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Abstract: Two-year periodic basal area increments (PBAI) of short-rotation *Populus* stands were followed through a 6-year rotation in monoclonal plots at three sites to assess variation in response patterns among 20 *Populus trichocarpa* Torr. & Gray × *Populus deltoides* Bartr. clones. Data were analyzed using a split-plot model for repeated measurements with the main effect of time and the time × clone interaction partitioned into their linear and quadratic orthogonal components. The form of the mean clone growth response was mainly quadratic with PBAI culminating during the second period at 145–160% of the rotation mean. Increments fell to 95–116% of the rotation mean during the following period. Response variation occurred mainly in the degree of linearity at two sites with clones varying in the rate of growth deceleration during the third period, while quadratic response variation was of prime importance at the third site. Changes in basal area levels among the topmost clones over the last stage of stand development were associated with the divergence in the linear and quadratic responses. Selection on the basis of interaction contrasts of periodic growth from monoclonal plot trials is discussed in terms of sustaining yield improvements and maintaining adaptation to short rotation strategies.

Résumé : L'auteur a étudié l'accroissement périodique en surface terrière (PBAI) de peuplements de *Populus* sur courtes révolutions afin de mesurer les différences de réponse parmi 20 clones de *Populus trichocarpa* Torr. & Gray × *Populus deltoides* Bartr. Les mesures furent prises à intervalles de 2 ans pendant une révolution de 6 ans. Les peuplements ont été établis sur trois sites et ils étaient constitués de parcelles monoclonales. Les données ont été analysées selon un modèle en tiroirs pour mesures répétées avec le temps comme effet principal et l'interaction temps × clone décomposée en ses composantes orthogonales linéaires et quadratiques. La réponse exprimée via la croissance moyenne des clones était principalement quadratique et la PBAI atteignait son maximum durant la seconde période avec des valeurs correspondant à 145–160% de la moyenne de l'ensemble de la révolution. Durant la période suivante, les augmentations ont chuté à 95–116% de la moyenne de l'ensemble de la révolution. Pour deux des sites, la variation de réponse se situait principalement dans le degré de linéarité, les clones démontrant des différences dans le taux de diminution de la croissance durant la troisième période. Pour le troisième site, la variation de réponse était principalement quadratique. Durant le dernier stade de développement des peuplements, les variations en surface terrière parmi les meilleurs clones étaient liées à l'écart entre les réponses linéaires et quadratiques. L'auteur discute de la sélection sur la base des contrastes d'interaction de la croissance périodique mesurée à partir de dispositifs à parcelles monoclonales, dans un contexte de maintien des améliorations en rendement et de maintien de l'adaptation lors de la mise en oeuvre de stratégies sur courtes révolutions.

[Traduit par la Rédaction]

Introduction

Short-rotation farming of hybrid poplar (*Populus*) has become well established in the Pacific Northwest within the last 15 years as part of the pulp and paper industry's hardwood fiber supply strategy. Over 20 000 ha are now being managed for the production of wood chips using highly developed genotypes grown in monoclonal blocks, density levels of 1500–2200 stems/ha, and 5- to 7-year rotations. DeBell et al. (1996) have described three stages of monoclonal *Populus* stand development in which growth rates rapidly accelerate with increasing biomass accumula-

tion to a maximum rate of relatively short duration, before a decline phase is entered when growth rates decrease under increasing crop competition. The key management objectives are to secure the acceleration phase by intensive cultivation and increases in plantation density within limits imposed by piece-size constraints and to harvest shortly after growth culmination before precipitous declines in periodic growth (Hall 1994).

The potential for ongoing genetic improvement has given rise to several controlled hybridization and clonal selection programs designed to increase yields as well as to maintain resistance to pathogens and wind throw (Stettler et al. 1988; Newcombe et al. 1994; Stanton 1995; Newcombe and Bradshaw 1996; Harrington and DeBell 1996; Newcombe and van Oosten 1997; Newcombe 2000). Preliminary clonal field trials accommodate large test populations by using close spacing and small plots that together promote intergenotypic competition and exaggerate clonal growth differences (Heilman and Stettler 1985; Ceulemans et al. 1992;

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DeBell and Harrington 1997). Culling in such early stage trials typically allows for a reliable identification of truncated portions of the test population by midrotation (Mohn and Randall 1971; Foster 1986; Brown et al. 1996). The concluding test stage is, by contrast, composed of a limited number of a highly refined set of clones planted in monoclonal plots where intracolon competition replaces intergenotypic interactions with a concomitant shift in selection emphasis from truncated populations to individual genotypes. How clone performance adjusts to this change in the nature of plot competition is not well understood but is recognized as one of the more important areas of research in *Populus* clonal improvement (Riemenschneider et al. 1996). Specifically, the schedule of evaluating monoclonal-plot yield trials and the timing of final selections could be affected if the clone response to the onset of intracolon crop competition differs in significant ways.

