Reprinted from

Forest Ecology and Management

Forest Ecology and Management 106 (1998) 115–123

Height-age and height-diameter relationships for monocultures and mixtures of eastern cottonwood clones

Steven A. Knowe [a,*], G. Sam Foster [b,1], Randall J. Rousseau [c], Warren L. Nance [d]

[a] *Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR 97331, USA*
[b] *US Forest Service, Southern Forest Experiment Station, Huntsville, AL 35762, USA*
[c] *Westvaco, Wickliffe, KY 42087, USA*
[d] *US Forest Service, Southern Forest Experiment Station, Gulfport, MS 39505, USA*

Received 4 August 1997; accepted 10 October 1997

ELSEVIER

Forest Ecology and Management

Aims and scope. forest Ecology *and Management* publishes scientific articles concerned with forest management and conservation, and in particular the application of biological, ecological and social knowledge to the management of man-made and natural forests. The scope of the journal includes all forest ecosystems of the world. A refereeing process ensures the quality and international interest of the manuscripts accepted for publication. The journal aims to encourage communication between scientists in disparate fields who share a common interest in ecology and natural-resource management, and to bridge the gap between research workers and forest managers in the field to the benefit of both. The journal should be of interest to research workers, managers and policy makers in forestry, natural resources, ecological conservation and related fields.

FOUNDING EDITOR
Laurence L. Roche, Murroe, Ireland

EDITORS-IN-CHIEF
For the Americas, Australia, New Zealand and the Pacific:
RF. Fisher
Department of Forest Science
Texas A&M University
College Station, TX 77843-2135, USA

For the rest of the world:
G.M.J. Mohren
Forest Production Ecology Group
Department of Vegetation Ecology
DLO-Institute for Forestry and Nature Research
P.O. Box 23
6700 AA Wageningen, The Netherlands

BOOK REVIEWS EDITOR
Margaret Ft. Gale
School of Forestry and Wood Products
Michigan Technological University
1400 Townsend Drive
Houghton, MI 49931, USA

EDITORIAL ADVISORY BOARD
G. Abrahamsen, Agricultural University of Norway, As, Norway
R. Alfaro, Canadian Forestry Service, Victoria, B.C., Canada
F. Andersson, Swedish University of Agricultural Sciences, Uppsala, Sweden
P.M.S. Ashton, Yale University, New Haven, USA
P. Attiwill, University of Melbourne, Parkville, Vic., Australia
J. Boyle, Oregon State University, Corvallis, USA
S. Brown, US Environmental Protection Agency, Corvallis, USA
I. Burke, Colorado State University, Fort Collins, CO, USA
J.C. Calvo, Institute of Technology, Cartago, Costa Rica
R.-J. Chen, University of Hong Kong, Pokfulan Road, Hong Kong
J.D. Deans, Institute of Terrestrial Ecology, Penicuik, Midlothian, UK
R.M. DeGraaf, USDA Forest Service, University of Massachusetts, Amherst, MA, USA
S. Diamandis, Forest Research Institute, Thessaloniki, Greece
D.P. Dykstra, CIFOR, Jakarta, Indonesia
E.P. Farrell, University College Dublin, Dublin, Ireland
P.M. Fearnside, Instituto Nacional de Pesquisas da Amazonia – INPA, Manaus-Amazonas, Brazil
P.H. Freer-Smith, Forestry Commission, Farnham, UK
0. Garcia, ENGREF, Nancy, France
D. Gilmore, Canadian Forest Products Ltd., Alberta, Canada
R.A. Goyer, Louisiana State University, Baton Rouge, LA, USA
J.B. Hall, University College of North Wales, Bangor, UK
F. Houllier, Institut National de la Recherche Agronomique, Montpellier, France
B.M. Kumar, Kerala Agricultural University, Kerala, India
J.P. Lassoie, Cornell University, Ithaca, NY, USA
J.N. Long, Utah State University, Logan, UT, USA
A.E. Lugo, International Institute of Tropical Forestry, Rio Piedras, PR, USA
J.A. Maghembe, SADCC/ICRAF Agroforestry Project, Zomba, Malawi
F. Makeschin, Institut für Bodenkunde und Standortslehre, Tharandt, Germany
DC. Malcolm, University of Edinburgh, Edinburgh, UK
E. Mälkönen, Finnish Forest Research Institute, Vantaa, Finland
M.A.R. Nahuz, Instituto de Pesquisas Tecnologicas, São Paulo, SP, Brazil
R. Paivinen, European Forestry Institute, Joensuu, Finland
S.G. Pallardy, University of Missouri, Columbia, MO, USA
R.F. Powers, Pacific Southwest Research Station, Redding, CA, USA
T. Pukkala, University of Joensuu, Joensuu, Finland
F.E. Putz, University of Florida, Gainesville, FL, USA
L. Rasmussen, RISO, Roskilde, Denmark
D.D. Reed, Michigan Technological University, Houghton, MI, USA
R. Sands, University of Canterbury, Christchurch, NZ
J.A. Stanturf, Stoneville, MS, USA
0. Sziklai, University of British Columbia, Vancouver, B.C., Canada
J.R. Toliver, USDA Forest Service, Washington, DC, USA
K. von Weissenberg, University of Helsinki, Helsinki, Finland
D. Whitehead, Manaaki Whenua Landacre Research, Lincoln, New Zealand

