term patterns of height development. Ease of use in conjunction with ecological classification systems favours this approach. The studies by Monserud (1984b, 1985), Payandeh (1991b) and Stansfield *et al.* (1991) are particularly interesting in this context because their productivity functions contain predictor variables integrating the effect of different ecological types. As this approach consists in deriving site productivity functions that associate growth trends with growth conditions, it has the potential to explain more variation in the long-term patterns of height development for a given data set. Consequently, it also has the potential to better meet one of the fundamental objectives of site index curves, which is to determine the long-term height growth pattern that a stand might achieve (Clutter *et al.* 1983). The basic methodology of this approach involves deriving site index curves from stem analysis data. The use of long-term remeasurement data from permanent sample plots has seldom been reported.

In this study, the objectives were (i) to derive site productivity functions for black spruce (*Picea mariana* [Mill.] B.S.P.) in relation to operational groups (OGs) as defined by the Ontario Forest Ecosystem Classification (FEC) system (Jones *et al.* 1983) using remeasurement data obtained from permanent sample plots, and

(ii) to examine if the shapes of the height growth curves could be reconciled with the ecological characteristics of different operational groups.

MATERIALS AND METHODS

Data were obtained from permanent sample plots established by the Spruce Falls Power and Paper Co. in the Clay Belt region of Northern Ontario, Canada (Fig. 1). While black spruce is the dominant species in the area, the following species are also found in association: jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), larch (*Larix laricina* [Du Roi] K. Koch), white birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), white cedar (*Thuja occidentalis* L.), and trembling aspen (*Populus tremuloides* Michx.). For the purpose of this study, only plots representing naturally regenerated stands originating after fire or harvesting in which black spruce comprised 60% or more of the basal area were examined. The majority of these sample plots had been remeasured several times, enabling the long-term development of individual stands to be assessed (Table 1). The number of measurements for individual plots varied between 1 and 12, and there were wide ranges in age, diameter at breast height (dbh), and height. More than half of the plots were remeasured at least eight times. Stand age was calculated as the number of years since harvesting or fire. Also, these plots were classified into their ecological groups using the Ontario FEC for the Clay Belt region. These are OGs defined on the basis of soil characteristics and the presence of specific understorey and overstorey species (Table 2).

The size of the sample plots varied between 0.10 acre (0.04 ha) and 1 acre (0.40 ha). Diameters (dbh) of all the trees in the sample plots were remeasured and then tallied by 1-inch (2.54 cm) classes. As tree height was measured only on subsample trees, the following relationship was derived to enable the computation of top height (largest 100 trees ha^{-1}):

$$(\text{Height} - 1.3) = b_1(\text{dbh}) + b_2(\text{age}) \qquad [1]$$

This equation was initially derived for every OG. However, subsequent analyses indicated that a single relationship for all the OGs was satisfactory:

$$(\text{Height} - 1.3) = 0.59848(\text{dbh}) + 0.03455(\text{age})$$
$$R^2 = 0.97,\ SE_E = 2.02 \qquad [2]$$

This relationship was used to compute top height for every sample plot and age of measurement. The top height values of the sample plots were classified into OGs, and the parameters of the Weibull function (Yang *et al.* 1978) were estimated through nonlinear regression:

$$\text{Top height} = b_0(1 - \exp^{-(b_1 \text{age})^{b_2}}) \qquad [3]$$

The derivation of this function for each OG was required to determine the height growth pattern within each OG and to estimate the site index of sample plots that did not have measurements taken at the reference age (50). Five site productivity functions that included dummy variables to represent differences between the operational groups were then derived. The first function was based upon the model derived by Monserud (1984b) for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in different habitat types:

$$H_{FEC} = \frac{b_1 S^{b_2}}{(1 - \exp^{(b_3 + b_4 \ln(\text{age}) + (a_1 Z_1 + a_2 Z_2 + \ldots)\ln(s))})} \qquad [4]$$

where H_{FEC} is top height for a given operational group and site index (S) at a given age Z_n indicates the presence (1) or absence (0) of operational groups for specific values of site indexes and ages, and a_n and b_n are parameters. The second function was based upon the function of Richards (1959) modified by Payandeh (1991b):

$$H_{FEC} = b_1\ S^{(a_1 Z_1 + a_2 Z_2 + \ldots)}\ (1 - \exp^{(-b_2 \text{age})})^{b_3} \qquad [5]$$

The next three functions were constrained to satisfy the condition that top height equals site index at the age of reference (50). The first one of this type consisted of the function derived by Hann and Scrivani (1987):

$$H_{FEC} = S\ \frac{(1 - \exp^{\exp(b_1 + (a_1 Z_1 + a_2 Z_2 + \ldots)\ln(\text{age}) + b_2 \ln(s))})}{1 - \exp^{\exp(b_1 + (a_1 Z_1 + a_2 Z_2 + \ldots)\ln(50) + b_2 \ln(S))})} \qquad [6]$$

The second constrained function was based upon the Richards (1959) function:

$$H_{FEC} = S\left\{\frac{(1 - \exp^{-((a_1 Z_1 + a_2 Z_2 + \ldots)\text{age})})}{(1 - \exp^{-((a_1 Z_1 + a_2 Z_2 + \ldots)50)})}\right\}^{(b_1 Z_1 + b_2 Z_2 + \ldots)} \qquad [7]$$

Figure 1. Location of the Clay Belt area in Ontario, Canada.

Table 1. Summary statistics for the database

	Minimum	Mean	Maximum	Standard deviation
Age	9	91	171	38.31
dbh (cm)	2.5	19.6	55.9	5.92
Height (m)	1.5	14.9	39.3	4.55

Observations: 10,424
Number of permanent sample plots: 44

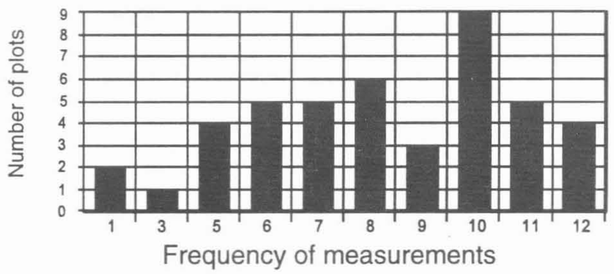
Statistics on the frequency of measurements

Table 2. Summary characteristics for the operational groups covered in this study (adapted from Jones *et al.* 1983)

	Operational group names	Common forest cover type[a]	Common soil texture	Common moisture regime[b]
5	Feathermoss-fine soil	BS, BS-JP, JP	fine loamy, clayey	3-6
7	Mixedwood-herb rich	PO, PO-BF-WS, PO-BS, PO-WB	clayey, fine loamy	2-4
8	Feathermoss-sphagnum	BS	fine loamy, clayey	5-6
9	Conifer-herb/moss rich	BS, WS-BF, WS-EWC	fine loamy, clayey	4-6
11	Ledum	BS	organic soil	7-8
12	Alnus-herb poor	BS, BS-EWC	organic soil	7-8
13	Alnus-herb rich	BS, BS-L-EWC, EWC	organic soil	7-8

[a] Abbreviations for tree species: BS, black spruce; JP, jack pine; BF, balsam fir; WB, white birch; EWC, eastern white cedar; L, larch; PO, trembling aspen or balsam poplar; WS, white spruce.

[b] Moisture regime codes: 2, fresh; 3, very fresh; 4, moderate moist; 5, moist; 6, very moist; 7, moderate wet; 8, very wet.