The present study investigated variation in the response of periodic basal area increment (PBAI) to three successive 2-year periods of stand development among 20 clones grown in monoclonal plots at three sites throughout a 6-year rotation during which periodic growth culminated. Basal area increment was chosen as the response variable because of its ease of measurement and its high correlation with biomass production. (The working relationship between stem basal area and biomass of 6-year-old hybrid trees is quite strong ($r^2 = 0.98$) and, although clonal differences in wood density and stem form are known, is reasonably consistent among those clones represented in this study (W.R. Schuette, personal communication).) The purpose of the investigation was to determine the linear and nonlinear nature of the PBAI response variation while assessing the impact of variation in each component on changes in clone rankings in cumulative basal area (CBA) during stand development.

Materials and methods

Two populations of several hundred hybrid poplar seedlings were bred at the University of Washington in 1980–1984. Each was composed of controlled-pollinated offspring of selected phenotypes of black cottonwood (*Populus trichocarpa* Torr. & Gray) from western Washington and British Columbia crossed with selected clones of eastern cottonwood (*Populus deltoides* Bartr.) from Texas, Mississippi, and southern Illinois in 1980 and 1981 or, in 1984, using *P. deltoides* clones from Oklahoma and Mississippi. Seedling nursery selections from each of the *P. trichocarpa* × *P. deltoides* hybrid populations were tested as clones in two separate primary field trials established in 1983 and 1986 on the lower Columbia River floodplain at Westport, Oreg. (46°08'N, 123°22'W). The soil is deep, moderately well drained with a loam – silt loam surface overlying a sandy loam to fine sand horizon. Both trials were established using 30- to 35-cm hardwood cuttings, 1.83 × 1.83 m spacing, and a completely randomized design in which each clone was represented by six single-ramet plot replicates.

Twenty clones, 13 from the 1983 trial and 7 from the 1986 trial, were selected at age 2 for continued testing using independent culling levels established for resistance to *Venturia* shoot blight, *Septoria* leaf spot, and *Melampsora* leaf rust; stem height and diameter; crown width; and earliness of spring growth initiation. There were no full-sib, but several half-sib, relationships within each group (Table 1). All selections were established in nursery beds in 1985 (1983 trial selections) or 1988 (1986 trial selections)

Table 1. Pedigrees of hybrid poplar clones included in 1989 secondary yield trials.

Clone	Female parent (<i>P. trichocarpa</i>) ^a	Male parent (<i>P. deltoides</i>) ^b
1983 trial selections		
11-5	WASH 67	MISS mix
11-11	WASH 67	MISS mix
15-26	CHI 80-1	ST1
19-61	CHI 80-2	ST66
23-91	MON 80-1	ST70
24-305	MON 80-2	ST1
46-158	ORT 80-1	S7C4
47-174	ORT 80-1	MO-243
49-177	ORT 81-3	S7C1
50-179	GF 93-968	IL-005
52-225	GF 93-968	IL-101
55-260	GF 93-968	S7C4
58-282	GF 93-972	IL-129
1986 trial selections		
184-402	RAN 91-568	OK 17-10
194-525	IFA 94-572	OK 17-10
195-529	IFA 94-572	OK 21-7
196-553	IFA 94-572	110804
198-567	HOH 95-875	110120
199-574	HOH 95-875	OK 1
200-604	HOH 95-876	OK 17-10

^aAll female *P. trichocarpa* parents originate from provenances in western Washington with the exception of British Columbia selections CHI 80-1 and CHI 80-2.

^b*Populus deltoides* parents originate from provenances in Mississippi (ST1, ST66, ST70, 110120, 110804, MISS mix); Texas (S7C1, S7C4), southern Illinois (IL-005, IL-101, IL-129, MO-243), and Oklahoma (OK1, OK 17-10, OK 21-7).

from which 30-cm hardwood cuttings were collected for the establishment of secondary yield trials in 1989. (Whereas cuttings of selections from the 1983 trial were taken from beds coppiced three times while cuttings of selections from the 1986 trial were produced from 1-year-old planted beds, there were slight differences in cutting caliper between the two sources that were otherwise quite similar.) Cuttings were collected in January and stored at -2°C until planted in April.

