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Eastern cottonwood clonal mixing study: intergenotypic competition effects

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Abstract

Intergenotypic competition of seven clones of eastern cottonwood (*Populus deltoides*) was evaluated in a replacement series experiment. A partial diallel competition design was used to choose pairs (binary sets) of clones for plot type treatments. Two separate treatments were established for each pair of clones, namely (1) 75% clone A: 25% clone B and (2) 25% clone A: 75% clone B. Twenty-one treatments were established in the study: seven pure clone treatments and 14 mixed treatments (seven pairs of clones each at two ratios). Two study sites (Vicksburg, Mississippi and Wickliffe, Kentucky) were used. Results are presented for stand ages two, three, and four years which corresponds to the lower to mid-length rotation for the species for a short rotation woody crop (either biomass for energy or fiber for pulp and paper). Average plot height at an age of 4 years was 13.23 m. Plot total yield was affected by intergenotypic competition. The type and level of response to mixing clones depended on the specific clones involved and the planting site. Usually, the most predictable opportunity for over- or underyielding when in binary mixture occurred for clones which differed substantially in pure plot growth and yield. The yield of mixtures of clones of more similar growth patterns sometimes differed significantly from that expected from an additive model, but this was less common. When significant differences did occur between pure clone yields and the yields of their binary mixtures, the plot yield was often a linear function of the proportion of the best clone. Overyielding of mixtures occurred, with additional yields of up to 27% of the mixture over the best clone's pure plot yield. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Genetic deployment; Genetic variance; Growth and yield modeling; Overyielding; Underyielding

1. Introduction

Forest geneticists know that genetic effects on forest stand productivity are strong, yet little is known regarding intergenotypic competition effects on stand productivity. Intergenotypic competition has been defined as the stress which is placed on a plant by the phenotype and spatial arrangement of the surrounding plants (Hinson and Hanson, 1961). A large body of scientific literature exists which demonstrates a varying impact of intergenotypic competition on agronomic crop yield, and this influence is often predictable (Trenbath, 1974; Harper, 1977; Wright, 1982). Given the long-lived nature and long economic

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rotation lengths of forest trees, competition is at least as important, if not more so, in forest trees than in annual agronomic crops. Among agronomic crops, perhaps perennial grasses, provide a better model for forest species than annual crops. Given the overwhelming importance of density competition on forest stand development, forest biometricians have concentrated a great deal of effort towards building this effect into growth and yield models (Clutter et al., 1983), yet accute lack of data has stymied their attempts to add genetic effects into their models.

Some attempts have been made to assess the magnitude of responses to intergenotypic competition with tree species. The studies can be divided generally into two categories: stand (plot) level and individual tree level. This categorization parallels a similar division for growth and yield models in forestry (Clutter et al., 1983). Most of the stand level studies of intergenotypic competition have been conducted in the field with an objective of assessing the difference in plot yield between pure and mixed plots. Generally these studies have included single-family or pure clonal plots as well as either (1) a single mixture plot with equal proportions of all families (Johnstone and Samuel, 1974; Rockwood, 1983; Williams et al., 1983; Hart, 1986) or clones (Markovic and Herpka, 1986; Lundkvist et al., 1992; DeBell and Harrington, 1993) or (2) binary mixtures at equal proportions (50% family A: 50% family B) (von Euler, 1993). In order for such studies to bridge the gap to provide stand level information, the plot sizes should be at least 25 measurement trees initially, and the trees must reach sufficient size and spacing to be well into competition. Due to their large size and long term nature, few such studies have been placed in the field. These studies have shown that a significant difference may (Williams et al., 1983; Lundkvist et al., 1992) or may not (Markovic and Herpka, 1986; DeBell and Harrington, 1993; von Euler, 1993) occur between the mean of the pure plots and the mean of the mixed plot(s). Although, of interest in investigating the effect of intergenotypic competition on stand level yield, an experimental approach with only two plot types does not aid in modifying growth and yield models, i.e., there is no predictive ability.

Many of the intergenotypic competition studies have been in controlled environments with very young trees and have focused attention at the individual tree level. This enables more complex studies to be installed with either seedling families (Adams et al., 1973; Tuskan and van Buijtenen, 1986; von Euler et al., 1993) or clones (Tauer, 1975; Adams, 1980). These study designs generally can be classified as a replacement series (Harper, 1977), in which the number of seedlings in a plot is fixed and the proportion of plants varies from 100% of one genetic entity (family or clone) to varying proportions of two or more. These designs permit the prediction of yields from the various treatments as well as detailed analyses of intergenotypic competition response at the individual tree level. von Euler et al. (1992) reported on a 16-year-old field study which is one of the few studies of this type in the literature.

Responses in replacement series experiments are classified as *complementary* (mixture equals the weighted mean of the pure treatments), *overyielding* (mixture exceeds weighted mean of the pure treatments), or *underyielding* (mixture is less than the weighted mean of the pure treatments). All of these response types have been observed with tree species (Adams et al., 1973; Tauer, 1975; Adams, 1980; Tuskan and van Buijtenen, 1986; von Euler et al., 1993). In essence, no single response dominates the results, hence general conclusions cannot be made; the result is family- or clone-specific. Furthermore, applicability of such results, with very small trees, to yield of forest stands is suspect, since evidence suggests that ontogenetic changes occur during stand development (Franklin, 1979; Foster, 1986).

Another approach that has been used by some researchers is to model competition effects in field genetic tests. This is an extension of the distance-dependent individual tree growth and yield model (Clutter et al., 1983) in which an assessment is made of the competitive effects of neighbors (via their height, dbh, or basal area and their distance to the subject tree). This competitive effect is subdivided into a genetic and environmental component (Nance et al., 1983; Hart, 1986; Magnussen, 1989) and used as an aid to predict future growth. Based on general principles, Nance (1983) used an individual-tree, growth and yield model to attempt to simulate the outcome of mixing families of loblolly pine (*Pinus taeda* L.). He found that the yield of mixed plantations may be predictable using the single family yields, but when combined in an additive model, the contribu-

tions of individual families to the total mixture yield was less predictable.