Publication information: *Forest* Ecology *and Management* (ISSN 0378-l 127). For 1998 volumes 100-l 10 are scheduled for publication. Subscription prices are available upon request from the Publisher. Subscriptions are accepted on a prepaid basis only and are entered on a calendar year basis. Issues are sent by surface mail except to the following countries where air delivery via SAL mail is ensured: Argentina, Australia, Brazil, Canada, Hong Kong, India, Israel, Japan, Malaysia, Mexico, New Zealand, Pakistan, PR China, Singapore, South Africa, South Korea, Taiwan, Thailand, USA. For all other countries airmail rates are available on request. Claims for missing issues should be made within six months of our publication (mailing) date.
Orders, claims, and product enquiries: please contact the Customer Support Department at the Regional Sales Office nearest you:
New York: Elsevier Science, P.O. Box 945, New York, NY 10159-0945, USA; Tel. (+1)212-633-3730,[Toll free number for North American customers: 1-888-4ES-INFO(437-4636)], Fax (+1)212-633-3680, E-mail usinfo-f@elsevier.com
Amsterdam: Elsevier Science, P.O. Box 211, 1000 AE Amsterdam, The Netherlands; Tel. (+31)20-485-3757, Fax (+31)20-485-3432, E-mail nlinfo-f@elsevier.nl
Tokyo: Elsevier Science, l-9-15, Higashi-Azabu 1-chome, Minato-ku, Tokyo 106-0044, Japan; Tel. (+81)3-5561-5033, Fax (+81)3-5561-5047, E-mail info@elsevier.co.jp
Singapore: Elsevier Science, No. 1 Temasek Avenue, #17-01 Millenia Tower, Singapore 039192; Tel. (+65)434-3727, Fax (+65)337-2230, E-mail asiainfo@elsevier.com.sg

ELSEVIER

Forest Ecology and Management 106 (1998) 115–123

Forest Ecology and Management

Height-age and height-diameter relationships for monocultures and mixtures of eastern cottonwood clones

Steven A. Knowe [a,*], G. Sam Foster [b,1], Randall J. Rousseau [c], Warren L. Nance [d]

[a] *Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR 97331, USA*
[b] *US Forest Service, Southern Forest Experiment Station, Huntsville, AL 35762, USA*
[c] *Westvaco, Wickliffe, KY 42087, USA*
[d] *US Forest Service, Southern Forest Experiment Station, Gulfport, MS 39505, USA*

Received 4 August 1997; accepted 10 October 1997

Abstract

Data from an eastern cottonwood clonal mixing study in Mississippi and Kentucky, USA, were used to test the effects of planting locations and genetics (clonal proportion\) on height–age and height–dbh functions. Planting locations, which accounted for 5.6% of the variation in observed dominant height growth (p = 0.0001), were more important than clonal proportions, which accounted for only 1.0% of the variation (p = 0.0077). Interactions between clones in mixtures were not significant (p = 0.9178), but three cases of over- and undercompensation paralleled those observed for basal area. Planting location\ were associated with differences in maximum height in the height-dbh function and clonal proportions were associated uith difference\ in height of trees with smaller than average dbh. Although statistically significant, the effects of planting location and clonal proportion were not important enough to incorporate into the final height–dbh model. ©1998 Elsevier Science B.V.

Keywords: *Populus deltoides*; Height growth; Relative height; Relative diameter; Intergenotypic competition

1. Introduction

Many of the forest plantations in North America have been established with genetically improved planting stock with no means to verify expected genetic gain. In addition, a fundamental understanding of intergenotypic competition and the role of genetic diversity in forest ecosystem function is lacking. Theoretical studies point to a potential advantage from some level of genetic diversity in forest stands (Libby, 1982; Roberds et al., 1990), but empirical studies (Williams et al., 1983; Markovic and Herpka, 1986; Tuskan and van Buijtenen, 1986) suggest a range of potential results. Growth and yield tnodels are needed to assess and verify the long-tertn biological and cconotnic impacts of tree improvetnent programs and deployment strategies for genetically improved families or clones. Modeling approaches could also be used to compare growth in

* Corresponding author. Rayonier, P.O. Box 819, Yulee, FL 32041, USA. Tel.: +1-904-225-5393; fax: +1-904-225-0370; e-mail: steve.knowe@rayonier.com.
[1] Current address: US Forest Service, Southern Research Station, Asheville, NC 28802, USA.

0378-1127/98/$19.00 © 1998 Elsevier Science B.V. All rights reserved
PII S0378-1127(97)00307-1

pure and mixed genotype plots, to identify different patterns of stand development. and to screen future genotypes.

Generally. growth models with interrelated components have been used to account for genetic differences. Only one function may need to be modified in order to incorporate genetic differences in growth models with interrelated components, whereas several functions may need to be modified in growth models with unrelated component equations (Burkhart and Matney, 1981). As a result, research has focused on incorporating genetic differences into height-age functions (Nance and Wells, 1981; Buford and Burkhart. 1985, 1987: Sprinz, 1987; Knowe and Foster. 1989) and height-diameter functions (Buford and Burkhart. 1985, 1987; Buford. 1986) because of their utility in expressing stand structure and dynamics in forest growth models.

Research involving large plots of similar genetic composition suggests that the basic growth relationships are similar among loblolly pine (*Pinus taeda* L.) seed sources and families. Golden et al. (1981) detected variations in height growth patterns among seed sources but determined that the differences were not of practical importance. Nance and Wells (1981) and Buford and Burkhart (1985,1987) detected significant differences in level (site index) but not shape (slope) of height-age profiles. Buford and Burkhart (1985,1987) and Buford (1986) reported similar results for height-diameter functions. Using more flexible models. differences in height growth patterns have been associated with loblolly pine seed sources (Sprinz, 1987) and half-sib families (Knowe and Foster. 1989).

Despite the need, very little growth and yield information is available for improved stands of species other than loblolly pine. For eastern cottonwood (*Populus deltoides* Bartr.), height–age curves (Cao and Durand, 1991a) and a system of compatible basal area and volume growth and yield equations (Cao and Durand, 1991b) have been developed for improved stands. Also, a diameter distribution prediction approach that accounts for specific clones and mixtures has been developed (Knowe et al., 1994). Foster (1985) showed that clones within stands accounted for 11% of the total variation in height at age 1 and 37% of the variation at age 7 for eastern cottonwood in Mississippi. This suggests that height-age and height-diameter models may need to account for specific clonal differences. The objective of this study was to develop equations for height-age and height-diameter relationships applicable to both monocultures and mixtures of eastern cottonwood clones.

