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Growth and stem quality responses to fertilizer application by 21 loblolly pine clones in the Virginia Piedmont

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ABSTRACT

Clonal forestry offers the opportunity to increase yields, enhance uniformity and improve wood characteristics. Intensive silvicultural practices, including fertilization, will be required to capture the full growth potential of clonal plantations. However, variation in nutrient use efficiency that exists among clones could affect growth responses. Our research objective was to determine the range of growth response and stem form quality due to fertilization in clones of *Pinus taeda*. A split-plot experimental design was used, with the whole plots being two levels of fertilizer application (fertilizer versus control) and the split plot factor being 25 clones. Whole plot treatments were blocked and replicated four times. Six years after planting and five years after fertilizer application, a repeated measures analysis showed fertilizer-by-time and clone-by-time interactions affected volume ($p < 0.10$). Clone-by-fertilizer interactions were observed for tree height, branch traits, and a metric of foliar display. These interactions were primarily due to scale-effect phenomena rather than rank shifts. The magnitude of fertilizer responses observed in a small number of genotypes suggests that knowledge of fertilizer responses in widely deployed genotypes, if developed prior to mid-rotation, may better optimize management of single-clone blocks. Our results further indicate that a range of possibilities exist for the design and application of clone-specific precision silvicultural systems.

1. Introduction

Clonal *Pinus taeda* (L.) plantations are currently limited in their deployment throughout the southeastern United States (Bettinger et al., 2009). However, increased production capabilities and the development of silvicultural systems specific to clonal plantations may result in a greater land area allocated to clonal plantations in the near future (Wright and Dougherty, 2006). One current barrier to the widespread deployment of clonal plantations is the higher cost per seedling versus mass control pollinated or improved open pollinated seedlings (Wright and Dougherty, 2007). In order to offset higher costs at planting, it has been argued that it is necessary to manage clonal plantations with a high level of silvicultural inputs to maximize growth rates and improve product class distribution at harvest (Dougherty, 2007; Wright and Dougherty, 2007). Fertilizer application is among the most commonly prescribed management activities currently in *P. taeda* plantations (Fox et al., 2007a), and likely will be a prescription for many clonal plantations in the future. The objective of this paper was to determine the range of stem growth, stem form, and two generalized growth efficiency metrics response to fertilizer application in a large number of clones. We further sought to ascertain if clone-by-fertilizer interactions for any of these traits occurred, and to determine if their occurrence might be of concern or represent unique opportunities for the management of clonal plantations and the selection of clones for deployment. To better assess implications for clonal selection, we examined clonal repeatability and between-trait clonal mean correlations.

Clones of *P. taeda* have been previously shown to vary significantly in their growth rates (Paul et al., 1997; King et al., 2008). Additionally, variable growth responses to fertilizer application have been observed among a small number of clones (King et al., 2008; Espinoza, 2009; Tyree et al., 2009b). However, we are aware of no information currently available in the literature on clonal fertilizer growth response involving more than eight clones of *P. taeda*. While information on clone-by-fertilizer interactions is currently based on small samples of clones, reports of clone-by-site interactions are inconsistent among trials planted with large numbers (e.g. >100) of clones (Paul et al., 1997; Baltunis et al., 2007). It remains uncertain to what extent genotype-by-environment interactions may play a role in operational clonal plantations, although it is important to note that even if such interactions occur at a low rate, they may remain an issue if they randomly occur in any of the relatively small number of high-performing clones that are selected and deployed over a wide geographic area. While potential genotype-

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by-environment or genotype-by-silviculture interactions clearly represent a challenge for the management of clonal plantations, they may also present a range of management opportunities. For instance, if highly responsive genotypes are identified prior to planting, appropriate silvicultural systems may be implemented to take full advantage of their potential growth responses to treatments (Roth et al., 2007).

Stem form defects such as forks, ramicorns, or sinuosity have previously been observed in *P. taeda* plantations, and have generally been associated with greater levels of silvicultural inputs, particularly fertilizer application, in some genotypes (McKeand et al., 2006; Espinoza, 2009). Forking is a dichotomous branching of the main leader, ramicorns are excessively steeply angled large branches, and sinuosity is a repeated deviation from vertical in the main leader. All are significant form problems that may reduce wood quality and yield at harvest. As with growth, based on a thorough review of the literature we are aware of no published reports on the effects of fertilizer application on stem form defects in a sample of more than six clones. More experiments involving a greater number of clones are required to determine the possible extent and severity of stem form responses to fertilizer application. Branch morphology, including branch diameter, angle, and number, also affects stem quality by determining the size and number of knots. Branch diameter and number have both been shown to increase with fertilizer application in *P. taeda*, although not to an extent that would negatively impact stem quality (Albaugh et al., 2006). In a study of two contrasting clones of *P. taeda*, allocation to branch biomass varied between clones in response to fertilizer application (Tyree et al., 2009a). It is uncertain to what extent branch morphology may vary among a larger number of clones, and how common clone-by-fertilizer interactions may be for branch morphology.