The 20 clones were installed in yield trials within fiber-production plantations at three floodplain sites near Scappoose, Oreg. (45°46'N, 122°53'W); Woodland, Wash. (45°54'N, 122°45'W); and Cathlamet, Wash. (46°12'N, 123°53'W). All are protected from river flooding and had been hayed or pastured prior to conversion to *Populus* culture. The soils are deep, somewhat poorly drained, common floodplain types in which a silt loam surface overlays a silt clay loam stratum. Annual precipitation, the foremost climatic parameter that distinguishes the three sites, averages 1129, 1576, and 2034 mm at Scappoose, Woodland, and Cathlamet, respectively. The mean maximum temperature during the April–September growing season is 24°C at Scappoose, 22°C at Woodland, and 20°C at Cathlamet.

Cuttings were stuck by hand into bedded rows 30 cm wide and 20 cm deep, to an approximate depth of 25 cm so that only the uppermost axillary bud was exposed. The three trials were managed with clean cultivation and protection from deer browsing during the 2-year establishment period. (Crown closure was completed during either the latter part of the second growing season or the early part of the third season for all clones at all sites.) Each site's

yield trial incorporated three randomized complete blocks within which each clone was represented by one 49-ramet (7 trees \times 7 trees) mono-clonal plot. Spacing was 3.05 \times 1.52 m. (Previous density trials had determined that recoverable wood fiber from a 6-year rotation is close to optimum at this spacing, during which time periodic basal area increment culminates during the third and fourth years.¹)

Plot CBA values were determined after the second, fourth, and sixth years by measurement of the breast-height diameter of each live stem within the interior 25-ramet plot. Data were then expressed as 2-year PBAI and analyzed by site using the following split-plot model (Steel and Torrie 1960; Snedecor and Cochran 1980) for repeated measurements combining the data from the three growth periods ending at ages 2, 4, and 6:

$$[1] \quad Y_{ijk} = \mu + b_i + c_j + bc_{(ij)} + t_k + tb_{(ki)} + tc_{(kj)} + tbc_{(kij)}$$

where Y_{ijk} is the PBAI of the j th clone during the k th 2-year time period measured in the i th block, b_i is the random effect of the i th block (1–3), c_j is the fixed effect of the j th clone (1–20), $bc_{(ij)}$ is the interaction of the i th block with the j th clone (whole-plot error a), t_k is the random effect of the k th time period (1–3), $tb_{(ki)}$ is the interaction of the k th time period with the i th block, $tc_{(kj)}$ is the interaction of the k th time period with the j th clone, and $tbc_{(kij)}$ is the interaction of the k th time period with the i th block and the j th clone (subplot error b). (Prior to the combined analyses, error variances were tested for heterogeneity among the three time periods using Bartlett's chi-square procedure. Chi-square statistics, each nonsignificant at $P < 0.05$, were $\chi^2 = 0.358$, 0.527, and 1.031, $df = 2$, for the Cathlamet, Scappoose, and Woodland data sets, respectively.)

The three sources of variation involving time (its main effect, its two first-order interactions (time \times block and time \times clone), and its second-order interaction (time \times block \times clone)) were each partitioned into their linear and quadratic orthogonal components. The form of the mean PBAI growth response of the 20-clone population was determined by testing the significance of the linear and quadratic components of the main effect of time against the same component of the time \times block interaction as recommended by Rowell and Walters (1976) and Gumpertz and Brownie (1993). To detect departures from the mean response, the significance of the two time \times clone interaction components was tested using the matching component of the second-order interaction. Linear and quadratic orthogonal contrasts of the difference between clonal PBAIs and each time period's mean increment were then computed to determine individual linear and nonlinear deviations from the mean growth response (i.e., interaction contrasts) following the approach of Hill and Baylor (1983). These were inspected for patterns of growth-response variation and then associated with age-related changes in clone CBA performance.