The third function was based upon the Weibull function and constrained in a manner similar to that of Burkhart and Tennent (1977):

$$H_{FEC} = s\frac{(1-\exp^{-((a_1Z_1+a_2Z_2+...)age)^{(b_1Z_1+b_2Z_2+...)}})}{1-\exp^{-((a_1Z_1+a_2Z_2+...)50)^{(b_1Z_1+b_2Z_2+...)}}} \quad [8]$$

Equations were evaluated by computing the coefficient of determination (R^2) and the standard error of estimate (SE_E). As suggested by Kvålseth (1985) and Cornell and Berger (1987) for nonlinear models, the coefficient of determination was computed as:

$$R^2 = 1-\frac{\sum(\text{observed values}-\text{predicted values})^2}{\sum(\text{observed values}-\text{mean}(\text{observed values}))^2} \quad [9]$$

Predictions obtained from the best equation derived were compared with measured height growth data from three independent data sets from the Clay Belt. The first two data sets were obtained from the studies of P.N. Ray *et al.* ("Polymorphic-nondisjoint site index curves for black spruce of the Ontario Claybelt", Univ. of Toronto) and Horton and Groot (1987). The third data set was extracted from the sample plot data bank of the Ontario Ministry of Natural Resources. All three sources contain height growth data obtained by destructive stem analysis. As top height was defined as the largest 100 trees ha^{-1}, comparisons were based on the largest individual tree within each plot because sample plot size was 10 m x 10 m.

RESULTS

Due to the low frequencies of data in some OGs, as well as for practical reasons, several OGs were merged on the basis of the similarity of their characteristics (Fig. 2); OGs 5 and 8, OGs 7 and 9, and OGs 12 and 13. Operational group 11 was left alone. The merged OGs will be referred to as OG 5/8, OG 7/9, and OG 12/13, respectively, in the remainder of the text. The Weibull function was then fitted to top height data of the remaining four OGs in two steps. First, the function was derived for each operational group such that it represented the general pattern of top height growth of all the sample plots. Second, sets of curves were derived within each new OG by varying the asymptote of the Weibull function (Table 3, Fig. 3). The growth pattern of each individual plot was then compared with predicted top height computed from the sets of curves. If there were large discrepancies between observed and predicted top heights, all the parameters of the Weibull function were refitted. This procedure was repeated until the trend in top height development of all the sample plots was adequately represented. The functions derived for each operational group (Table 3) were then used to estimate the site index of the sample plots that did not have measurements taken at the age of reference (50 years). This approach implied deriving anamorphic curves within each new OG.

For the five site productivity functions derived, the inclusion of OGs as dummy variables was significant (Table 4). Equations (5), (6), (7), and (8) fitted the data much better than eq. (4). As suggested by Kvålseth (1985), the negative coefficient of determination indicates that eq. (4) was not appropriate for this data set. Lower standard errors of estimate were obtained with the constrained models (eqs. (6), (7), and (8)) than with those that were not (eqs. (4) and (5)). Top height data from the best model within each category (eqs. (5) and (8)) were plotted for every OG and different values of site index (Figs. 4 and 5). Despite the fact that eq. (5) resulted in a relatively high coefficient of determination and a low standard error of estimate, it did not perform as well as eq. (8): it failed to differentiate OG 5/8 from OG 11 and resulted in relatively large differences between top height at the reference age and site index, particularly for low site index values (Figs. 4 and 5).

Predicted top heights from eq. (8) were compared with observed top heights from the independent data sets (Fig. 6a-d). For brevity, only a representative subset of trees that were not suppressed were selected from low to high site indexes within each operational group. Differences between predicted and observed top heights were within 1 m in most cases. Residual values greater than 1 m were obtained for some ages only in OGs 7/9 and 12/13. Despite this, all predicted top heights represented well the different patterns of change in top height within different operational groups for quite different values of site indexes.

	- Low rate of decomposition - Herb poor - Shrub layer dominated by ledum - Nutrient poor - Dominated by black spruce - Gradation down slope	- High rate of decomposition - Herb and shrub rich - Nutrient rich - Mixed stands - Telluric water movement
- Mineral soils - Upland	Operational groups 5 and 8	Operational groups 7 and 9
- Organic soils - Lowland	Operational group 11	Operational groups 12 and 13

Figure 2. Similarities and differences in the characteristics of the operational groups that were analyzed for merging operational groups 5 and 8, 7 and 9, and 12 and 13.

Table 3. Parameters of the Weibull function $\left\{\text{Top height} = b_0(1 - \exp^{-(b_1 \text{age})^{b_2}})\right\}$ derived within each operational group

Operational group	**Parameters**			
	b_0		**b_1**	**b_2**
	Minimum	**Maximum**		
5/8	34.53731	56.53731	3.38404×10^{-3}	0.88519
7/9	258.2006	698.2006	6.58216×10^{-5}	0.64065
11	14.10571	38.10571	1.27190×10^{-2}	1.45966
12/13	19.47148	43.47148	8.35929×10^{-3}	0.75656

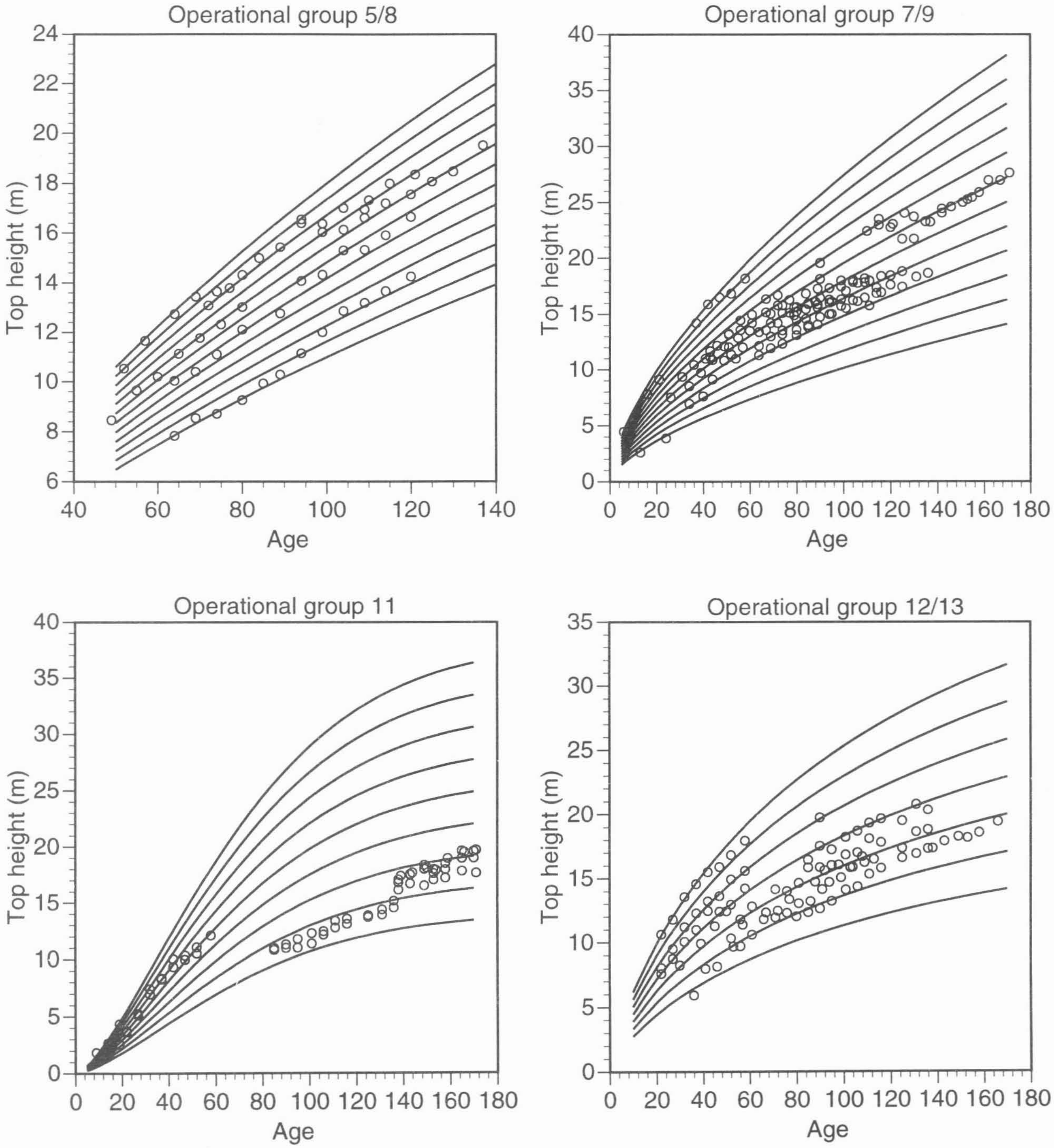

Figure 3. Observed top heights and Weibull function derived for each grouping of operational groups.