2. Methods

2.1. Data

Details of the eastern cottonwood clonal mixing study are given by Knowe et al. (1994). The study was established in 1984 on two randomly-selected sites near Fitler, MS (33°N, 91°W) and Wickliffe. KY (37°N, 89°W), and included seven randomly-selected clones originating from northeastern Texas, northwestern Louisiana. and between Vicksburg and

Table 1
Eastern cottonwood clones and diallel mixtures represented in replacement series experiments near Fitler, MS, and Wickliffe, KY

Code	Clone number	Origin	Mixtures (3:1 ratio)			
			4	5	6	7
1	ST231	Issaquena Co., MS	x	x		
2	S7C1	Brazos Co., TX		x	x	
3	S7C4	Brazos Co., TX			×	x
4	S7C8	Brazos Co., TX				×
5	ST75	Issaquena Co., MS				
6	ST238	Bolivar Co., MS				
7	ST66	Issaquena Co., MS				

Each binary mixture consisted of 2 treatment plot types: 75% clone A and 25% clone B; and 25% clone A and 75% clone B. A mixture treatment of equal proportions of each clone (1:1 ratio) was also included.

Greenville, MS (Table I). Although widely-separated geographically, the planting locations are typical of eastern cottonwood sites along the Mississippi River and are similar with respect to soil texture and fertility, precipitation, length of growing season, site preparation, and post-planting cultural treatments.

Each location included four randomized complete block replications of 22 plots of 36 measurement trees (with an internal border row) in a replacement series arrangement: seven monoculture plots; 14 binary mixture plots representing a subset from a partial diallel mixing design; and one all-clone mixture plot with all seven clones at equal proportions. Each binary mixture was represented by two plots: 75% of clone A and 25% of clone B and 25% of clone A and 75% of clone B. Clones in mixtures were randomly assigned to planting spots in each plot (i.e. noncontiguous clone plots). One clone in the all-clone mixture included an extra tree that was excluded from the present analyses. To insure adequate survival, two SO-cm long unrooted cuttings were planted at each planting spot and thinned to one tree per planting spot in August. 1984. Measurements of total height and dbh were obtained for the interior 36 trees (0.047 ha) at the end of the second, third, and fourth growing seasons. Virtually all of the mortality occurred during the first two growing seasons.

2.2. Analysis of height growth patterns

When developing height-age curves, Curtis et al. (1974) recommended using either a fixed number of trees per acre or a fixed percentage of surviving trees to calculate average dominant height (H). In similar studies, dominant height has been based on the taller two-thirds (Nance and Wells, 1981) and the taller one-half (Boyer, 1983: Golden et al., 1981; Knowe and Foster, 1989; Knowe, 1994) of surviving trees at each age. Buford and Burkhart (1985, 1987) designated the tallest 2.50 trees/ha (100 trees/ac) as dominant height. For the present study, H was defined as the average height of the taller one-third of surviving trees at each age, which is equivalent to the tallest 250 trees/ha.

Two mathematical models that have been used to describe height growth patterns were considered for the eastern cottonwood clonal mixing study. The nonlinear form of a logarithmic model used for loblolly pine by Nance and Wells (198 1) and Buford and Burkhart (1985, 1987), is shown as an algebraic difference formulation (Borders et al., 1984) obtained by assuming that the asymptote defines curve shape:

$$H_2 = H_1 \exp\left\{\beta\left(A_2^{-1} - A_1^{-1}\right)\right\} + \varepsilon \qquad (1)$$

where H_2 = dominant height (m) at end of growth period, H_1 = dominant height (m) at start of growth period, A_1 = plantation age (years) at end of growth period, A_1 = plantation age (years) at start of growth period, β = rate of height growth, and ε = random error.

An exponential growth model developed by Richards (1959) has been used for loblolly pine by Sprinz (1987) and Knowe and Foster (1989), for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) by Knowe (1994), and for red alder (*Alnus rubra* Bong.) by Knowe and Hibbs (1996). The algebraic difference formulation (Borders et al., 1984) obtained by assuming that the asymptote defines curve shape is:

$$H_2 = H_1\left(\frac{1 - \exp(-\beta A_2)}{1 - \exp(-\beta A_1)}\right)^{\theta} + \varepsilon \qquad (2)$$

where θ = shape parameter and other terms are as previously defined. In both of these functions, the rate parameter (β) determines how rapidly the asymptotic height is approached, with larger values resulting in rapid attainment of maximum height. The shape parameter in Eq. (2) determines the degree of curvature; values equal to 1.0 indicate that maximum growth rate occurs at young ages and declines linearly; larger values indicate sigmoid growth patterns. Replacing H_2 with site index (S) and A_2 with base age (A_1) produces an equation for predicting either dominant height or site index. Desirable features of these equations are any base age for site index may be selected, each curve has an implied asymptote, and $H_1 = S$ when $A_1 = A_1$.