Lastly, plot CBA data were submitted to a combined-site analysis to discern the sensitivity of clone rankings to a change in site using the following model:

$$[2] \quad Y_{ijl} = \mu + s_l + b_{i(l)} + c_j + sc_{ij} + bc_{ij(l)}$$

where Y_{ijl} is the age-6 plot CBA of the j th clone in the i th block at the l th site, s_l is the random effect of the l th site (1–3), $b_{i(l)}$ is the random effect of the i th block (1–3) at the l th site, c_j is the fixed effect of the j th clone (1–20), sc_{ij} is the interaction of the l th site with the j th clone, and $bc_{ij(l)}$ is the interaction of the j th clone with the i th block at the l th site (pooled experimental error). (The χ^2 test for heterogeneity of error variance among the three sites was not significant at $P < 0.05$, $\chi^2 = 2.55$, $df = 2$.)

Results and discussion

Cumulative plot basal area following 6 years averaged 0.309 m²/plot for all 20 clones at both Cathlamet and Woodland. The standard error of the clone means was 0.029 m²/plot at Cathlamet and 0.031 m²/plot at Woodland. The range among clones was 0.407–0.223 m²/plot at Cathlamet and 0.395–0.224 m²/plot at Woodland. CBA was 6% higher at Scappoose, averaging 0.329 m²/plot with a standard error of 0.024 m²/plot and a clonal range of 0.398–0.260 m²/plot. The highest CBA means at each site approximate the level (0.406 m²/plot) at which biomass production is maximized by hybrid poplar on the lower Columbia River floodplain (Schuette 1995). Mirroring these site differences in basal area were parallel differences in survival. Survival at age 6 averaged 84% at both Cathlamet and Woodland but 87% at Scappoose where the highest basal area was measured. (Nearly all of the mortality occurred during the first 2 years; that which occurred after the establishment period resulted exclusively from a combination of stem girdling by field voles and windthrow rather than from competition among the test trees.) The range among clones in survival was 67–100% at Cathlamet, 67–99% at Scappoose, and 57–93% at Woodland, each of which coincides with survival rates reported for hybrid poplar mono-clonal test plots (Ceulemans et al. 1992). Covariation among clonal means in CBA and survival at age 6 was consistently but weakly associated (Pearson's correlation coefficient, $r = 0.49$, 0.45, and 0.46 at Cathlamet, Scappoose, and Woodland, respectively, each significant at $P < 0.05$). A stronger association may have been realized if a wider range in survival rates among the clones (e.g., 40–100%) had been observed and if mortality had not been well dispersed throughout the plots (Chambers and Borralho 1997).

Clone CBA means at age 2 were not highly correlated with age-6 means at either Cathlamet or Scappoose ($r = 0.50$ and 0.62, significant at $P < 0.05$ and 0.01, respectively) but were moderately well associated at Woodland ($r = 0.80$, significant at $P < 0.01$). The strength of the correlation improved appreciably, however, when clone means were compared between ages 4 and 6 ($r = 0.91$, 0.88, and 0.96, at Cathlamet, Scappoose, and Woodland, respectively, each significant at $P < 0.01$). These coefficients do not vary among sites (nonsignificant χ^2 test of homogeneity at $P < 0.05$, $\chi^2 = 2.448$, $df = 2$), and their pooled value (0.92) suggests the general efficacy of scheduling mono-clonal plot selections at age four.

Growth during the first 2 years of establishment was relatively modest at Cathlamet and Woodland amounting to 32 and 28% of the respective site's mean periodic increment (Table 2). At Scappoose, the basal area accrual during this time was proportionally greater equaling 59% of the mean increment. Growth accelerated dramatically into the second period with PBAI values amounting to 145–160% of the site's mean increment. Growth then declined in the final period, although it still slightly exceeded the mean increment at Cathlamet and Woodland with PBAI values equaling 108 and 116% of the mean. However, at Scappoose, the final period's PBAI fell below the mean increment measuring

¹ 1984 hybrid poplar spacing trial. Data are on file at Fort James Corp., Camas, Wash.

Table 2. Progression of 2-year periodic basal area increments (PBAI) in the development of short-rotation clonal stands of hybrid poplar at each of three sites.

Site	Stand development period			Mean periodic increment
	First (years 1–2)	Second (years 3–4)	Third (years 5–6)	
Cathlamet	0.033	0.165	0.111	0.103
Scappoose	0.065	0.159	0.105	0.110
Woodland	0.029	0.161	0.119	0.103

Note: Values are square metres per 25-ramet plot (116 m²).