Research results are needed to enable the prediction of forest stand growth and yield with either pure or mixed families or clones. Such results should be generated from field studies using: (1) relatively large plots, (2) some type of replacement series design, (3) a tree spacing similar to that used operationally, and (4) data collected over a range of ages. The current study was initiated with eastern cottonwood (*Populus deltoides* Bartr.) clones with these factors in mind. We chose to focus our analyses at the stand level rather than at the individual tree level. This decision was conditioned somewhat by the fact that a growth and yield model for eastern cottonwood already exists (Cao and Durand, 1991), and it operates at the stand level. Previous research with the same data as in the current study was intended to incorporate intergenotypic competition into predicting diameter distributions (Knowe et al., 1993), which is one component of many stand level growth and yield models. For eastern cottonwood clones, the clonal proportions in the stand directly affected stand basal area which indirectly affected the diameter distributions (Knowe et al., 1993). Clonal proportion also directly influenced minimum diameter; and along with the direct effect of different clones, it also caused skewed distributions. Foster and Knowe (1995) also utilized the same cottonwood data as in the current study in order to develop a growth and yield model. They used the basal area prediction function and the diameter distribution function from Knowe et al. (1993) in combination with a height-dbh function that they developed. Stand volumes were then simulated using the model. Simulations were performed for mixtures and monocultures of an underyielding pair of clones, an overyielding pair of clones, and a complimentary pair of clones. The simulations predicted various mixture proportions of the underyielding clones to yield 3–4% less total volume than expected based on their pure clone performance, overyielding clones to yield 2% more total volume than expected, and the complimentary clones to yield about the same total volume as expected.

The objectives of the current study were to: (1) determine the yielding ability of representative cottonwood clones in monocultures (pure plots) and mixtures, and (2) test the hypothesis that per area volume of binary mixtures of clones is a linear function of the per area volumes of the two constituent clones in monoclonal plots.

2. Materials and methods

2.1. Experimental design

We used a partial competition diallel similar to the full half-diallel of Hill and Shimamoto (1973); Hill (1974) as an experimental design. Seven clones of eastern cottonwood (Table 1), (hereinafter termed cottonwood) were chosen at random from the tree improvement programs of Crown Zellerbach (subsequently the program and land was purchased by James

Table 1
Plot types in the competition diallel with seven eastern cottonwood clones and their geographic origin[a]

Clone B	Clone A						
	ST244	S7C1	S7C4	S7C8	ST75	ST238	ST66
ST244	×			×[b]	×		
S7C1		×			×	×	
S7C4			×			×	×
S7C8				×			×
ST75					×		
ST238						×	
ST66							×

[a] Clones S7C1, S7C4, and S7C8 originated in Brazos County, Texas, Latitude 30°38′N, Longitude 96°21′W; ST238 was from Bolivar County, Mississippi, Latitude 34°00′N, Longitude 90°20′W; and ST66, ST75, and ST244 were from Issaquena County, Mississippi, Latitude 32°43′N, Longitude 90°20′W.

[b] Each binary clone mixture is represented by two plot types: 75% clone A: 25% clone B and 25% clone A: 75% Clone B.

Table 2
Plot types in the eastern cottonwood intergenotypic competition study

Group number	Clone (s)	Plot ratio (%)	Coded variable (PROP[a])
1	S7C8	100	1.00
1	S7C8:ST244	75:25	0.75
1	S7C8:ST244	25:75	0.25
1	ST244	100	0.00
2	S7C4	100	1.00
2	S7C4:ST238	75:25	0.75
2	S7C4:ST238	25:75	0.25
2	ST238	100	0.00
3	ST75	100	1.00
3	ST75:ST244	75:25	0.75
3	ST75:ST244	25:75	0.25
3	ST244	100	0.00
4	S7C4	100	1.00
4	S7C4:ST66	75:25	0.75
4	S7C4:ST66	25:75	0.25
4	ST66	100	0.00
5	S7C1	100	1.00
5	S7C1:ST75	75:25	0.75
5	S7C1:ST75	25:75	0.25
5	ST75	100	0.00
6	S7C8	100	1.00
6	S7C8:ST66	75:25	0.75
6	S7C8:ST66	25:75	0.25
6	ST66	100	0.00
7	S7C1	100	1.00
7	S7C1:ST238	75:25	0.75
7	S7C1:ST238	25:75	0.25
7	ST238	100	0.00

[a] PROP is the proportion of the most productive clone of the pair of clones in the group, so that the regression coefficients were positive.

River) and Westvaco. These clones were considered to be a random sample from the tested, first generation population of cottonwood in the lower Mississippi Valley. Twenty-one plot types were arranged in the partial diallel (Table 1): 7 monoclonal plots (one plot per clone) and seven binary mixtures, each at two ratios (75% clone A: 25% clone B and the reverse) (7 mixtures×2 ratios=14 plot types) (Table 2). Clones were assigned to positions within the diallel without reference to their inherent growth characteristics; hence, clone pairs were not purposefully matched based on characteristics. The 50:50% mixture was deleted from the study due to the constraint of the study's large size and the fact that it is less informative in the model than the two chosen mixture plot types.

2.2. Field design and measurements

The 21 plot types were arranged in a randomized complete block design with four replications in each of the two sites: site 1 near Vicksburg, Mississippi (latitude 33°N, longitude 91°W) and site 2 near Wickliffe, Kentucky (latitude 36°49′N, longitude 89°7′W). Sixty-four trees were planted per plot (0.086 ha) in an 8×8 tree square configuration with approximately a 3.7×3.7 m tree spacing. The outer row served as an interior border row with an inner 36 tree (6×6) measurement plot (0.048 ha). For binary mixture plots, the clones were assigned to planting spots at random and care was taken to maintain the correct ratios in both the border rows and the inner measurement plots.