Eastern cottonwood measurements obtained between ages 2 and 4 were arranged into a single set consisting of two nonoverlapping growth intervals (2-3 and 3-4). According to Borders et al. (1988), real growth series from remeasured plots or trees are less likely to have problems with serial correlation

Table 2
Comparison of height-age models for eastern cottonwood in a clonal mixing study

Equation and model[a]	R^2	$\sqrt{MSE}$	β(s.e.)	θ(s.e.)
(1) $H_2 = H_1 \exp\{\beta(A_2^{-1} - A_1^{-1})\}$	*0.7812*	*2.47*	*– 2.577666 (0.026999)*	–
(2) $H_2 = H_1((1 - \exp(-\beta A_2))/(1 - \exp(-\beta A_1)))^{\theta}$	*0.7842*	*2.46*	*0.619186 (0.030615)*	*2.524839* (0.135079)

Equation numbers correspond to those used in text.
[a] H_2 = dominant height (m) at end of growth period, H_1 = dominant height (m) at start of growth period. A_2 = plantation age (years) at end of growth period, A_1 = plantation age (years) at start of growth period, β = rate parameter, and θ = shape parameter.

when the data are arranged in non-overlapping growth intervals rather than all possible intervals. Preliminary regressions were obtained by fitting both height-age models to pooled data for all locations, monocultures, and mixtures combined. Both models accounted for about 78% of the variation in height growth (Table 2). However, projected heights at age 10 were appreciably less for Eq. (2) than those obtained by using the model developed by Cao and Durand (1991a) and Eq. (1) (Fig. 1). Therefore, Eq. (1) was selected for additional testing of planting locations and clonal differences.

The hypothesis of planting location and genetic effects on the rate parameter (β) of eastern cottonwood height-age model was explored by calculating additional sum of squares between full and reduced regression models (Neter et al., 1985). Differences in the rate parameter due to planting locations were tested by incorporating an indicator variable for the Kentucky location.

$$\beta_l = \mathrm{PO} + \beta_{01} L$$

where L = 0 if Fitler, 1 if Wickliffe. Polymorphism among clones and mixtures was incorporated using

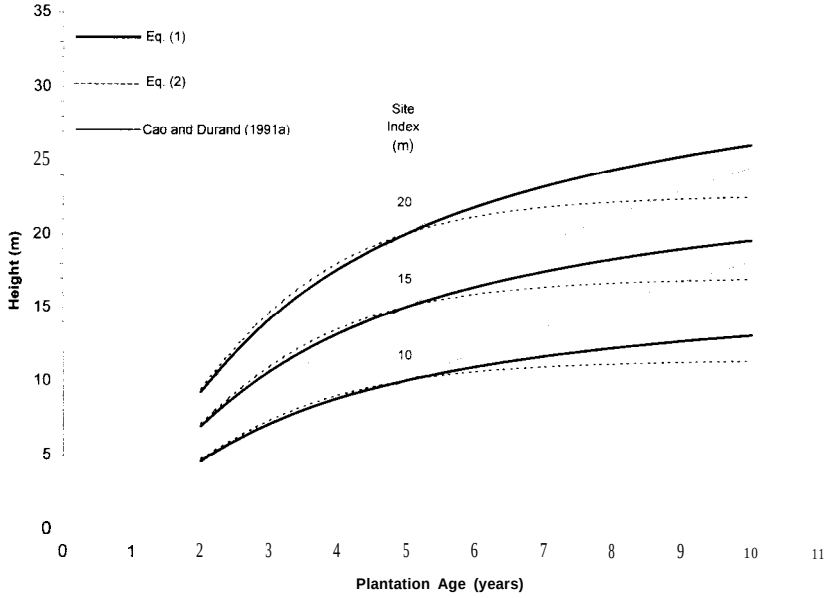

Fig. 1. Comparison of height-age curves developed for eastern cottonwood plantations in Mississippi and Kentucky, USA. Equation numbers refer to equations used in text.

the proportion of each clone in monocultures or mixtures.

$$\beta_c = \beta_0 + \sum_{i=1} \beta_i p_i$$

where p_i = proportion of the i^{th} clone in monoculture or mixture at time of planting. and $\sum_{i=}^{6}, p_i \leq 1.0$. β_0 represented the rate parameter for all clones combined and the β_i's represented adjustments to β_0 for the proportion of the i^{th} clone in mixture. An important implication of this formulation is that interactions between clones in mixtures are expressed by the linear function of proportions when β_c is included **in** Eq. (1). The combined effect of planting locations and clonal proportions was incorporated as follows:

$$\beta_{lc} = \beta_0 + \beta_{01} L + \sum_{i=1} \beta_i p_i$$

with terms as previously defined. Interactions between proportions of specific clones in mixtures were incorporated by using the expression developed by Knowe et al. (1994) for basal area predictions:

$$\beta_{lcx} = \beta_0 + \beta_{01} L + \sum_{i=1}^{6} b_i p_i + \sum_{j=4}^{5} b_{1j} p_j p_1 + \sum_{k=5}^{6} b_{2k} p_k p_2 + \sum_{l=6}^{7} b_{3l} p_l p_3 + \beta_{47} p_7 p_4$$

$$= \beta_0 + \beta_{01} L + (\beta_1 + \beta_{14} p_4 + \beta_{15} p_5) p_1 + (\beta_2 + \beta_{25} p_5 + \beta_{26} p_6) p_2 + (\beta_3 + \beta_{36} p_6 + \beta_{37} p_7) p_3 + (\beta_4 + \beta_{47} p_7) p_4 + \beta_5 p_5 + \beta_6 p_6$$

The β_i parameters represent the effect of clones in monocultures or mixtures and the β_{ij} parameters represent the interactions with other clonal proportions in mixtures. For example, the parameters β_{14} and β_{15} represent adjustments of clone ST244 according to the proportion of clones S7C8(p_4) or ST75 (p_5) in mixture. The sign of each β_{ij} parameter indicates overcompensation if positive and undercompensation if negative. Equations incorporating planting locations, clonal differences, and interactions were compared to Eq. (1) as the reduced model. Additional comparisons were made for testing the significance of incorporating clones to the model with planting locations and for incorporating interactions between clones in mixtures to the model with planting locations and clonal proportions.