95% of that value. These large periodic differences in growth led to pronounced time effects in the analyses of variance in which PBAI culmination during the second period was described by a growth response in which the quadratic component predominated ($P < 0.001$ – 0.05), accounting for the majority of the time variance at all three sites (Table 3). Variance due to the linear portion of the time response, while consistently less than its quadratic counterpart, was nonetheless important at Scappoose ($P < 0.05$) and Woodland ($P < 0.025$).

Individual clone growth responses did not deviate qualitatively from the population mean response to the extent that PBAI culminated during the second period in all 20 cases. However, significant quantitative variation ($P < 0.001$ and 0.01) in one or both components of the time \times clone interaction variance was found at each site, although the pattern of variation differed among the sites (Table 3). The response variance was effected mainly through the degree of linearity at Cathlamet and Scappoose, where mean squares associated with the time \times clone (linear) interaction were nearly double those of the time \times clone (quadratic) interaction mean square. (Despite the linear interaction component's prominence, the quadratic component was yet significant at Scappoose.) The trend was reversed at Woodland, however, where the time \times clone (quadratic) interaction mean square was 3.5 times the size of the mean square of its linear interaction counterpart. (The underlying site factors that accounted for the lesser importance of linear interactions at Woodland were not clear. But given that the time (linear) mean square in relation to the time (quadratic) mean square was proportionally larger here than at the other sites, the lack of clone departures from the mean linear response may not be incongruent.) The weightier importance of linear response variations at Cathlamet and Scappoose was also evident in those sites' clone range in linear interaction contrasts, each of which was more than twice as large as the corresponding range at Woodland (Table 4). Conversely, the range among clone quadratic interaction contrasts at Woodland was noticeably wider than those at Cathlamet and Scappoose attesting to the importance of that site's nonlinear variation. Neither the linear nor the quadratic interaction contrasts were associated with clonal survival rates; with the exception of a relatively weak association between the number of surviving trees and quadratic interaction contrasts at Cathlamet ($r = -0.48$, significant at $P < 0.05$), no other significant correlations were observed.

Interpretation of the interaction contrast variation could be made through its association with the distribution of clone

means mainly following the second and final periods of stand development (Table 5). (CBA distributions were not, by comparison, as strongly associated with either interaction component after the first period.) Clones that exhibited positive linear interaction contrasts tended towards elevated CBA means at all sites especially after the final period. Clones 49-177 and 52-225 illustrated this trend with increases in standardized CBA deviations between age 4 and 6 and above-average linear interaction contrasts observed at all three sites (Tables 6–8). Quadratic interaction contrasts, on the other hand, produced the expected inverse association with CBA distributions that was maximized at midrotation (Table 5). Clones 47-174 and 50-179 typified the response showing large negative quadratic interactions at most sites (Tables 6–8). Accordingly both clones were highly placed in age-4 CBA distributions. However, after growth culmination, clones 47-174 and 50-179 in all but one case moved downward in the age-6 distributions mostly showing negative linear contrasts and steeper rates of PBAI growth deceleration by comparison with the more moderate rates of growth reduction of clones 49-177 and 52-225 (Figs. 1–3).

Linear interactions are a measure of a clone's ability to extend a portion of the maximum growth phase into the final phase when basal area increments normally decline under increasing intraclonal crop competition. Variable biomass growth patterns during stand development have been previously reported in *Populus* monoclonal plot trials and linked to varying tolerance of crop competition (Ceulemans et al. 1992; DeBell et al. 1996, 1997; Scarascia-Mugnozza et al. 1997). The present study lacking plot density as an experimental factor cannot, however, discern to what degree the response variation was actually a reflection of adaptations to crowding. Nonetheless, to the extent that linear interaction contrasts represent clonal ability to forestall third-period declines due to increasing crop competition, they are a way to quantify selections that may sustain yield improvements as stand productivity increases approach their limits (DeBell et al. 1997).

Yet, growth response patterns may also have been partially affected by *Melampsora* leaf rust infection. Clones 49-177 and 52-225 show good levels of field resistance to *Melampsora medusae* Thuem. f.sp. *deltoidae* Shain relative to the susceptibility of clones 50-179 and 47-174 (Newcombe et al. 1994) in which the accumulative effects of annual leaf defoliation may have been manifested in below-average performances during the final period of stand development. A similar relationship in which the effect of stem canker on basal area growth rate increases with stand age in hybrid poplar has been reported by Lo et al. (1995).