Each site was prepared by removal of all debris, disking, and subsoiling (along the planting lines). Unrooted, 50 cm long stem cuttings were planted in the subsoil trenches in December 1983 and February 1984 at site 1 and site 2, respectively. Two cuttings were planted at each spot, and if both survived, one was chosen at random and cut during August, 1984. Normal cultural treatments (such as weed control) were followed (McKnight, 1970) at both sites. Measurements were taken following growing seasons two, three, and four: (1) total height at ages two (HT2), three (HT3), and four (HT4) and (2) diameter at breast height (dbh) at ages two (DBH2), three (DBH3), and four (DBH4). Total tree volume (o.b.) was calculated at ages two (TVOL2), three (TVOL3), and four (TVOL4) following Mohn and Krinard (1971):

$$\mathrm{TVOL(o.b.)} = (0.21099 + 0.00221\mathrm{DBH}^2\mathrm{HT}).028 \quad (1)$$

where the 0.028 multiplier was used to convert ft^3 to m^3.

2.3. Analyses

For analytical purposes, the plot types were divided into seven groups, each with four plot types: pure clone plots for two clones and the two mixture plots which contained the same two clones (Table 2). For example, group 1 contained pure plots for clones S7C8 and ST244 as well as a plot with 75% S7C8:25% ST244 and another plot with 25% S7C8:75% ST244.

Due to the diallel design, each clone was included in two different groups.

A two-way analysis of variance was conducted, by group and site for each age, based on either plot means (HT and DBH) or plot totals (TVOL). The sources of variation included (4) plot types, (4) replications, and error with three, three, and nine degrees of freedom, respectively. Plot types were considered to be fixed effects, and replications were assumed to be random. If plot type effects were significant at $p=0.05$, then a Tukey's w-procedure test (Steel and Torrie, 1960) was conducted for mean separation.

If significant differences occurred among plot types within a group, the hypothesis of a linear relationship between plot yield and the proportion of the best clone of the binary clone group in a replacement series (Table 2) was tested also. The replacement series has been used extensively in competition studies (Hill, 1974; Harper, 1977). If the regression is linear, then intermediate yields can be predicted using the pure plot yields. A variable (PROP) was created, for each of the four plot types within each group, in which the replacement series proportion was coded as 1.00, 0.75, 0.25, or 0.00 (Table 2). This variable referred to the proportion of the most productive clone of the pair, so that the regression coefficients were usually positive.

Regression lines (yield regressed on clone proportion) were compared for coincidence between the two sites, neglecting replication effects in the model. This test was conducted for each of the seven groups only for TVOL4. The full model included a dummy variable for site while the reduced model did not include a site effect (Neter and Wasserman, 1974). The F-statistic included 2 and 28 degrees of freedom, and significance was tested at $p=0.05$. There was a significant difference in regression equations between the two sites for all the seven groups. Then, a similar test was conducted, by site and clone group, for coincidence in regression equations among the four replications. The full model included replication effects while the reduced model did not. The F-statistic had 6 and 8 degrees of freedom and was tested for significance at $p=0.05$. The regression equations for the four replications per site were not significantly different at either site for any of the groups.

Based on these results, separate regression equations were calculated at each site in which total plot volume was regressed against clone proportion (PROP). This regression was calculated for plot volume at ages two, three, or four (TVOL2, TVOL3, or TVOL4) as the dependent variable. A stepwise regression approach (Neter and Wasserman, 1974) was used to select the best model by testing PROP, $PROP^2$, and $PROP^3$ as possible independent variables in the model.

In order to better understand the results of mixing effects, observed values for the mixture plots were compared to predicted values. The predicted values were based on an additive model in which the predicted values were weighted averages of the pure clone plots.

$$TVOL_{75A:25B} = (.75 \times TVOL_A) + (.25 \times TVOL_B) \quad (2)$$

$$TVOL_{25A:75B} = (.25 \times TVOL_A) + (.75 \times TVOL_B) \quad (3)$$

where, $TVOL_{75A:25B}$ predicted volume of plot with mixture of 75% clone A and 25% clone B; $TVOL_{25A:75B}$ predicted volume of plot with mixture of 25% clone A and 75% clone B; $TVOL_A$, actual volume of plot with 100% clone A; $TVOL_B$, actual volume of plot with 100% clone B.

The ratio of observed to predicted plot volume provided a measure of departure from linearity. Values greater than 1.0 indicated overyielding mixtures, and values less than 1.0 indicated underyielding mixtures. Values equal to 1.0 indicated complementary mixtures. A Chi-square test was used to test the significance of departure of expected from observed TVOL values at each test site, not of the ratio itself. The actual TVOL values for the four replications per site for each mixture treatment were used in the Chi-square test, which provided three degrees of freedom. Significance was tested at $p=0.05$.

3. Results and discussion

3.1. General

Survival and growth of the tests were good. Survival at age four was 91.1% at site 1 (with a clonal range of 83–94%) and 84.3% at site 2 (with a clonal range of 65–88%). This was facilitated at least partially by initially planting two cuttings per spot with subsequent thinning. Total height averaged 6.97, 10.78, and

13.23 m at ages 2, 3, and 4, respectively. Plot volume averaged 2.86 m^3 at age 4 which would equate to 59.60 m^3ha^{-1}.

Test site 2 was substantially more productive than site 1. By age 4, total height, dbh, and plot volume at site 2 were 13.86 m, 14.92 cm, and 3.25 m^3, respectively, compared to 12.65 m, 12.83 cm, and 2.46 m^3 for site 1.

Differences among clones in pure plots were substantial by age four years. By age 4 in pure plots, clone S7C8 was the tallest (13.79 m, site 1; 14.56 m, site 2), had the greatest dbh (13.83 cm, site 1; 16.00 cm, site 2), and had the greatest plot volume but only at site 1 (3.15 m^3) (Tables 3–6). Clone ST244 had the greatest TVOL4 at site 2 (3.51 m^3). In contrast, also at age 4, clone ST244 was shortest (11.29 m, site 1; 12.94 m, site 2), but clone ST238 had the smallest dbh (11.61 cm, site 1; 13.61 cm, site 2) and smallest plot volume (2.02 m^3, site 1; 2.52 m^3, site 2). Hence, the best pure clone performance, for plot volume, exceeded the worst pure clone performance by 55% and 40% at sites 1 and 2, respectively.