Table 4. Regression models of site productivity functions

Regression equation [a]	R^2	SE_E
(4) $H = \dfrac{0.68737S^{1.35869}}{(1 - \exp^{(-2.23034 - 0.11103\ln(age) + (0.57333Z_5 + 0.53614Z_7 + 0.59629Z_{11} + 0.60221Z_{12})\ln(S))})}$	-0.44	5.3150
(5) $H = 4.40364S^{(0.93412Z_5 + 0.90995Z_7 + 0.94960Z_{11} + 0.88247Z_{12})}\ (1\ \exp^{(-0.00419age)})^{0.75289}$	0.96	0.9133
(6) $H = S\,\dfrac{(1 - \exp^{\exp^{(-32.63982 + (0.76455Z_5 + 0.63544Z_7 + 0.77527Z_{11} + 0.53181Z_{12})\ln(age) - 0.00212\ln(S))}})}{1 - \exp^{\exp^{(-32.63982 + (0.76455Z_5 + 0.63544Z_7 + 0.77527Z_{11} + 0.53181Z_{12})\ln(50) - 0.00212\ln(S))}})}$	0.98	0.6819
(7) $H = S\left\{\dfrac{(1 - \exp^{(-(0.00754Z_5 + 0.00198Z_7 + 0.01308Z_{11} + 0.00720Z_{12})\ age)})}{(1 - \exp^{(-(0.00754Z_5 + 0.00198Z_7 + 0.01308Z_{11} + 0.00720Z_{12})\ 50)})}\right\}^{(0.99628Z_5 + 0.00158Z_7 - 0.00597Z_{11} - 0.00731Z_{12})}$	0.98	0.5636
(8) $H = S\,\dfrac{(1 - \exp^{-((0.00745Z_5 + 0.00139Z_7 + 0.01086Z_{11} + 0.00805Z_{12})age)^{(1.02311Z_5 + 0.70808Z_7 + 1.29923Z_{11} + 0.76670Z_{12})}})}{(1 - \exp^{-((0.00745Z_5 + 0.00139Z_7 + 0.01086Z_{11} + 0.00805Z_{12})50)^{(1.02311Z_5 + 0.70808Z_7 + 1.29923Z_{11} + 0.76670Z_{12})}})}$	0.98	0.5645

[a] (4): based on the function used by Monserud (1984b).
(5): based on the function used by Payandeh (1991b).
(6): based on the function used by Hann and Scrivani (1987).
(7): based on the Richards function.
(8): based on the Weibull function.

Note: H, top height (m); S, site index (m) at a base age of 50 years; Z_5, Z_7, Z_{11}, Z_{12}, dummy variables, i.e., $Z_5 = 1$ for operational group 5/8, $Z_7 = 1$ for operational group 7/9, $Z_{11} = 1$ for operational group 11, and $Z_{12} = 1$ for operational group 12/13.

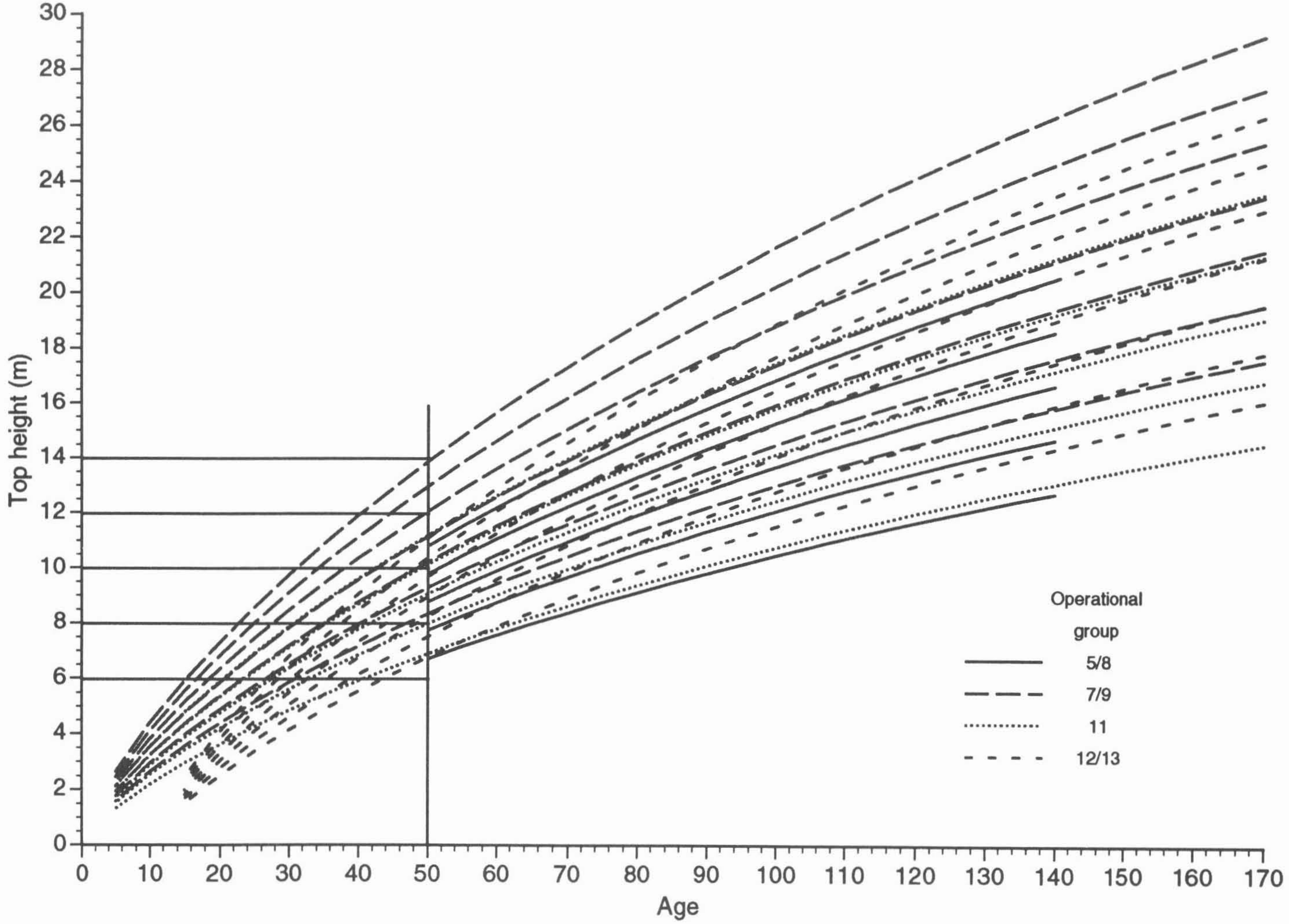

Figure 4. Graph of the site index curves obtained from the function used by Payandeh (1991b) (eq. (5)).