Finally, the age-6 CBA distribution of clones varied significantly ($P < 0.01$) across the three sites as indicated by the site \times clone interaction term in the combined-site analysis (Table 9). The importance of this interaction should be viewed, however, in context of the overall clone variance, the magnitude of which exceeded by nearly 2.5 times the site \times clone interaction variance. The clones registering the largest rotation basal areas (49-177, 0.387 m²/plot; 52-225, 0.355 m²/plot; 47-174, 0.352 m²/plot; 200-604, 0.350 m²/plot) were individually present in the upper half of the age-6 CBA clone distributions at either two (47-174, 200-604) or all three sites (49-177, 52-225) (Tables 6–8). These clones also represent most

Table 3. Mean squares from analyses of variation in 2-year periodic basal area increments (PBAI) at each of three sites.

Source of variation	df	Cathlamet		Scappoose		Woodland	
		MS	P	MS	P	MS	P
Block	2	0.006 520 12	0.0001	0.002 628 16	0.0001	0.003 859 60	0.0001
Clone	19	0.002 485 56	0.005	0.001 593 14	0.005	0.002 196 62	0.025
Error a	38	0.000 823 33		0.000 563 67		0.000 938 84	
Time	2						
Linear	1	0.182 632 18	0.100	0.047 404 22	0.050	0.243 253 87	0.025
Quadratic	1	0.348 324 37	0.050	0.216 602 89	<0.001	0.302 907 57	0.025
Time × block	4						
Linear	2	0.013 497 66		0.001 387 58		0.004 279 06	
Quadratic	2	0.010 346 56		0.000 170 50		0.003 170 36	
Time × clone	38						
Linear	19	0.001 027 18	0.010	0.000 780 27	0.001	0.000 303 91	>0.250
Quadratic	19	0.000 552 51	>0.250	0.000 403 81	0.001	0.001 068 08	0.001
Error b	76						
Linear	38	0.000 421 71		0.000 141 14		0.000 280 12	
Quadratic	38	0.000 474 05		0.000 117 02		0.000 329 37	

Table 4. Range among clones in contrasts of the linear and quadratic components of the time × clone interaction, compared with each site's mean contrast of the linear and quadratic time response.

Site	Mean linear contrast	Clone range in linear interaction contrast ^a	Mean quadratic contrast	Clone range in quadratic interaction contrast ^a
Cathlamet	0.078	0.050 to -0.038	-0.186	0.054 to -0.079
Scappoose	0.040	0.049 to -0.041	-0.148	0.041 to -0.087
Woodland	0.090	0.021 to -0.020	-0.174	0.101 to -0.081

Note: Values are square metres per 25-ramet plot (116 m²). The linear and quadratic interaction contrasts each average to zero.

^aMinimum and maximum values of the linear or quadratic contrast of the difference between each clone's individual PBAI time response and the mean PBAI time response of the 20-clone population.

Table 5. Pearson coefficients of correlation between individual clone orthogonal estimates of the linear and quadratic contrasts of the time × clone interaction and cumulative plot basal area (CBA) for the three stand development periods at each of three sites.

Site	First period (years 1 and 2)		Second period (years 3 and 4)		Third period (years 5 and 6)	
	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic
Cathlamet	0.03	-0.28	0.52	-0.77	0.82	-0.49
Scappoose	-0.46	-0.21	-0.13	-0.60	0.34	-0.35
Woodland	0.19	-0.64	0.32	-0.89	0.57	-0.75

of the parental *P. deltooides* provenances used in hybridization (Table 1). Both features of first-generation *P. trichocarpa* × *P. deltooides* hybrids, good site adaptability and recruitment from varied parental sources, are generally recognized as key components of successful clonal improvement programs (Stettler et al. 1988; Wu and Stettler 1996).

Conclusion

Despite the reasonably strong phenotypic correlations between plot basal area at ages 4 and 6, variable PBAI re-

sponses over the last stage of stand development were observed that could affect the final selections from yield trials that conclude a multistage testing program. Clones 15-26 at Cathlamet (Table 6), 52-225 at Scappoose (Table 7), and 49-177 at Woodland (Table 8) each improved their performance considerably during the last period, affecting not only the final rank of clones but, more importantly, the actual yield projections that ultimately determine the cost-benefit analysis of the mass propagation and commercial deployment of newly developed selections. Consequently, the choice of individual clones for production purposes should be deferred

Table 6. Upper half of the Cathlamet age-4 CBA distribution.