3.2. Analyses of variance

The lack of coincidence between the regression models for the two sites led to the decision to conduct separate analyses of variance by site. General principles were sought due to the complexity of the analysis of variance and mean separation results. Considering all groups, traits, and ages, a significant difference usually occurred among plot types within a group only if the pure plots of the two clones in the respective group were significantly different (Tables 3–6). In only five of the 50 statistically significant cases, a mix was different from one or both of the pure clone plots in its group when the two pure clone plots were statistically the same. Therefore, in general, it appears

Table 3
Significance of plot type effects for eastern cottonwood in mixture groups 1 and 2 analyzed separately by location, for height (HT, m), dbh (DBH, cm), and total plot volume (TVOL, m^3) at ages 2, 3, and 4 years

Location	Trait	Group 1						Group 2					
		PROP[a]						PROP[a]					
		Plot type	Rep	1.00	0.75	0.25	0.00	Plot type	Rep	1.00	0.75	0.25	0.00
1	HT2	**	NS	7.87^{a}	7.40^{a}	6.45^{b}	6.08^{b}	*	NS	7.38^{ab}	7.63^{a}	6.93^{bc}	6.61^{c}
	HT3	**	NS	11.81^{a}	11.30^{a}	9.63^{b}	9.31^{b}	**	NS	11.34^{ab}	11.68^{a}	10.49^{bc}	9.87^{c}
	HT4	**	NS	13.80^{a}	12.76^{ab}	11.62^{bc}	11.29^{c}	NS	*	13.09	13.50	12.45	12.35
	DBH2	**	NS	8.98^{a}	8.45^{ab}	7.15^{bc}	6.91^{c}	**	NS	7.71^{a}	8.18^{a}	6.89^{b}	6.34^{b}
	DBH3	*	NS	12.16^{a}	11.65^{ab}	10.42^{b}	10.52^{b}	**	**	10.89^{ab}	11.52^{a}	10.03^{bc}	9.51^{c}
	DBH4	NS	NS	13.83	13.43	12.51	13.00	**	*	12.82^{ab}	13.53^{a}	12.17^{bc}	11.61^{c}
	TVOL2	**	NS	0.91^{a}	0.81^{ab}	0.58^{bc}	0.51^{c}	**	NS	0.70^{a}	0.71^{a}	0.53^{b}	0.48^{b}
	TVOL3	**	NS	2.16^{a}	1.96^{ab}	1.38^{bc}	1.30^{c}	**	*	1.71^{a}	1.78^{a}	1.27^{b}	1.18^{b}
	TVOL4	**	NS	3.15^{a}	2.82^{ab}	2.24^{b}	2.24^{b}	**	**	2.63^{ab}	2.71^{a}	2.08^{bc}	2.02^{c}
2	HT2	NS	NS	7.32	6.81	6.92	6.57	*	NS	6.89^{ab}	7.16^{a}	6.95^{ab}	6.34^{b}
	HT3	**	*	11.64^{a}	10.93^{b}	10.91^{b}	10.57^{b}	NS	NS	10.99	11.11	11.15	10.23
	HT4	NS	NS	14.56	13.71	13.71	12.94	NS	NS	13.85	13.91	14.36	13.64
	DBH2	NS	NS	8.63	7.89	8.80	8.01	**	NS	7.62^{a}	7.98^{a}	7.50^{a}	6.47^{b}
	DBH3	NS	NS	13.72	13.19	13.74	13.13	**	NS	12.13^{a}	12.41^{a}	11.87^{ab}	11.17^{b}
	DBH4	NS	NS	16.00	15.78	16.03	15.91	NS	NS	14.14	14.49	14.03	13.61
	TVOL2	NS	NS	0.58	0.51	0.70	0.63	**	*	0.62^{a}	0.70^{a}	0.59^{ab}	0.43^{b}
	TVOL3	NS	NS	1.85	1.68	2.15	2.06	**	*	1.86^{a}	2.04^{a}	1.77^{a}	1.36^{b}
	TVOL4	NS	NS	3.02	2.87	3.55	3.51	*	*	3.04^{ab}	3.34^{a}	3.03^{ab}	2.52^{b}

NS: not significantly different at $p=0.05$.
* Significantly different at $p=0.05$.
** Significantly different at $0.05<p\leq0.01$.
Means within a group and trait/age combination (a row) which share the same letter superscript are not significantly different at $p=0.05$.
[a] PROP defined in Table 2.

Table 4
Significance of plot type effects for eastern cottonwood in mixture groups 3 and 4, analyzed separately by location, for height (HT, m), dbh (DBH, cm), and total plot volume (TVOL, m^3) at ages 2, 3, and 4 years

Location	Trait	Group 3						Group 4					
		PROP[a]						PROP[a]					
		Plot type	Rep	1.00	0.75	0.25	0.00	Plot type	Rep	1.00	0.75	0.25	0.00
1	HT2	**	NS	7.06[a]	6.51[ab]	5.79[b]	6.08[b]	NS	NS	7.38	7.64	6.76	6.63
	HT3	*	NS	10.36[a]	9.46[ab]	8.74[b]	9.31[ab]	NS	NS	11.34	11.13	10.30	9.82
	HT4	NS	NS	11.65	11.91	11.04	11.29	NS	NS	13.09	13.55	12.52	12.49
	DBH2	NS	NS	7.89	7.22	6.50	6.91	NS	NS	7.71	8.01	6.96	6.75
	DBH3	NS	NS	11.00	10.55	9.82	10.52	NS	NS	10.89	11.30	9.86	9.88
	DBH4	NS	NS	12.90	12.72	12.25	13.00	NS	NS	12.82	13.19	12.00	11.94
	TVOL2	NS	NS	0.62	0.51	0.48	0.51	NS	NS	0.70	0.75	0.61	0.52
	TVOL3	NS	NS	1.42	1.19	1.15	1.30	NS	NS	1.71	1.76	1.40	1.22
	TVOL4	NS	NS	2.09	2.02	2.05	2.24	NS	NS	2.64	2.77	2.33	2.08
2	HT2	NS	NS	6.88	6.62	6.78	6.57	NS	NS	6.89	6.91	6.46	6.43
	HT3	NS	NS	10.72	10.62	10.82	10.57	NS	NS	10.99	10.88	10.75	10.56
	HT4	NS	NS	13.35	13.20	13.21	12.94	NS	NS	13.84	13.80	14.18	13.68
	DBH2	NS	NS	8.01	7.90	8.57	8.01	NS	NS	7.62	7.84	7.19	7.15
	DBH3	NS	NS	12.87	12.92	13.54	13.13	NS	NS	12.13	12.47	12.12	12.14
	DBH4	*	NS	14.98[b]	15.20[ab]	16.11[a]	15.91[ab]	NS	NS	14.14	14.45	14.64	14.85
	TVOL2	NS	*	0.65	0.57	0.62	0.63	NS	NS	0.62	0.66	0.56	0.50
	TVOL3	NS	*	2.03	1.82	1.96	2.06	NS	NS	1.86	1.99	1.85	1.67
	TVOL4	NS	NS	3.27	3.01	3.26	3.51	NS	NS	3.04	3.26	3.38	3.07