2.3. *Analysis of height–diameter relationships*

Both age-dependent and age-independent expressions for tree position with respect to its competitors have been shown to be important in modeling height growth of Douglas-fir (Ritchie and Hann, 1986; Hann and Ritchie, 1988; Knowe. 1994). A height-diameter model developed for loblolly pine by Borders and Patterson (1990) and subsequently applied to young Douglas-fir by Knowe (1994), based on dominant height and relative diameter, was considered for eastern cottonwood.

$$h_i = \lambda_1 H\left\{1 - \lambda_2 \exp[-\lambda_3 (d_i / D_q)]\right\} + \varepsilon \qquad (3)$$

where h_i = height of i^{th} tree (m), H = dominant height (m), d_i = dbh of i^{th} tree (cm>, and D_q = quadratic mean dbh (cm). Advantages of this function are its flexibility and compatibility with stand functions for dominant height, basal area, and survival. λ_1 expresses the maximum height as a function of dominant height, with larger values indicating taller maximum tree heights. λ_2 is the lower asymptote, with large values indicating shorter trees at small diameters and small values indicating taller trees. λ_3 indicates the rate at which the asymptotic height is attained, with large values indicating that maximum tree height is rapidly approached. Relative diameter (d_i/D_q) in these functions expressed the position of each tree in the stand. Values of relative diameter less than 1 .O indicated trees that were smaller than average; values greater than 1.0 indicated trees that were larger than average. The height-diameter pairs for individual trees and the corresponding quadratic mean diameters and dominant heights on all plots, locations, and measurement ages were combined into a single dataset for analyses.

The hypotheses of different height-diameter relationships for locations and clones were tested by expressing each parameter as a function of indicator variables or clonal proportions.

$$\lambda_{il} = \lambda_{i0} + \lambda_{i1} L$$

$$\lambda_{ic} = \sum_{j=1}^{7} \lambda_{ij} p_j$$

with variables as previously defined. Residual sum of squares for full and reduced regression models

were compared (Neter et al., 1985) by using Eq. (3) as the reduced model.

3. **Results**

3.1. *Height-age function*

Incorporating an indicator variable for planting locations into the rate parameter (β_1) was significant (p = 0.0001) and accounted for 5.6% additional variation in height growth (Table 3). Clonal proportions (β_c) was also significant (p = 0.0077) and accounted for about 1% additional variation in height growth. Inclusion of both planting locations and clonal proportions into the rate parameter (β_{lc}) was significant (p = 0.0001) and accounted for 6.6% additional variation in height growth, which is slightly more than the additive effects. Comparison of the mode1 with both planting locations and clonal proportions in the rate parameter to the model with planting locations alone indicated that the addition of clonal proportions was significant (p = 0.0011). The model with interaction between clones in mixtures was significant (p = 0.000 1) and accounted for 6.7% of the variation in height growth. However, comparison of the model with interaction terms in the rate parameter to the model with both planting locations and clonal proportions indicated that the addition of interactions was not significant (p = 0.9178). Although different height growth rates were associated with certain clonal interactions, these differences were much less important than those associated with planting locations and clonal proportions. The magnitude and sign of parameter estimates suggests undercompensation in mixtures involving ST75 and either ST238 or S7C1 and overcompensation in mixtures involving S7C4 and ST238. These patterns of interactions in the height-age function are identical to those observed in a basal area prediction function developed for this study (Knowe et al., 1994).

The parameter estimates and standard errors (s.e.) for the height-age function are:

$$\beta_{lc} = \underset{(0\ 077849)}{2\ 562862} + \underset{(0\ 045648)}{0\ 513454}L - \underset{(0\ 106642)}{0.198376}p_1 - \underset{(0\ 102357)}{0\ 286997}p_2 - \underset{(0\ 111591)}{0\ 318960}p_3 - \underset{(0\ 110711)}{0\ 345909}p_4 - \underset{(0\ 106124)}{0\ 431640}p_5 - \underset{(0\ 103817)}{0.073135}p_6$$

3.2. *Height-diameter function*

For all three parameters of the height-dbh function, incorporating indicator variables for planting locations or clonal proportions into the parameter (β_1) were significant (p = 0.0001) but accounted for less than 0.02% additional variation in height (Table 4). Planting locations were associated with differences in maximum height (λ_1), suggesting that trees of the same relative diameter are slightly taller at the Mississippi location than at the Kentucky location. Clonal proportions were associated with differences in lower asymptote (h,). The estimated parameters suggested that, for trees with smaller than average dbh in stands with the same quadratic mean dbh and dominant height, clones ST75, ST244, and S7C8 are slightly taller than the other clones and that clone S7C1 trees are slightly shorter. The differences in

Table 3
Explained variation (R^2) and partial analysis of variance for testing the effects of planting locations and clonal proportions on rate of height growth in the height-age function for eastern cottonwood

Model	R^2	Partial R^2	*df*	SSE	*F*	Prob. > *F*
Reduced	0.7812		348	2124.23		
Planting locations (β_1)	0.8372	0.0560	347	1580.61	119.477	0.000 1
Clones (β_c)	0.7909	0.0097	342	2029.68	3.200	0.0077
Locations and clones (β_{lc})	0.8474	0.0662	341	1480.96	24.703	0.0001
Locations and interactions (β_{lcx})	0.8486	0.0674	334	1469.48	10.629	0.0001

Table 4
Explained variation (R^2) and partial analysis of variance for **testing the effects of planting location\ and** clonal **proportions on parameters of the height-diameter** function for eastern cottonwood

Model	R^2	Partial R^2	*df*	*SSE*	*F*	Prob. $>F$
Reduced	0.9498		16609	**7025.76**		
Asymptote (λ_1)						
Planting locations (λ_{11})	**0.9499**	**0.000 I**	16608	**70 16.54**	**21.822**	**0.0001**
Clonal proportions (λ_{1c})	0.9499	**0.000** 1	**16603**	**7014.36**	**4.407**	**0.0002**
Lower asymptote (λ_2)						
Planting locations (λ_{21})	**0.9398**	**0.000 *I***	**16608**	**7023.75**	**7.1**17	**0.000** I
Clonal proportion% (λ_{2c})	0.9500	***0.0002***	16603	6996.03	**I**1.758	**0.000 I**
Rate (λ_3)						
Planting locations **(A,,**)	0.9499	0.0001	**I6** 608	**7019.93**	13.792	**0.000** I
Clonal proportions (λ_{3c})	0.9499	0.0001	**I 6**603	**7007.97**	**7.024**	**0.0001**

height-dbh relationships may reflect differential responses to changes in light quality and quantity (Ballare et al., 1990, 199 1).