Clone	CBA ₄	s ₄ ^a	CBA ₆	s ₆ ^b	Linear	Quadratic
184-402	0.239	1.49	0.400	1.83	0.046	-0.020
49-177	0.238	1.45	0.407	1.97	0.050	0.000
199-574	0.232	1.22	0.353	0.88	0.002	-0.032
200-604	0.220	0.79	0.338	0.59	0.006	-0.030
50-179	0.215	0.61	0.305	-0.07	-0.032	-0.020
47-174	0.213	0.56	0.302	-0.13	-0.013	-0.079
24-305	0.212	0.53	0.349	0.81	0.026	-0.004
58-282	0.211	0.47	0.308	-0.01	-0.018	-0.023
15-26	0.210	0.45	0.354	0.91	0.037	-0.007
52-225	0.208	0.35	0.332	0.47	0.016	-0.012

Note: The means of CBA at ages 4 and 6 and orthogonal contrasts of the time × clone interaction were measured in square metres per 25-ramet plot (116 m²).

^aStandardized deviation of age-4 CBA mean, calculated as the difference between clone mean and site mean (0.198 m²/plot) divided by the phenotypic standard deviation among clone age-4 CBA means (0.028 m²/plot).

^bStandardized deviation of age-6 CBA mean, calculated as the difference between clone mean and site mean (0.309 m²/plot) divided by the phenotypic standard deviation among clone age-6 CBA means (0.050 m²/plot).

Table 7. Upper half of the Scappoose age-4 CBA distribution.

Clone	CBA ₄	s ₄ ^a	CBA ₆	s ₆ ^b	Linear	Quadratic
47-174	0.281	2.05	0.393	1.60	0.000	-0.087
50-179	0.264	1.42	0.361	0.80	-0.037	0.003
55-260	0.254	1.06	0.365	0.90	-0.010	-0.004
15-26	0.249	0.91	0.378	1.21	0.015	-0.002
49-177	0.246	0.77	0.373	1.10	0.021	-0.016
11-11	0.239	0.55	0.331	0.05	-0.031	0.010
52-225	0.239	0.53	0.398	1.72	0.049	0.039
195-529	0.231	0.26	0.356	0.68	0.021	0.002
194-525	0.230	0.22	0.342	0.35	0.009	-0.011
46-158	0.230	0.22	0.308	-0.52	-0.026	-0.040

Note: CBA means at ages 4 and 6 and orthogonal contrasts of the time × clone interaction were measured in square metres per 25-ramet plot (116 m²).

^aStandardized deviation of age-4 CBA mean. Calculated as the difference between clone mean and site mean (0.224 m²/plot) divided by the phenotypic standard deviation among clone age-4 CBA means (0.028 m²/plot).

^bStandardized deviation of age-6 CBA mean. Calculated as the difference between clone mean and site mean (0.329 m²/plot) divided by the phenotypic standard deviation among clone age-6 CBA means (0.040 m²/plot).

until completion of a full rotation, especially in view of the sizeable contribution of late-rotation growth rates to harvest stocking levels. This evaluation could also benefit from a direct inspection of interaction contrasts of periodic growth in addition to cumulative plot basal area. Clones characterized by positive linear responses are well suited to the prevalent short-rotation management strategy that through genetic and cultural means seeks to lengthen the maximum growth phase while minimizing the impact of pests and adverse weather events. Clones whose superiority flags after the intermediate stages of stand development could require extended cultivation to mitigate poor performance during the concluding rotation stages. For example, *Venturia populina* (Vuill.) Fabric spring defoliation of moderately susceptible genotypes de-

Table 8. Upper half of the Woodland age-4 CBA distribution.

Clone	CBA ₄	s ₄ ^a	CBA ₆	s ₆ ^b	Linear	Quadratic
200-604	0.251	1.76	0.395	1.85	0.012	-0.056
50-179	0.240	1.45	0.350	0.87	-0.019	-0.081
49-177	0.232	1.22	0.381	1.54	0.017	-0.016
47-174	0.226	1.05	0.362	1.14	0.020	-0.064
195-529	0.210	0.58	0.337	0.60	0.009	-0.035
11-5	0.207	0.49	0.344	0.41	0.017	-0.010
199-574	0.200	0.30	0.304	-0.11	-0.020	-0.022
52-225	0.199	0.28	0.335	0.57	0.015	0.004
11-11	0.198	0.23	0.328	0.41	0.005	0.014
55-260	0.197	0.21	0.321	0.27	0.000	0.004

Note: CBA means at age 4 and 6 and orthogonal contrasts of the time × clone interaction were measured in square metres per 25-ramet plot (116 m²).