NS: not significantly different at $p=0.05$.
* Significantly different at $p=0.05$.
** Significantly different at $0.05<p\leq 0.01$.
Means within a group and trait/age combination (a row) which share the same letter superscript are not significantly different at $p=0.05$.
[a] PROP defined in Table 2.

that clones must be significantly different in order for their binary mixtures to be also significantly different.

For HT4, significant differences occurred among plot types within a group for only two of the seven groups: group 1 (clones S7C8 and ST244) at site 1 and group 5 (clones S7C1 and ST75) at site 1 only. One explanation for this may be in the fact that clones S7C8 and S7C1 were the tallest and second tallest clones in pure plots while clones ST75 and ST244 ranked sixth and seventh out of seven clones in pure plots. Significant differences occurred between the plot types when the two clones in the group were dissimilar in performance.

Results were less clearcut for DBH4 compared with HT4. Significant differences occurred among plot types within a group for four of the seven groups, but only one of the groups was common with the results for HT4. Groups 2 (clones S7C4 and ST238) at site 1 only, 3 (clones ST75 and ST244) at site 2 only, 6 (clones S7C8 and ST66) at site 2 only, and 7 (clones S7C1 and ST238) at site 1 only showed significant differences among plot types for DBH4 (Tables 3–6). Based on clonal ranking using pure plot performance for either HT4 or DBH4, the clones in either groups 2 or 3 were very close in ranking. It was surprising that clones with no difference in pure plot HT4 performance, as with groups 2, 3, 6, and 7 would have significant DBH4 differences between clones. It is noteworthy that clone ST238 was involved in two of the four pairs of significantly different clones.

The pattern of plot type differences for total plot volume at age four (TVOL4) was somewhat different than either HT4 or DBH4. Significant differences occurred among plot types for groups 1 (clones S7C8 and ST244) at site 1, 2 (clones S7C4 and ST238) at both sites, and 7 (clones S7C1 and ST238) at both sites. In the case of group 1, S7C8 was the tallest clone while ST244 was the shortest

Table 5
Significance of plot type effects for eastern cottonwood in mixture groups 5 and 6, analyzed separately by location, for height (HT, m), dbh. (DBH, cm), and total plot volume (TVOL, m^3) at ages 2, 3, and 4 years

Location	Trait	Group 5						Group 6					
		PROP[a]						PROP[a]					
		Plot type	Rep	1.00	0.75	0.25	0.00	Plot type	Rep	1.00	0.75	0.25	0.00
1	HT2	NS	NS	7.779	7.325	7.106	7.057	*	NS	7.871[a]	7.546[ab]	7.290[ab]	6.631[b]
	HT3	NS	NS	11.726	11.183	10.619	10.357	NS	NS	11.805	11.200	10.923	9.818
	HT4	*	NS	13.637[a]	13.021[ab]	12.074[ab]	11.649[b]	NS	NS	13.792	13.319	13.286	12.486
	DBH2	NS	NS	8.645	8.114	7.803	7.891	**	NS	8.976[a]	8.258[ab]	7.633[ab]	6.754[b]
	DBH3	NS	NS	11.895	11.318	11.001	11.001	*	NS	12.164[a]	11.529[ab]	10.717[ab]	9.876[b]
	DBH4	NS	NS	13.682	13.272	13.065	12.896	NS	NS	13.830	13.428	12.888	11.940
	TVOL2	NS	NS	0.841	0.677	0.639	0.622	**	NS	0.913[a]	0.756[ab]	0.694[ab]	0.521[b]
	TVOL3	NS	NS	2.028	1.643	1.516	1.417	*	NS	2.156[a]	1.807[ab]	1.644[ab]	1.218[b]
	TVOL4	NS	NS	3.015	2.520	2.306	2.087	NS	NS	3.147	2.797	2.729	2.080
2	HT2	NS	NS	7.080	7.221	7.266	6.883	**	NS	7.323[a]	7.117[a]	6.365[b]	6.431[b]
	HT3	NS	NS	11.300	11.691	11.199	10.724	**	*	11.642[a]	11.296[ab]	10.320[c]	10.564[bc]
	HT4	NS	NS	14.025	14.315	14.146	13.349	NS	NS	14.559	14.492	13.244	13.686
	DBH2	NS	NS	7.899	8.139	8.491	8.010	NS	NS	8.625	8.045	7.343	7.153
	DBH3	NS	NS	12.685	12.933	12.970	12.871	**	NS	13.716[a]	12.945[ab]	12.263[b]	12.138[b]
	DBH4	NS	NS	14.769	14.870	15.085	14.984	*	NS	16.002[a]	15.068[a]	14.751[a]	14.855[a]
	TVOL2	NS	NS	0.639	0.741	0.758	0.655	NS	NS	0.583	0.734	0.542	0.502
	TVOL3	NS	NS	2.009	2.385	2.207	2.025	NS	NS	1.852	2.324	1.741	1.671
	TVOL4	NS	NS	3.267	3.750	3.643	3.275	NS	NS	3.022	3.905	3.051	3.072

NS: not significantly different at $p=0.05$.
* Significantly different at $p=0.05$.
** Significantly different at $0.05<p\leq 0.01$.
Means within a group and trait/age combination (a row) which share the same letter superscript are not significantly different at $p=0.05$.
[a] PROP defined in Table 2.

clone, however, clone ST244 had better than average rank among clones for dbh and total plot volume. Clones S7C1 and ST238 in group 7 had widely disparate pure plot ranking for HT4 and DBH4. In group 2, clone S7C4 was average ranked in HT4 but of low rank among the clones for DBH4 while clone ST238 was low rank for all traits.