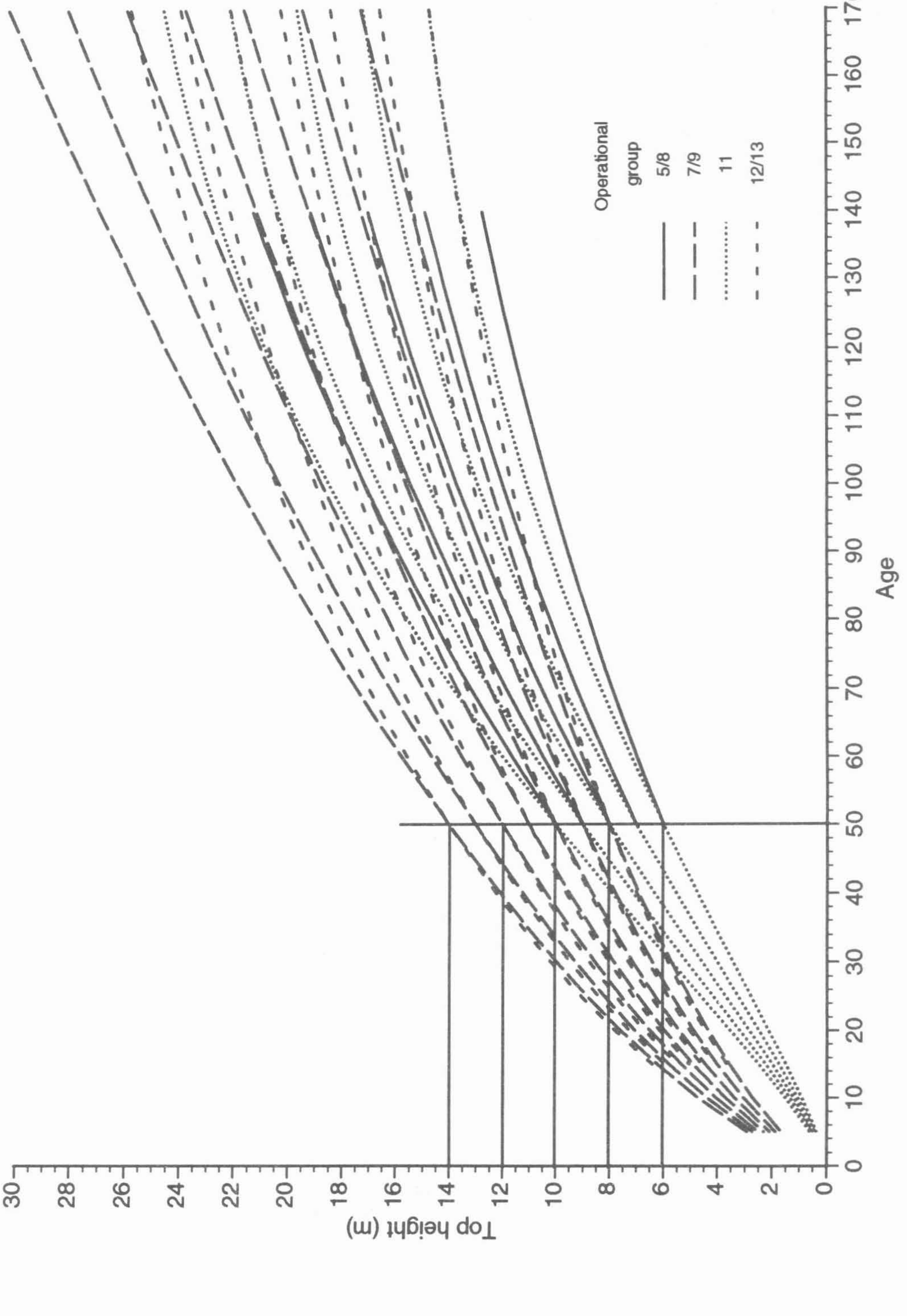

Figure 5. Graph of the site index curves obtained from the function based on the Weibull function (eq. (8)).

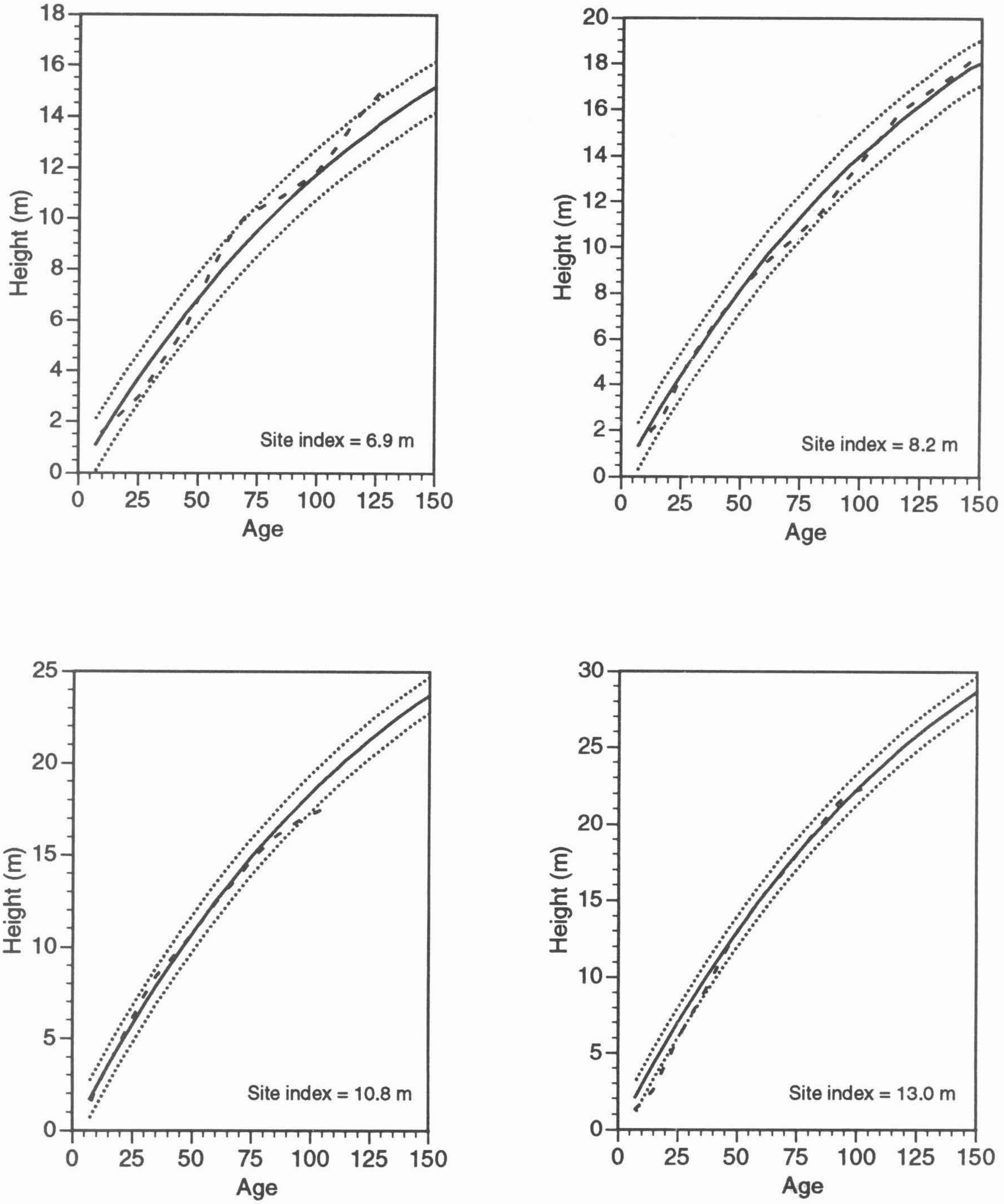

Figure 6a. Comparison between observed (- - - -) and predicted (——) top heights for operational group 5/8. (·········: limits of ±1 m for the predicted values).