The final height-dbh function is as follows:

$$h_i = 1.266303\,H\left\{1 - 0.973\,136 \times \exp\left[-1.567133\left(d_i/D_q\right)\right]\right\} \quad (4)$$

The standard errors are 0.008440, 0.014526, and 0.040366. respectively.

4. Discussion and conclusions

Unlike the studies involving loblolly pine families (Sprinz, 1987; Knowe and Foster, 1989) and competition control treatments in young Douglas-fir plantations (Knowe, 1994), the more flexible Richards (1959) function did not provide a substantial improvement in fit over the simpler exponential function to the height-age data for eastern cottonwood clones. In the present study, both equations resulted in similar patterns of residuals and R^2 values. However, the nonlinear form of the logarithmic function provided more realistic estimates of dominant height when extrapolated beyond the range of observed ages. Furthermore, using the less-flexible nonlinear form of the logarithmic function did not preclude detecting significant differences among eastern cottonwood clones, as reported for loblolly pine seed sources and families by Nance and Wells (198 1), Buford and Burkhart (1985, 1987), and Buford (1986).

Based on the proportion of explained variation, differences in planting locations appear to be more important than clones (genetic variation) in determining height growth patterns of eastern cottonwood. However, the planting locations were widely separated, which may have exaggerated the differences in planting locations compared with more similar sites. When compared to planting location effects, differences in height growth patterns among the seven eastern cottonwood clones were relatively small. When selecting superior genotypes or in evaluating the long-term consequences of genetic deployment strategies, slight differences in height growth patterns may reflect important differences in stand dynamics. Therefore, differences in growth patterns should be recognized even though differences in predicted heights are relatively small. In addition, the clonal mixing study included only seven clones, all of which were randomly selected from an operational tree improvement program. Hence, a larger sample might include a greater range in growth response. Eastern cottonwood is a monoecious species, but no differences between sexes have been observed in growth traits (Farmer, 1964; Ying and Bagley, 1976).

As with basal area and diameter distribution prediction models (Knowe et al., 1994), interactions between proportions of specific clones in binary mixtures were not statistically significant in either the height-age or the height-dbh functions. The

clones that exhibited over- and under-compensation in the basal area prediction model (Knowe et al., 1994) exhibited similar trends in the height-age function. This suggests that intergenotypic competition may affect both allometric relationships and stand dynamics. For that reason, modification of only one function in forest growth models involving interrelated components may not always be adequate for incorporating genetic differences.

As with the height-age function, differences in the height-diameter function were small. This is in general agreement with results obtained for loblolly pine families (Buford and Burkhart, 1985, 1987; Buford, 1986) and competition control treatments in young Douglas-fir plantations (Knowe, 1994). Planting locations were associated with differences in maximum height, reflecting the impacts of environmental variation on height-age curves. Clones were associated with differences in the height of trees with smaller than average diameter. Taller trees at high levels of interclonal competition may indicate reallocation of photosynthate to shoot growth at the expense of cambial growth because of competition (Waring, 1987). Another possibility is an escape mechanism from competition (Ballare et al., 1990, 1991). A photomorphic response may occur in trees as a result of changes in light quality (ratio of red to far-red light) and quantity (reduction of photons in the red and the far-red wavelengths).

References

Ballare, C.L., Scopel, A.L., Sanchez, R.A., 1990. Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. Science 247, 329–332.

Ballare, C.L., Scopel, A.L.. Sanchez, R.A., 1991. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. Plant Cell Environ. 14, 57-65.

Borders, B.E., Patterson, W.D., 1990. Projecting stand tables: a comparison of the Weibull diameter distribution method, a percentile-based projection method. and a basal area growth projection method. For. Sci. 36. 413-424.

Borders, B.E., Bailey, R.L., Ware. K.D., 1984. Slash pine site index from a polymorphic model by joining (splining) nonpolynomial segment?, with an algebraic difference method. For. Sci. 30, 41 l-423.

Borders, B.E., Bailey. R.L., Clutter, M.L., 1988. Forest growth models: parameter estimation using real growth series. In: Ek, A.R., Shifley. S.R., Burk, T.E. (Eds.), Proceedings of IUFRO Forest Growth Modeling and Prediction Conf., 24–28 August 1987, Minneapolis, MN, USDA For. Serv. Gen. Tech. Rep. NC-120, North Central For. Exp. Stn., St. Paul. MN, pp. 660-667.

Boyer, W.D., 1983. Variation\ in height-over-age curves for young loblolly pine plantationa. For. Sci. 29, 15–27.

Buford, M.A., 1986. Height-diameter relationships in loblolly pine seed sources. For. Sci. 32, 812–815.

Buford, M.A., Burkhart, H.E., 1985. Dynamics of improved loblolly pine plantations and the implications for modeling growth of improved stands. In: Proceedings of 18th South. For. Tree Improve. Conf., 21–23 May 1985, Univ. South. Mississippi, Long Beach, MS, pp. 170–174.

Buford, M.A., Burkhart. H.E., 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. For. Sci. 33, 707–724.