It was tempting to elicit widely disparate differences in total height and resultant competition for light as the major mechanism behind intergenotypic competition. However, it was obvious from the data that for DBH4 and TVOL4 several other factors were interacting, namely: genotype differences in the height-dbh allometry and site effects.

3.3. Trend analysis

Regression analyses were used to test for a linear relationship between total plot volume at age two (TVOL2), three (TVOL3), or four (TVOL4) and clone proportion in a replacement series with two clones. Stepwise regression with a polynomial model was used to determine the best model for groups 1, 2, 6, and 7, which had demonstrated significant differences among plot types in analysis of variance (Tables 3–6).

As mentioned earlier, a lack of coincidence between the regression models for the two sites occurred, leading to the decision to pursue separate analyses by site. Reasons for the different patterns of pure clonal performance as well as intergenotypic competition between sites can only be hypothesized. Clearly, in the case of some clonal groups, clonal rank for TVOL4 was reversed between sites 1 and 2 (Table 3 and Fig. 1) indicating genotype × environment interaction. In the case of group 1, not only were the clonal ranks for TVOL4 reversed but also the pattern of mixture performance was reversed (Table 3 and

Table 6
Significance of plot type effects for eastern cottonwood in mixture group 7 analyzed separately by location, for height (HT, m), dbh (DBH, cm), and total plot volume (TVOL, m^3) at ages 2, 3, and 4 years

Location	Trait	PROP[a]					
		Plot type	Rep	1.00	0.75	0.25	0.00
1	HT2	**	NS	7.78[a]	7.32[a]	7.25[ab]	6.61[b]
	HT3	**	**	11.73[a]	10.75[b]	11.05[ab]	9.87[c]
	HT4	NS	NS	13.64	12.75	13.15	12.35
	DBH2	**	NS	8.65[a]	7.80[ab]	7.37[b]	6.34[c]
	DBH3	**	*	11.90[a]	10.84[ab]	10.68[bc]	9.51[c]
	DBH4	**	NS	13.68[a]	12.43[ab]	12.82[ab]	11.61[b]
	TVOL2	**	**	0.84[a]	0.73[ab]	0.61[bc]	0.49[c]
	TVOL3	**	**	2.03[a]	1.69[ab]	1.53[b]	1.17[c]
	TVOL4	**	*	3.01[a]	2.50[ab]	2.48[ab]	2.02[b]
2	HT2	NS	NS	7.08	7.11	6.75	6.34
	HT3	*	NS	11.30[a]	11.29[a]	11.07[ab]	10.23[b]
	HT4	NS	NS	14.03	14.21	14.29	13.64
	DBH2	*	NS	7.90[a]	7.85[a]	7.14[ab]	6.47[b]
	DBH3	*	NS	12.69[a]	12.35[a]	11.85[ab]	11.17[b]
	DBH4	NS	NS	14.77	14.35	14.21	13.61
	TVOL2	*	NS	0.64[a]	0.66[a]	0.57[ab]	0.43[b]
	TVOL3	**	NS	2.01[a]	2.01[a]	1.86[ab]	1.36[b]
	TVOL4	*	NS	3.27[ab]	3.29[a]	3.28[ab]	2.52[a]

NS: not significantly different at $p=0.05$.
* Significantly different at $p=0.05$.
** Significantly different at $0.05<p\leq0.01$.
Means within a group and trait/age combination (a row) which share the same letter superscript are not significantly different at $p=0.05$.
[a] PROP defined in Table 2.

Fig. 1). Results with agronomic crop species have indicated that competitive ability can vary dramatically with the level of soil fertility (Sakai, 1961). Major differences in climatic factors (e.g., length of growing season, average winter low temperatures, rainfall pattern) may also have caused resulting shifts in phenology of the various clones.

For group 1, clone proportion (PROP) explained a significant amount of the variation in TVOL2, TVOL3, and TVOL4 at site 1 only. Furthermore, the relationship between TVOL and PROP was linear at ages two and three, with R^2 values of 0.79 and 0.69, respectively (Table 7). At age four, only $PROP^2$ was significant with an R^2 of 0.63.

With group 2, clone proportion again displayed a significant linear relationship with TVOL2, TVOL3, or TVOL4 at site 1 with R^2 values of 0.57, 0.56, and 0.37, respectively (Table 7). At site 2, the best model included both PROP and $PROP^2$ as significant independent variables with R^2 of the model of 0.50 and 0.52 for TVOL2 and TVOL3, respectively. None of the tested models were significant for TVOL4 at site 2.

Regression results for group 6 were significant for site 1 only. In this case, PROP referred to the proportion of clone S7C8 in a replacement series with clone ST66 (Fig. 1). Clone proportion (PROP) again was significant, indicating a linear relationship with R^2 values of 0.62, 0.52, and 0.35 for TVOL2, TVOL3, and TVOL4, respectively (Table 7). None of the tested models were significant at site 2.