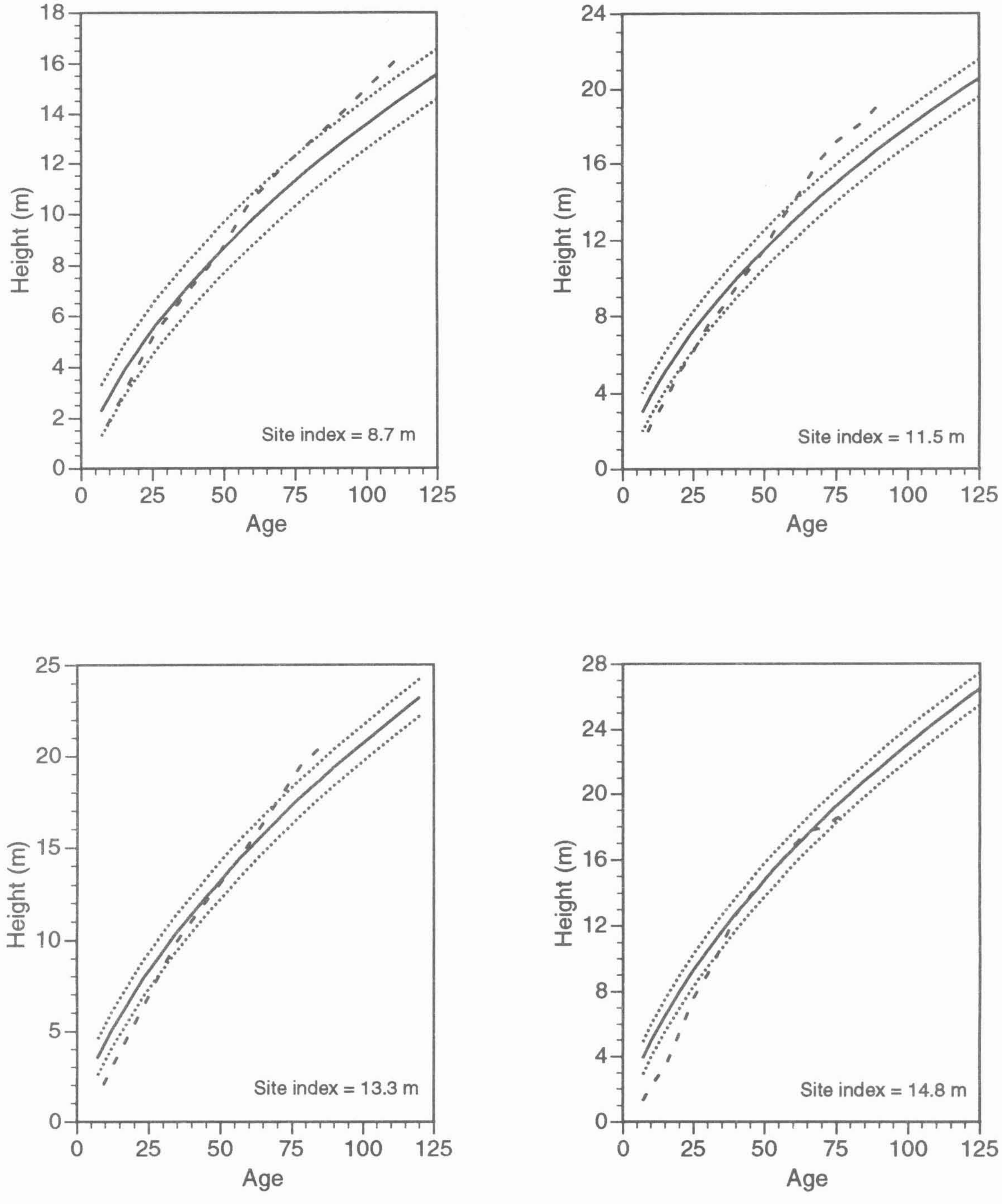

Figure 6b. Comparison between observed (- - - -) and predicted (——) top heights for operational group 7/9. (·········: limits of ±1 m for the predicted values).

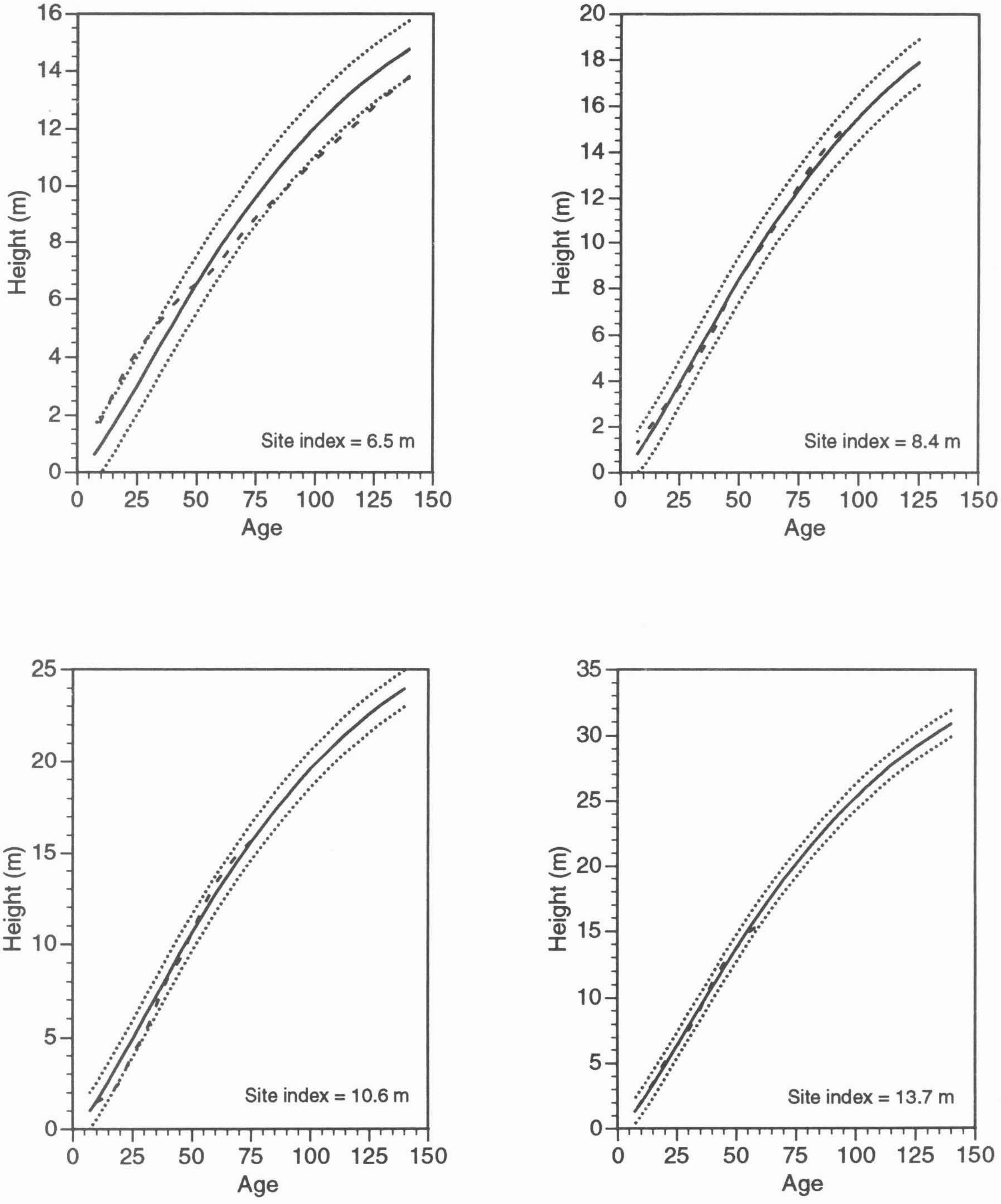

Figure 6c. Comparison between observed (- - - -) and predicted (——) top heights for operational group 11. (·········: limits of ±1 m for the predicted values).