Crown morphology, or the size and spatial distribution of foliage and branches throughout the canopy, is an important determinant of growth efficiency. Crown morphology and growth efficiency, or the amount of stem volume produced per unit foliage, have been shown to vary among different *Pinus* species (Xiao et al., 2003). Among open-pollinated families of *P. taeda* genotypic variability in crown morphology has been observed and correlated to growth (McCrady and Jokela, 1996; Chmura et al., 2007). A trial with 300 clones of *P. taeda* similarly found differences in crown morphology that were related to growth (Emhart et al., 2007). Differences in clonal crown morphology offer the opportunity to select individual clones based both on different growth efficiency and different crown-based ideotypes (Martin et al., 2001; Emhart et al., 2007; Nelson and Johnsen, 2008). In doing so it is important to account for clonal repeatability of traits and to examine between trait correlations. For instance, clones that consistently maintain a narrow-crown with high repeatability could be planted at a low density to maximize growth rates and production of high-quality sawtimber without problems associated with large branches or ramicorns. Further data on potential clone-by-fertilizer interactions in crown morphology are required before such clone-specific silvicultural systems can be successfully applied.

Numerous studies have examined the effects of fertilizer application on crown morphology without accounting for genotypic variability. It is widely accepted that fertilizer application results in an increase in leaf-area at the whole crown scale (Vose and Allen, 1988; Dalla-Tea and Jokela, 1991; Albaugh et al., 1998). Increased leaf area in response to fertilizer application has been shown to result in greater allocation to stem mass (Colbert et al., 1990; Samuelson et al., 2004). However, a number of studies among open-pollinated trees have found little effect of fertilizer application on crown morphology other than increased leaf area (Xiao et al., 2003; Yu et al., 2003; Chmura et al., 2007). Clone-by-fertilizer interactions for crown morphology have been observed in a field trial with a pair of clones with contrasting ideotypes (Tyree et al., 2009b). However, studies examining clone-by-fertilizer interactions among a greater number of clones will be required to better elucidate the extent of these interactions and the range of silvicultural possibilities they may present.

2. Materials and methods

2.1. Site, study, and plant material descriptions

Our study was installed at the Reynolds Homestead Forestry Research Center on a typical site in the upper Piedmont of Patrick County, Virginia, USA (latitude: 36°40′N, longitude: 80°10′W). The site is 320–340 m in elevation with topography consisting of gradually sloping hills. Average annual precipitation is 1300 mm and mean annual temperature is 12.8 °C. Soils located at the site include a Fairview sandy clay loam (fine, kaolinitic, mesic Typic Kanhapludults) and a French loam (fine-loamy over sandy or sandy-skeletal, mixed, active, mesic Fluvaquentic Dystrudepts). Soils generally have a truncated Ap horizon leading directly into a clayey B horizon as a result of extensive erosion due to poor agricultural practices over the last several centuries.

A split-plot experimental design was installed and replicated four times. The whole-plot treatment was control versus fertilizer application. Fertilizer was hand-banded at a rate of 224 kg ha^{-1} of diammonium phosphate and 184 kg ha^{-1} of ammonium nitrate per each application, equivalent to 103 kg ha^{-1} of elemental N and 45 kg ha^{-1} of elemental P per application. Fertilizer was applied on May 4, 2004, May 4, 2006, and July 16, 2008. The sub-plot treatment consisted of 25 clones in single-tree plots, with a single ramet of each clone per plot. Clonal material was donated by the Forest Biology Research Cooperative (Gainsville, Florida, USA). All clones were rooted cuttings from crosses of the Loblolly Pine Lower Gulf Elite Breeding Population that includes Atlantic Coastal Plain and Florida provenances. Further information on the mating design used to produce these clones is available in Kayihan et al. (2005). Clones are labeled by letter according to each cross, and are numbered by genotype within each cross (i.e. B1 and B2 are full-sib to one another but not to A). The site was cleared of competing vegetation with glyphosate (Round Up®), ripped, and the planting rows were shallowly cultivated. Seedlings were hand planted at 3.0-by-2.5 m spacing in May 2003. A border row of open-pollinated seedlings was planted around each plot. Complete weed control was maintained in all plots for the first two years. After the first two years the rows were mowed at least twice per year to control competing vegetation. Prior to root growth between plots, we dug trenches and lined them with plastic between the plots to ensure fertilizer did not contaminate control plots. Further descriptions of this trial are available in King et al. (2008) and Tyree et al. (2008).