Burkhart, H.E., Matncy, T.G.. 1981. Growth and yield modeling —a place for genetic improvement effects. In: Proceedings of 16th South. For. Tree Improve. Conf., 27-28 May 1981, VPI and SU. Blacksburg. VA. pp. 6–11.

Cao, Q.V., Durand, K.M.. 1991a. Site index curves for eastern cottonwood in the lower Mississippi Delta. South. J. Appl. For. 15,28–30.

Cao, Q.V., Durand, K.M., 1991b. A growth and yield model for improved eastern cottonwood plantations in the lower Mississippi Delta. South. J. Appl. For. 15,213–216.

Curtis, R.O., DeMars, D.J., Herman, F.R.. 1974. Which dependent variable in site index-height&age regressions?. For. Sci. 20. 74-87.

Farmer, R.E. Jr., 1964. Sex ratio and sex-related characteristics in eastern cottonwood. Silvae Gcnct. 13, 116–118.

Foster. G.S., 1985. Provenance variation of eastern cottonwood in the lower Mississippi Valley. Silvae Genet. 35,32–38.

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.

Hann, D.W., Ritchie, M.W., 1988. Height growth rate of Douglas-fir: a comparison of model forms. For. Sci. 34, 165–175.

Knowe, S.A., 1994. Effect of competition control treatment!, on height-age and height-diameter relationships in young Douglas-fir plantations. For. Ecol. Manage. 67. 101–111.

Knowe, S.A., Foster. G.S.. 1989. Application of growth models for simulating genetic gain of loblolly pine. For. Sci. 35, 21 l-228.

Knowe, S.A., Hibbs, D.E.. 1996. Stand structure and dynamics of young red alder as affected by planting density. For. Ecol. Manage. 82, 69-85.

Knowe, S.A.. Foster, G.S., Rousseau, R.J., Nance, W.L.. 1994. Eastern cottonwood clonal mixing study: predicted diameter distribution. Can. J. For. Res. 24. 405–414.

Libby, W.J., 1982. What is a safe number of clones per plantation'? In: Heybroek. H.M., Stephan, B.R., von Weissenburg, K. (Eds.), Rcsistancc to Diseases and Pests in Forest Trees. Centre for Agric. Publ.Doc., Wagcningen. Netherlands, pp. 342–360.

Markovic. J., Herpka, I., 1986. Plantations in short rotations. In:

Guzina, V. (Ed.). Poplars and Willows in Poplar Research Institute, Novi Sad. Yugoslavia. pp. 182–197.

Nance, W.L., Wells. O.O., 1981. Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. In: Proceedinga of 16th South. For. Tree Improve. Conf., 27-2X May 1981, VPI and SU. Blacksburg, VA. pp. 86-96.

Neter, J., Wasserman, W.. Kutner. M.H.. 1985. Applied Linear Statistical Models. 2nd cdn. Richard D. Irwin, Homewood, IL.

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

Ritchie, M.W.. Hann, D.W.. 1986. Development of a tree height growth model for Douglas-fir. For. Ecol. Manage. 15, 135–145.

Roberds, J.H., Namkoong, G., Skropps, T., 1990. Genetic analysis of risk in clonal populations. Theor. Appl. Genet. 79, 84 I-848.

Sprinz, P.T., 1987. Effects of genetically improved stands on growth and yield principles. In: Proceedings of 19th South. For. Tree Improve. Conf., 16–18 June 1987, Texas A&M Univ.. College Station, TX, pp. 338–348.

Tuskan, G.A., van Buijtenen, J.P., 1986. Inherent differences in family response to inter-family competition in loblolly pine. Silvae Genet. 35, 112–118.

Waring, R.H.. 1987. Characteristics of trees predisposed to die. BioScience 37, 569–574.

Williams, C.G., Bridgewater, F.E., Lambeth, C.C., 1983. Performance of single family versus mixed family plantation blocks of loblolly pine. In: Proceedings of 17th South. For. Tree Improve. Conf., 6-9 June 1983, Univ. Georgia, Athens, GA, pp. 194–20 I.

Ying, C.C., Bagley, W.T.. 1976. Genetic variation of eastern cottonwood in an eastern Nebraska provenance study. Silvae Genet. 25. 67–73.

Forest Ecology and Management

Submission of manuscripts.
Manuscripts should be submitted in triplicate. Authors from the Americas, Australia, New Zealand and the Pacific are requested to send their manuscripts to Forest Ecology and Management, Dr. Richard F. Fisher, Department of Forest Science, Texas A&M University, College Station, TX77843-2135, USA; all other authors are requested to send their manuscripts to the Editorial Office, Forest Ecology and *Management,* P.O. Box 181,1000 AD Amsterdam, The Netherlands.

Authors in Japan please note: Upon request, Elsevier Science Japan will provide authors with a list of people who can check and improve the English of their paper (before *submission).* Please contract our Tokyo office: Elsevier Science Japan, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo 106-0044, Japan; tel. (+81)-3-5561-5033; fax (+81)-3-5561-5047.

Electronic manuscripts: Electronic manuscripts have the advantage that there is no need for the rekeying of text, thereby avoiding the possibility of introducing errors and resulting in reliable and fast delivery of proofs.
For the initial submission of manuscripts for consideration, hardcopies are sufficient. For the processing of *accepted* papers, electronic versions are preferred. After final *acceptance,* your disk plus two, final and exactly matching printed versions should be submitted together. Double density (DD) or high density (HD) diskettes (3.5 or 5.25 inch) are acceptable. It is important that the file saved is in the native format of the wordprocessor program used. Label the disk with the name of the computer and wordprocessing package used, your name, and the name of the file on the disk. Further information may be obtained from the Publisher.

Enquiries concerning manuscripts and proofs: questions arising after acceptance of the manuscript, especially those relating to proofs, should be directed to Elsevier Science Ireland Ltd., Bay 15K, Shannon Industrial Estate, Shannon, Co. Glare, Ireland, tel. (+353-61) 471944; fax (+353-61) 472144.