^aStandardized deviation of age-4 CBA mean. Calculated as the difference between clone mean and site mean (0.189 m²/plot) divided by the phenotypic standard deviation among clone age-4 CBA means (0.035 m²/plot).

^bStandardized deviation of age-6 CBA mean. Calculated as the difference between clone mean and site mean (0.309 m²/plot) divided by the phenotypic standard deviation among clone age-6 CBA means (0.047 m²/plot).

Fig. 1. Variation among selected clones in PBAI growth response to three 2-year periods of stand development at Cathlamet.

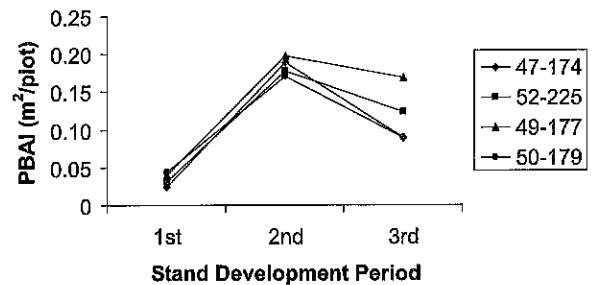


Fig. 2. Variation among selected clones in PBAI growth response to three 2-year periods of stand development at Scappoose.

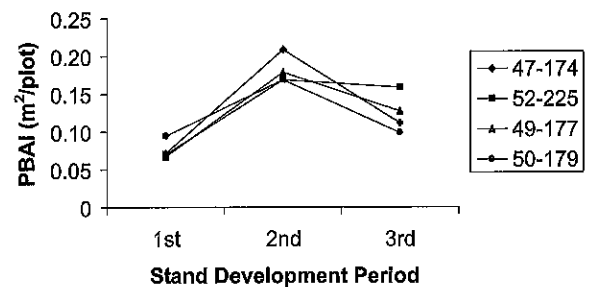


Fig. 3. Variation among selected clones in PBAI growth response to three 2-year periods of stand development at Woodland.

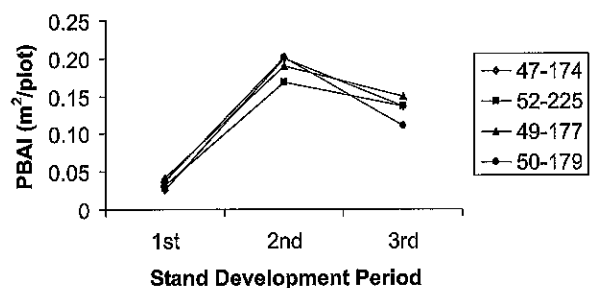


Table 9. Combined analysis of variance in cumulative plot basal area (CBA) at age 6.

Source of variation	df	MS	P
Site	2	0.008 479 95	>0.25
Block(site)	6	0.013 007 87	0.0001
Clone	19	0.010 046 74	0.01
Site × clone	38	0.004 389 60	0.01
Error	114	0.002 325 84	

ployed in monoclonal blocks may not be fully expressed until the late stages of stand development, allowing for greater light penetration, increased weed cover, and an outbreak of stem girdling by field voles, the control of which requires extended mechanical tillage (Newcombe and van Osten 1997). Alternatively, where polyclonal deployment is pursued, interaction contrasts may have utility in choosing clones with complementary growth patterns for compatibility trials that have been proposed to both increase productivity while reducing the risk of pest outbreaks (Libby 1982, 1987).

Time × clone (linear) interactions notwithstanding, it may still be well advised to make anticipatory selections at the conclusion of the second period's acceleration phase to expedite the commercial deployment of those clones that actually exhibit rotation-age superiority. However, doing so would likely require selection intensities that allow for those clones that assert superiority within the rotation's final period. Performance during the establishment period, while not generally correlated closely with growth response pattern or rotation-age performance, is yet not unimportant. Because of the amount of cultivation expended during stand establishment, the rapidity with which selected clones occupy a site is advantageous in that stands quickly grow beyond the browse line and eliminate herbaceous weed competition by shading, thereby obviating costly deer fencing and protracted mechanical weed control. Accordingly, performance during the establishment stage should not be forgotten in selection analyses but perhaps included as a separate but valuable criterion.

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