With group 7, the regression relationship was linear and significant for TVOL2, TVOL3, and TVOL4 at both sites (Table 7 and Fig. 1). The R^2 values for TVOL2, TVOL3, and TVOL4 were 0.71, 0.60, and 0.42, respectively at site 1 and 0.41, 0.42, and 0.30, respectively at site 2. Note that the significance level of $p=0.06$ for TVOL4 at site 2 was slightly lower than for the rest of the models, yet it was accepted as statistically significant in this case because of its

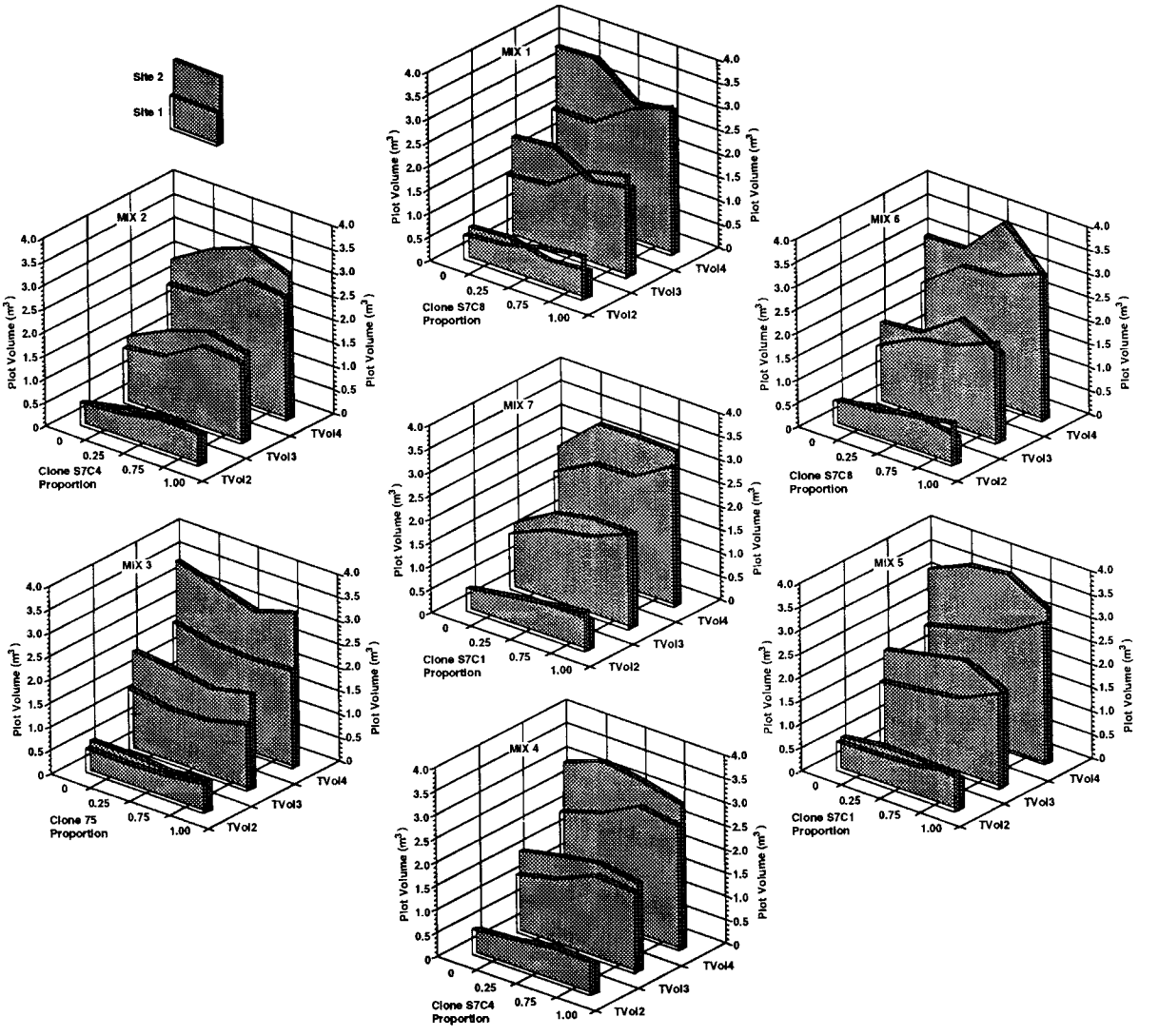

Fig. 1. Total plot volume at ages 2 (TVOL2), 3 (TVOL3), and 4 (TVOL4) as a function of proportion of the best clone in a replacement series study of eastern cottonwood clones planted at 2 sites. There are 7 groups (mixes) of pairs of clones.

closeness to the 0.05 level and the complete pattern which it signifies.

Similarities were apparent from these results. When the regression model was significant, the independent variable was usually PROP rather than $PROP^2$ or $PROP^3$ which indicated that the relationship was generally linear. There were a few exceptions to this trend with $PROP^2$ replacing PROP once and augmenting PROP in two cases. These results indicate that when significant differences occurred among plot types in a two-clone replacement series with cottonwood that the mixture plot yields were intermediate to the two pure clone plot yields, and the expected mixture plot yields could be predicted with a reasonable accuracy. A note of caution must be given in that this generalization was site specific for some of the clone groups and that the strength of the relationship decreased somewhat from ages two to four (note the declining R^2 values). Tuskan and van Buijtenen (1986) found that the response of a family of loblolly pine to

Table 7
Regression of total plot volume of eastern cottonwood clones at ages 2 (TVOL2), 3 (TVOL3), or 4 (TVOL4) on clonal proportion (PROP) in a replacement series with groups 1, 2, 6, and 7 of binary clone mixtures