Advertising information: Advertising orders and enquiries may be sent to: International: Elsevier Science, Advertising Department, The Boulevard, Langford Lane, Kidlington, Oxford, OX5 1GB, UK; tel. (+44) (0) 1865 843565; fax (+44) (0) 1865 843976. **USA and Canada: Elsevier Science** Inc., Mr. Tino DeCarlo, 655 Avenue of the Americas, New York, NY 10010-510, USA; tel. (+1) 212 633 3815; fax (+1) 212 633 3820. **Japan: Elsevier Science Japan, Marketing Service, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo 106-0044, Japan tel.** (+81)-3–5561-5033; **fax** (+81)-3-5561-5047.

US mailing info: Forest Ecology *and Management* (0378-1121) is published monthly by Elsevier Science B.V. (Molenwerf 1, Postbus 211,1000 AE Amsterdam). Annual subscription price in the USA is US$ 2307.00 (valid in North, Central and South America), including air speed delivery. Second class postage rate is paid at Jamaica, NY 11431.
USA POSTMASTERS: Send address changes to Forest *Ecology and* Management Publications Expediting, Inc., 200 Meacham Avenue, Elmont, NY 11003.
AIRFREIGHT AND MAILING in the USA by Publications Expediting Inc., 200 Meacham Avenue, Elmont, NY 11003.

***Forest Ecology and Management* has no page charges**

For a full and complete Guide for Authors, please refer to Forest Ecology and Management, Vol. 100, Nos. l-3, **pp.** 103-106. The instructions can also be found on the World Wide Web: access under http://www.elsevier.nl or http://www.elsevier.com

Copyright © 1998, Elsevier Science B.V. All rights reserved.

0378-1127/98/$19.00

⊗ **The paper used** in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in The Netherlands

LANDSCAPE AND URBAN PLANNING

An International Journal of Landscape Ecology, Landscape Planning and Landscape design

Editor-in-Chief:
J.E. Rodiek, College of Architecture, Texas A&M University, College Station, TX 77843-3137, USA

AIMS AND SCOPE

A journal concerned with conceptual, scientific and design approaches to land use. By emphasizing ecological understanding and a multi-disciplinary approach to analysis and planning and design, it attempts to draw attention to the interrelated nature of problems posed by nature and human use of land. In addition, papers dealing with ecological processes and interactions within urban areas, and between these areas and the surrounding natural systems which support them, will be considered. Papers in which specific problems are examined are welcome. Topics might include but are not limited to landscape ecology, landscape planning and landscape design. Landscape ecology examines how heterogeneous combinations of ecosystems are structured, how they function and how they change. Landscape planning examines the various ways humans structure their land usechanges.Landscape design involves the physical strategies and forms by which land use change is actually directed. *Landscape and Urban Planning* is based on the premise that research linked to practice will ultimately improve the human made landscape.

Editorial Advisory Board:
I.D. Bishop, *Parkville, Vic.*, Australia,
E.G. Bolen, Wilmington, NC, *USA*,
I.D. Bruns, *Schorndorf, Germany*,
J.B. Byrom, Edinburgh, UK,
T.C. Daniel, *Tucson, AZ, USA*,
R.M. DeGraaf, *Amherst, MA, USA*,
J.G. Fabos, *Amherst, MA, USA*,
S. Gonzalez Arbiso, *Madrid*, Spain,
M. Hough, *Etobicoke*, ON, Canada,
P. Jacobs, *Montreal PO, Canada*,
D.S. Jones, *Melbourne, Vic., Australia*,
H. Lavery, *Milton, Qld., Australia*,
W.M. Marsh, *Flint*, MI, *USA*,
D.L. Mitchell, *Dallas, TX, USA*,
D.G. Morrison, *Athens, GA, USA*,
J.I. Nassauer, *St. Paul, MN, USA*,
M. Neilscher, *Guelph*, ON, Canada,
D.D. Patterson, Vancouver, *BC*, Canada,
A. Ramos, *Madrid, Spain*,
P. Shepard, *Claremont, CA, USA*,
O.R. Skage, *Alnarp, Sweden*,
R.C. Smardon, Syracuse, NY, USA,
G. Sorte, *Alnarp, Sweden*,
F. Stearns, *Rhinelander, WI, USA*,
R.C. Szaro, *Washington, DC, USA*,
J.W. Thomas, La *Grande, OR, USA*,
P.J. Trowbridge, Ithaca, NY, USA,
T.H.D. Turner *London, UK*,
M.J. Vroom, *Wageningen, The Netherlands*.
W.V. Wendler, College *Station, TX, USA*,
B.-E. Yang, *Seoul, Korea*,
E.H. Zube, *Tucson, AZ, USA*

ELSEVIER
SCIENCE PUBLISHERS

ABSTRACTED/INDEXED IN
Applied Ecology Abstracts, Biological Abstracts, Current Contents B & S, Environmental Periodicals Bibliography, Geobase, Geographical Abstracts, LandSearch.

1994 SUBSCRIPTION DATA

Volumes 28-30 (in 9 issues)
Subscription price:
Dfl. 1080.00 (US $584.00)
incl. Postage
ISSN 0169-2046

Elsevier Science Publishers,
P.O. Box 211, 1000 AE Amsterdam,
The Netherlands
Fax: (020) 5803-203

Customers in the USA and Canada:
Elsevier Science Publishers
P.O. Box 945, Madison Square Station,
New York, NY 10160-0757, USA
Fax: (212) 633-3680

The Dutch Guilder price quoted applies worldwide, except in the Americas (North, Central and South America) The US Dollar price quoted applies in the Americas only Non VAT registered customers in the European Community should add the appropriate VAT rate applicable in their country to the price.