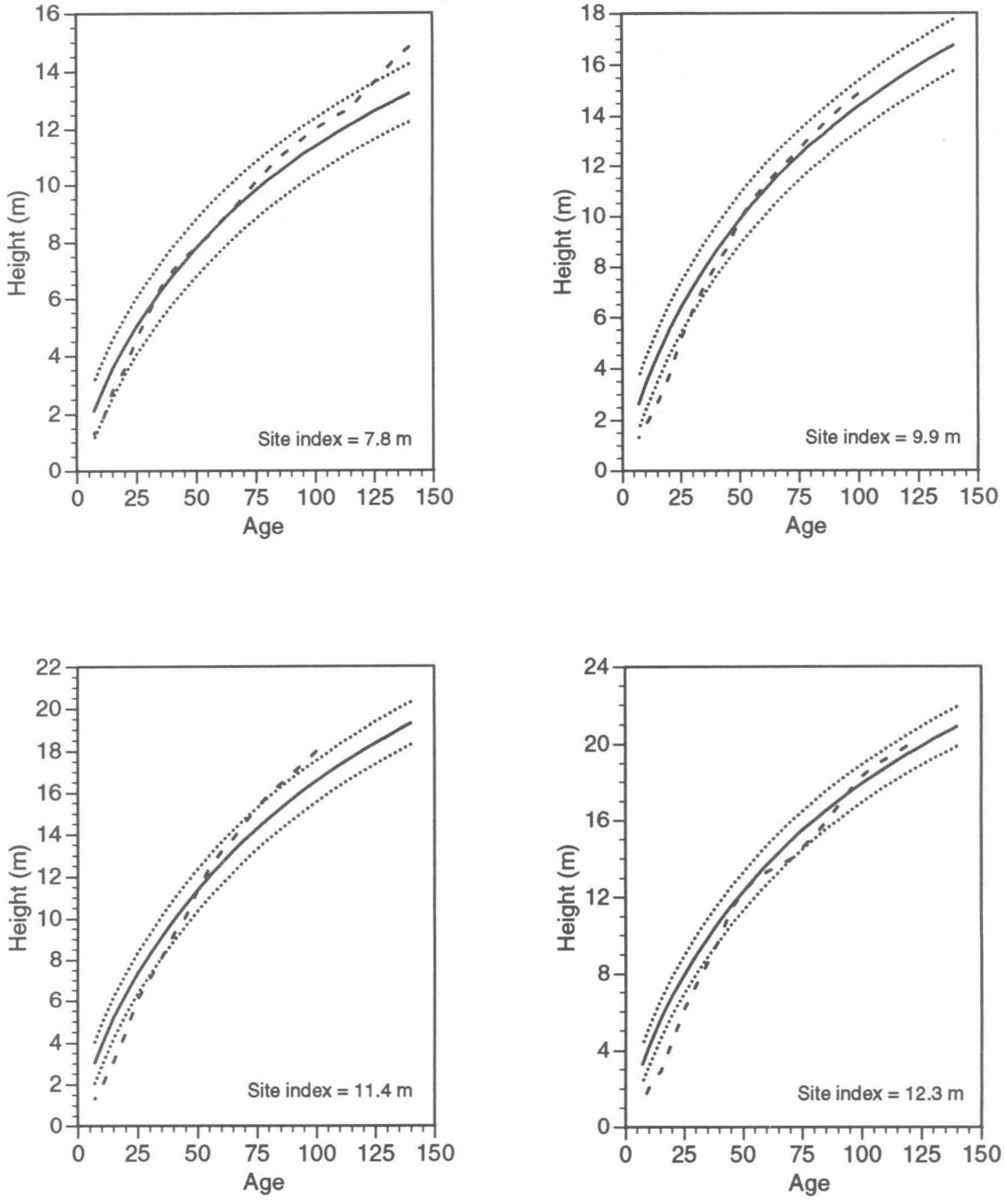

Figure 6d. Comparison between observed (- - - -) and predicted (——) top heights for operational group 12/13. (·········: limits of ±1 m for the predicted values).

DISCUSSION

The comparison of the long-term height growth patterns of the OGs suggests a polymorphic pattern (Figs. 4 and 5). Even though some OGs have very close site index values at age 50, they can have quite different productivities beyond this reference age. This indicates that the stratification of stands into different ecological groups was justified. Furthermore, this approach constitutes an efficient way to represent differences resulting from specific ecological characteristics associated with the OGs. This is also a more convenient approach than relating several environmental parameters such as soil nutrient content or climatic factors to site index values. Two reasons may be considered to support this assertion. First, the measurement of all environmental factors associated with growth may be expensive and time consuming. Second, existing studies have not resulted in the derivation of strong relationships representing the complex interactions between environmental factors and site index (e.g., Payandeh 1986, Brown and Marquard 1988, Walters *et al.* 1990, Klinka and Carter 1990, Monserud *et al.* 1990, Gale *et al.* 1991, Tamminen 1993). Even though a good fit was obtained with eq. (5), it did not differentiate the OGs as well as eqs. (7) and (8). This result, and the fact that relatively large differences were obtained between site index and top height at age 50 with eq. (5), suggest that it is preferable to derive functions constrained to satisfy the condition that top height equals site index at base age in order to represent more adequately the differences in long-term height development patterns of different ecological forest types.

The polymorphism resulting from the different OGs may be explained by their ecological characteristics (Jones *et al.* 1983). The height growth pattern obtained for OG 7/9 will be used as a basis of comparison because it is believed that its nutrient and moisture regimes represent the optimum site conditions for black spruce (e.g., Lowry 1975, Viereck and Johnston 1990). Despite the fact that OG 7/9 is characterized by better drainage and nutrition conditions than OG 5/8 (Table 2; Fig. 2), the latter showed higher productivity after the age of reference for the same values of site indexes (Fig. 5). The presence of severe competition from other species in OG 7/9 might explain this trend: OG 5/8 is dominated by black spruce while OG 7/9 consists of mixed stands (Table 2, Fig. 2). A detailed review of the literature produced little conclusive evidence of competitive interactions between black spruce and white spruce, balsam fir, balsam poplar, and white birch. Newton and Smith (1991), for example, concluded that balsam fir had no significant impact on the growth of black spruce. However, the studies of Payandeh (1984, 1991a) suggest that white spruce, balsam poplar, and trembling aspen might have a negative effect on the growth of black spruce because of their faster growth rates both in dbh and height.

The relatively low productivity of OG 11 at young ages suggests that seedlings were growing in poor conditions, which is consistent with the observations of Munson and Timmer (1989). This OG consists of an organic soil with a thick fibric horizon that is not well decomposed, and there is little groundwater flow. Both studies by Lieffers and Rothwell (1986) and Czapowskyj *et al.* (1986) suggested that the high water table in this ecosystem probably has a negative effect on seedling growth. Even though the extent of competitive interactions was not investigated, the establishment and growth of black spruce seedlings is also likely inhibited by the presence of Labrador-tea (*Ledum groenlendicum* Retzius). The studies by Chapin (1983) and Grigal *et al.* (1985), for example, indicated that Labrador-tea grows much faster than black spruce seedlings. In particular, Chapin (1983) observed that Labrador-tea produces leaf biomass and uptake nutrients more rapidly than black spruce.