Group	Parameter	TVOL2		TVOL3		TVOL4	
		Site		Site		Site	
		1	2	1	2	1	2
1	b_0	0.495^{**}		1.241^{**}		2.222^{**}	
	b_1	0.415^{**}		0.917^{**}		0.955^{**}	
	Variable	$PROP^{**}$	NS	$PROP^{**}$	NS	$PROP^{2**}$	NS
	R^2	0.79		0.69		0.63	
2	b_0	0.488^{**}	0.424^{**}	1.170^{**}	1.354^{**}	1.994^{**}	
	b_1	0.240^{**}	0.845^{*}	0.629^{**}	2.078^{*}	0.742^{*}	
	Variable	$PROP^{**}$	$PROP^{*}$	$PROP^{**}$	$PROP^{*}$	$PROP^{*}$	NS
	b_2		-0.645^{*}		-1.565		
	Variable		$PROP^2$		$PROP^{2*}$		
	R^2	0.57	0.50	0.56	0.52	0.37	
6	b_0	0.552^{**}		1.298^{**}		2.248^{**}	
	b_1	0.338^{**}		0.815^{**}		0.881^{*}	
	Variable	$PROP^{**}$	NS	$PROP^{**}$	NS	$PROP^{*}$	NS
	R^2	0.62		0.52		0.35	
7	b_0	0.507^{**}	0.470^{**}	1.234^{**}	1.517^{**}	2.105^{**}	2.786^{**}
	b_1	0.324^{**}	0.206^{**}	0.743^{**}	0.582	0.800^{**}	0.605^{1}
	Variable	$PROP^{**}$	$PROP^{**}$	$PROP^{**}$	$PROP^{**}$	$PROP^{**}$	$PROP^{1}$
	R^2	0.71	0.41	0.60	0.42	0.42	0.30

NS: not significantly different at $p=0.05$.
[1] Significantly different at $p=0.06$.
[*] Significantly different at $p=0.05$.
[**] Significantly different at $0.05<p\leq 0.01$.
The variable PROP is explained in Table 2.

average competitor values was non-linear rather than linear, hence, mixture plot yield was specific to each family x competition combination.

The ratio of observed to expected total plot yield at age four (TVOL4) provided another method to understand intergenotypic competition. A Chi-square statistic was calculated to help judge the statistical significance of the observed departure from the expected value assuming a linear function. About half of the observed values departed significantly from expected at site 1 (Table 8). Slightly more than half of the ratios were less than 1.0 for site 1 indicating a tendency for the mixtures to underyield, however, the opposite pattern occurred at site 2. The largest example of overyielding at site 1 (ratio=1.16) occurred when 75% clone ST66 was mixed with 25% clone S7C8 (Table 8). The yield of this mixture was still intermediate between the two pure clone yields. The second largest example of overyielding (ratio=1.11) resulted from mixing 25% clone ST66 with 75% clone S7C4 (Table 8). In this case, this mixture actually overyielded (TVOL4=2.77 m^3) the best clone's (S7C4) pure plot yield (TVOL4=2.64 m^3). In general the ratios indicated mixture yields within 10% of the predicted values based on an assumption of a linear (additive) relationship between the total plot yield of mixtures and the relative proportion of the best clone.

For some reason, the mixtures at site 2 tended to overyield their expected values (Table 8). In fact, this occurred in 11 of the 14 cases. The largest total plot yield in the entire study was at site 2 with a mixture of 75% clone S7C8 and 25% of clone ST66 (TVOL4=3.91 m^3) compared with the best clone, in the group, yield (TVOL4=3.07 m^3). This mixture represented an increase of 27% yield over the best pure clone. The reasons for the generally non-linear pattern of mixture yield at site 2 compared with site 1 are unknown. One possible explanation is that site 2 is

Table 8
Ratio of observed to expected plot volume yield at age four (TVOL4) for pure cottonwood clones (on diagonals) and binary mixtures at two ratios (75% clone A:25% clone B and vice versa) at two locations (location 1 above diagonal and location 2 below diagonal)

Clone B	Clone A						
	ST244	S7C1	S7C4	S7C8	ST75	ST238	ST66
				0.97^{aNS}	0.95^{NS}		
ST244	1.00			0.91^{bNS}	0.93^{*}		
					0.99^{*}	1.09^{*}	
S7C1		1.00			0.91^{*}	0.90^{NS}	
						0.96^{NS}	1.01^{*}
S7C4			1.00			1.09^{NS}	1.11^{*}
	1.05^{NS}						1.16^{*}
S7C8	0.91^{*}			1.00			0.97^{*}
	0.94^{*}	1.15^{*}					
ST75	0.90^{NS}	1.11^{*}			1.00		
		1.07^{*}	1.15^{*}				
ST238		1.21^{*}	1.14^{*}			1.00	
			1.07^{*}	1.29^{*}			
ST66			1.10^{*}	1.00^{NS}			1.00

[a] Plot type for 75% clone A: 25% clone B.
[b] Plot type for 25% clone A: 75% clone B.
[NS] Not significantly different at $p=0.05$.
[*] Significantly different at $p \leq 0.05$.

located considerably north of the original location of the seven clones (Table 1). There is some reordering of the clone ranks between the two sites for dbh and total plot yield based on pure clone plot values, yet the ranks for height were identical. Furthermore, the average yield at site 2 was substantially greater than site 1, yet both sites are considered to be good cottonwood sites. So if the mixture behavior at site 2 was some type of adaptation phenomenon, it did not harm the overall yield. The average survival of clone S7C8 was lower at site 2 (65.3%) than at site 1 (94.4%), which supports the hypothesis of some type of adaptation phenomenon.

4. Conclusion

Yield of stands of eastern cottonwood clones can be affected by intergenotypic competition. The type and level of response to mixing clones depended on the specific genotypes involved and the planting site. There was some tendency for clones which differed substantially in their growth and yield to offer the most predictable opportunity for over- or underyielding when in mixture. The yield of clones of more similar growth and yield occasionally differed significantly from expected in an additive model, but reasons for this behavior were not apparent. When significant differences do occur between pure clone yields and the yields of their binary mixtures, the response is often a linear function of the proportion of the best clone. Overyielding of mixtures is demonstrated in the current study, with additional yields of up to 29% of the mixture over its expected yield and 27% of the mixture over the best clone's pure plot yield. Traits such as crown architecture and root system architecture must be assessed in an attempt to enhance the predictability of response to mixing. Strong efforts must be made to integrate results from this study and other similar studies into growth and yield models. It will be impossible to establish experiments with all available clones in all possible combinations, therefore, models must be constructed which can be used to predict mixture yields from pure clone plot information. Additional studies of this type (replacement series) must be established in the field in order to provide the information needed to build the growth and yield models.

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