Even though OG 12/13 consists of organic soils, which can be unfavourable to black spruce (Jeglum 1974; Lowry 1975; Payandeh 1978), its relatively good productivity in terms of height growth may be explained by the movement of telluric water in the ecosystem, providing good influx of nutrients and appropriate aerobic growing conditions, and possibly by the presence of nitrogen-fixing alder. Its productivity was close to OG 7/9 until age 50, and then started declining. For the same values of site index, this OG had lower productivity than OG 11. This may be due to (1) a restriction in the rooting zone of older trees, and (2) stand density. Compared with the other operational groups, OG 12/13 has relatively shallow rooting zones because of fluctuations in the depth of the water table. In general, the stands within this OG are less dense and tend to break up easily due to windthrow (see Smith *et al.* 1987). Trees in OG 11 are less susceptible to windthrow because of deeper rooting zones and the presence of a thick fibric horizon, both of which contribute to better stand stability.

The proportionality assumption within each operational group was valid for the range of ages considered. Therefore, the models derived integrated both a polymorphic approach to explain the patterns resulting from the different OGs and an anamorphic approach to represent the variability within each operational group.

The graphical comparison of predicted top heights from eq. (8) with observed top heights from the independent data sets was satisfactory. In most cases, the relatively large departures between observations and predictions occurred late in the life of the stands. Even though there were cases with relatively large errors at young and old ages, the observed top heights followed the trend derived from eq. (8). As previously mentioned, only a subset of the data bank is illustrated in Fig. 6. Except for trees found to be suppressed at young ages, the other top height data from the independent data sets were also relatively close to top height data derived from eq. (8). The larger differences obtained between observed and predicted top heights with suppressed trees indicate that the dominant trees used to evaluate site productivity must be selected carefully by examining the history of the stand in detail (Monserud 1984a).

CONCLUSIONS

The integration of basic ecological information and polymorphic site index curves provided a good explanation of the growth pattern within each OG. These results suggest that such an approach constitutes a practical and efficient way of integrating ecological characteristics into site index equations. The only additional requirement consists in identifying the OG of the stands whose potential productivities are being evaluated. This approach provides improved estimation of the long-term height growth pattern.

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REFERENCES

Alemdag, I.S. 1988. Site index equations for white spruce in the Northwest Territories, Canada. For. Ecol. Manage. 23:61-71.

Alemdag, I.S. 1991. National site-index and height-growth curves for white spruce growing in natural stands in Canada. Can. J. For. Res. 21:1466-1474.

Amateis, R.L.; Burkhart, H.E. 1985. Site index curves for loblolly pine plantations on cutover site-prepared lands. South. J. Appl. For. 9:166-169.

Bailey, R.L.; Clutter, J.L. 1974. Base-age invariant polymorphic site curves. For. Sci. 20:155-159.

Biging, G.S. 1985. Improved estimates of site index curves using a varying-parameter model. For. Sci. 31:248-259.

Borders, B.E.; Bailey, R.L.; Ware, K.D. 1984. Slash pine site index from a polymorphic model by joining (splining) nonpolynomial segments with an algebraic difference method. For. Sci. 30:411-423.

Brown, J.H.; Marquard, R.D. 1988. Site index of yellow-poplar in relation to soils and topography in the Allegheny Plateau of Ohio. North. J. Appl. For. 5:34-38.

Burkhart, H.E.; Tennent, R.B. 1977. Site index equations for radiata pine in New Zealand. N. Z. J. For. Sci. 7:408-416.

Cao, Q.V. 1993. Estimating coefficients of base-age-invariant site index equations. Can. J. For. Res. 23:2343-2347.

Cao, Q.V.; Durand, K.M. 1991. Site index curves for eastern cottonwood plantations in the Lower Mississippi Delta. South. J. Appl. For. 15:28-30.

Carmean, W.H. 1968. Tree height-growth patterns in relation to soil and site. Pages 499-512 *in* Tree growth and forest soils. 3rd N. Am. Forest Soils Conf. Proc., Oregon State University Press, Corvallis.

Carmean, W.H. 1972. Site index curves for upland oaks in the Central States. For. Sci. 18:109-120.

Carmean, W.H. 1975. Forest site quality evaluation in the United States. Adv. Agron. 27:209-269.

Chapin, F.S., III. 1983. Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest. Can. J. For. Res. 13:773-781.

Cieszewski, C.J.; Bella, I.E. 1989. Polymorphic height and site index curves for lodgepole pine in Alberta. Can. J. For. Res. 19:1151-1160.

Clutter, J.L.; Fortson, J.C.; Pienaar, L.V.; Brister, G.H.; Bailey, R.L. 1983. Timber management: a quantitative approach. John Wiley & Sons, New York.

Cornell, J.A.; Berger, R.D. 1987. Factors that influence the value of the coefficient of determination in simple linear and nonlinear regression models. Phytopathology 77:63-70.

Corns, I.G.W.; Pluth, D.J. 1984. Vegetational indicators as independent variables in forest growth prediction in west-central Alberta, Canada. For. Ecol. Manage. 9:13-25.

Curtis, R.O.; Diaz, N.M.; Clendenen, G.W. 1990. Height growth and site index curves for western white pine (*Pinus monticola*) in the Cascade range of Washington and Oregon. USDA For. Serv. Res. Pap. PNW-RP-423.

Czapowskyj, M.M.; Rowke, R.V.; Grant, W.J. 1986. Growth and nutrient status of black spruce seedlings as affected by water table depth. USDA For. Serv. Res. Pap. NE-RP-591.

Daniel, T.W.; Helms, J.A.; Baker, F.S. 1979. Principles of silviculture. 2nd ed. McGraw-Hill Book Company, New York.

Dolph, K.L. 1987. Site index curves for young-growth California white fir on the western slopes of the Sierra Nevada. USDA For. Serv. Res. Pap. PSW-185.

Dolph, K.L. 1991. Polymorphic site index curves for red fir [*Abies magnifica*] in California and southern Oregon. USDA For. Serv. Res. Pap. PSW-206.

Gale, M.R.; Grigal, D.F.; Harding, R.B. 1991. Soil productivity index: predictions of site quality for white spruce plantations. Soil Sci. Soc. Am. J. 55:1701-1708.

Gilmore, D.W.; Briggs, R.D.; Seymour, R.S. 1993. Stem volume and site index equations for European larch in Maine. North. J. Appl. For. 10:70-74.

Goelz, J.C.G.; Burk, T.E. 1992. Development of a well-behaved site index equation: jack pine in north central Ontario. Can. J. For. Res. 22: 776-784.

Golden, M.S.; Meldahl, R.; Knowe, S.A.; Boyer, W.D. 1981. Predicting site index for old-field loblolly pine plantations. South. J. Appl. For. 5:109-114.

Gordon, A.M.; Williams, P.A.; Taylor, E.P. 1989. Site index curves for Norway spruce in Southern Ontario. North. J. Appl. For. 6:23-26.

Graney, D.L.; Burkhart, H.E. 1973. Polymorphic site index curves for Shortleaf Pine in the Ouachita mountains. USDA For. Serv. Res. Pap. SO-85.

Green, R.N., Marshall, P.L., and Klinka, K. 1989. Estimating site index of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) from ecological variables in southwestern British Columbia. For. Sci. 35:50-63.

Grigal, D.F.; Buttleman, C.G.; Kernik, L.K. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can. J. Bot. 63:2416-2424.

Hacker, W.D.; Bilan, M.V. 1991. Site index curves for loblolly and slash pine plantations in the post oak belt of east Texas. South. J. Appl. For. 15:97-100.

Hann, D.W.; Scrivani, J.A. 1987. Dominant-height-growth and site-index equations for Douglas-fir and ponderosa pine in southwest Oregon. Oregon State University, Forest Research Laboratory, Res. Bull. 59.

Horton, B.J.; Groot, A. 1987. Development of second-growth black spruce stands on peatlands in northeastern Ontario. Canada-Ontario Forest Resource Development Agreement, Internal report.

Huang, S. 1994. Ecologically based reference-age invariant polymorphic height growth and site index curves for white spruce in Alberta. Alberta Environmental Protection Land and Forest Services, Forest Management Division, Technical Report Pub. No. T/308.

Jeglum, J.K. 1974. Relative influence of moisture-aeration and nutrients on vegetation and black spruce growth in northern Ontario. Can. J. For. Res. 4:114-126.

Jones, R.K.; Pierpoint, G.; Wickware, G.M.; Jeglum, J.K.; Arnup, R.W.; Bowles, J.M. 1983. Field guide to forest ecosystem classification for the clay belt, site region 3e. Ont. Min. Nat. Resour., Toronto, Ontario.

Ker, M.F.; Bowling, C. 1991. Polymorphic site index equations for four New Brunswick softwood species. Can. J. For. Res. 21:728-732.

Klinka, K.; Carter, R.E. 1990. Relationships between site index and synoptic environmental factors in immature coastal Douglas-fir stands. For. Sci. 36:815-830.

Kvålseth, T.O. 1985. Cautionary note about R^2. Am. Stat. 39:279-285.

Lieffers, V.J.; Rothwell, R.L. 1986. Effects of depth of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. Can. J. For. Res. 16:1201-1206.

Lowry, G.L. 1975. Black spruce site quality as related to soil and other site conditions. Soil Sci. Soc. Am. Proc. 39:125-131.

Monserud, R.A. 1984a. Problems with site index: an opinionated review. Pages 167-180 *in* Forest land classification: experiences, problems, perspectives: Symposium Proceedings. *Edited by* J. Bockheim. Department of Soil Science, University of Wisconsin, Madison, WI.

Monserud, R.A. 1984b. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. For. Sci. 30:943-965.

Monserud, R.A. 1985. Applying height growth and site index curves for inland Douglas-fir. USDA For. Serv. Res. Pap. INT-347.

Monserud, R.A.; Moody, U.; Breuer, D.W. 1990. A soil-site study for inland Douglas-fir. Can. J. For. Res. 20:686-695.

Munson, A.D.; Timmer, V.R. 1989. Site-specific growth and nutrition of planted *Picea mariana* in the Ontario Clay Belt. I. Early performance. Can. J. For. Res. 19:162-170.

Newnham, R.M. 1988. A modification of the Ek-Payandeh nonlinear regression model for site index curves. Can. J. For. Res. 18:115-120.

Newton, P.F. 1992. Base-age invariant polymorphic site index curves for black spruce and balsam fir within central Newfoundland. North. J. Appl. For. 9:18-22.

Newton, P.F.; Smith, V.G. 1991. Volume growth relationships within mixed black-spruce/balsam-fir stands. For. Ecol. Manage. 40:131-136.

Nieppola, J. 1993. Understorey plants as indicators of site productivity in *Pinus sylvestris* L. stands. Scand. J. For. Res. 8:49-65.

Payandeh, B. 1978. A site index formula for peatland black spruce in Ontario. For. Chron. 54:39-41.

Payandeh, B. 1984. Dimensional relationships for several tree species from the spruce-fir forest types of northwestern Ontario. Can. For. Serv. Res. Notes 4:18-20.

Payandeh, B. 1986. Predictability of site index from soil factors and lesser vegetation in northern Ontario forest types. Can. For. Serv., Inf. Rep. O-X-373.

Payandeh, B. 1991a. Plonski's (metric) yield tables formulated. For. Chron. 67:545-546.

Payandeh, B. 1991b. Composite site-productivity functions for northeastern Ontario black spruce. New For. 5:1-12.

Payandeh, B.; Wang, Y. 1994. Relative accuracy of a new base-age invariant site index model. For. Sci. 40:341-348.

Phillips, G.B. 1992. Development of site index curves for *Eucalyptus rubida* Deane et Maiden growing in Lesotho. Commonw. For. Rev. 71:197-202.

Quenet, R.V.; Manning, G.H. 1990. Site index equations for black spruce and white spruce in the Yukon. For. Can. Pacific For. Cent. Inf. Rep. BC-X-317.

Rayner, M.E. 1991. Site index and dominant height growth curves for regrowth karri (*Eucalyptus diversicolor* F. Muell.) in south-western Australia. For. Ecol. Manage. 44:261-283.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

Schmoldt, D.L.; Martin, G.L.; Bockheim, J.G. 1985. Yield-based measures of northern hardwood site quality and their correlation with soil-site factors. For. Sci. 31:209-219.

Smith, V.G. 1984. Asymptotic site-index curves, fact or artifact? For. Chron. 60:150-156.

Smith, V.G.; Watts, M.; James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Can. J. For. Res. 17: 1080-1091.

Stansfield, W.F.; McTague, J.P.; Lacapa, R. 1991. Dominant-height and site-index equations for ponderosa pine in east-central Arizona. Can. J. For. Res. 21:606-611.

Steinbrenner, E.C. 1979. Forest soil productivity relationships. Pages 199-222 *in* Forest soils of the Douglas-fir region. *Edited by* P.E. Heilman, H.W. Anderson, and D.M. Baumgartner. Washington State University, Cooperative Extension Service, Pullman.

Strong, W.L.; Pluth, D.J.; LaRoi, G.H.; Corns, I.G.W. 1991. Forest understory plants as predictors of lodgepole pine and white spruce site quality in west-central Alberta. Can. J. For. Res. 21:1675-1683.

Tamminen, P. 1993. Estimation of site index for Scots pine and Norway spruce stands in South Finland using site properties. Folia For. 819.

Viereck, L.A.; Johnston, W.F. 1990. *Picea mariana* (Mill.) B.S.P. - black spruce. Pages 227-237 *in* Silvics of North America: 1. Conifers. *Coordinated by* R.M. Burns, and B.H. Honkala. USDA For. Serv., Agriculture Handbook 654, Vol. 1.

Walters, D.K.; Sloan, J.P.; Kurmis, V. 1990. Aspen site index as related to plant indicators. Pages 337-340 *in* Aspen Symposium '89 - Proceedings, 25-27 July 1989, Duluth, Minnesota. *Edited by* R.D. Adams. USDA For. Serv. Gen. Tech. Rep. NC-40.

Wang, G.G.; Marshall, P.L.; Klinka, K. 1994. Height growth pattern of white spruce in relation to site quality. For. Ecol. Manage. 68:137-147.

Wang, Q.; Wang, G.G.; Coates, K.D.; Klinka, D. 1994. Use of site factors to predict lodgepole pine and interior spruce site index in the sub-boreal spruce zone. British Columbia Ministry of Forests, Research Note No. 114.

Williams, P.A.; Gordon, A.M.; Taylor, E.P. 1990. Site index curves and site factors affecting the growth of white pine in southern Ontario. North. J. Appl. For. 7:183-186.

Yang, R.C.; Kozak, A.; Smith, J.H.G. 1978. The potential of Weibull-type functions as flexible growth curves. Can. J. For. Res. 8:424-431.

Zahner, R. 1962. Loblolly pine site curves by soil groups. For. Sci. 8:104-110.

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