2.2. Data collection

Stem height was measured each year in the dormant season. Prior to trees reaching 1.37 m ground-line diameter was measured with calipers. Following the third growing season dbh was measured annually with calipers until the trial was harvested after the sixth growing season. A simple biomass index was calculated for the first year by multiplying height by the square of ground-line diameter. This biomass index was used as a covariate in analyses of stem volumes from years three through six. Stem volume was calculated using empirical equations from Burkhart (1977) for outside the bark volume of plantation grown trees.

Stem form was assessed following the third, fifth, and sixth growing seasons. Each tree was given a binary score for the presence or absence of stem forking and ramicorns. Only forks that were present for at least two previous growing seasons were scored.

The number of ramicorns was not recorded, only their presence or absence. Sinuosity was scored based on a subjective categorical system where a score of one indicated no sinuosity, two indicated sinuosity was evident but not severe, three indicated sinuosity was severe and might still be present at the end of a 20 year rotation, and four indicated that sinuosity was so severe that it would either severely limit growth, or would still be present at the end of a 20 year rotation.

A number of crown metrics were quantified on the same dates stem form was assessed. For a single representative whorl of branches nearest to 1.37 m above ground-line, crown width of an inter-row branch was measured, the number of primary branches was counted, and the angle and basal diameter of the average branch in each whorl was scored on a categorical basis. Crown volume was then calculated as a cone based on crown width and total tree height, since all measurements on this trial were prior to crown closure, and live-crown ratios were all approximately equal to unity. After calibrating the measurer's eye with a protractor on the first several trees, branch angle was visually assessed and assigned to one of four categories numbered one to four for branch angles from horizontal of 0° to 15°, 15° to 30°, 30° to 45°, and greater than 45°, respectively. Branch basal diameter was similarly assigned to one of four categories numbered one through four for branch diameters of 0–0.5 cm, 0.5–1 cm, 1–2 cm, and greater than 2 cm, respectively. The number of flushes in the previous growing season was also tallied.

The winter of 2005–2006 was relatively severe, and included several unusual periods of prolonged subfreezing temperatures, and several precipitation events that resulted in the accumulation of up to 1 cm of ice. These events offered the opportunity to examine the range of response among different genotypes to cold damage. Damage hypothesized to be the result of this unusual cold was observed on the leaders of a number of ramets. Cold damage was scored for all ramets in March 2006 according to a subjective categorical score. A score of 0 was given to trees with no observable damage, 0.5 to trees where only the tips of the needles of the top whorl were minimally affected, 1 to trees where the terminal buds of the top whorl were minimally affected, 2 to trees with the terminal buds of the top two or three whorls and the leader were markedly affected, and 3 to trees with severe dieback of the top. Only one tree was included in the most severe category, so categories two and three were combined for further analysis.

Two different methods were employed in order to assess growth efficiency, or unit stem produced per unit foliage. First, we calculated the stem to crown volume ratio. Assuming that crown volume may be used as an inexact surrogate for leaf area, this ratio can be interpreted as the volume of wood produced per unit foliage. We recognize that this approach is simplistic, and ignores differences in photosynthetic rates, specific leaf area, and foliar display. The second method involved the harvest of a single representative branch from the north side of each tree on January 4, 2006, after the third growing season. Foliage and branches were separated, oven dried, and weighed. Foliar mass was then expressed on a branch mass basis to account for differences in harvested branch size and to better represent crown development (Xiao et al., 2003). These data were then compared with growth in the fourth growing season as another indicator of growth efficiency, where the mass of foliage from a single branch was a surrogate for the total foliar mass of the tree. We recognize that this approach is also simplistic, as the foliar mass from a single branch may not be representative of the entire canopy.

2.3. Statistical analysis

Prior to analysis, all variables were checked for assumptions of normality and heteroscedasticity. Where assumptions were violated variables were power transformed. All means and standard errors presented are of untransformed data. Analyses were performed in SAS Software Version 9.2 (SAS Institute Inc., Cary, North Carolina, USA). All analyses included appropriate error structures for a split-plot experimental design (block and fertilizer-by-block interactions). Repeated measures data was analyzed in PROC MIXED with either an unstructured, compound symmetry, or first-order autoregressive covariance structure selected utilizing information criteria in the output. Some models failed to converge, despite dependent variables having been transformed to normal and checked for outliers. This was likely a result of limited sample size, the inclusion of covariates, and complex model structures. These variables (height, dbh, stem volume) were analyzed in PROC GLM with all appropriate time and time-by-treatment interactions included in the model. Clone was treated as a fixed effect, and first-year covariates of height, ground-line diameter, and biomass index were included in these models.

Variables measured at only one date were analyzed in PROC MIXED, also with clone treated as a fixed effect. Categorical, count, and binary data (sinuosity, ramicorns, forks, cold damage, branch number, branch diameter, branch angle, flush number) were analyzed with PROC LOGISTIC. Problems arose with the analysis of forking, ramicorn, and cold damage data due to the quasi-complete separation (QCS) of data points. QCS occurs when one or more independent variables perfectly predict the dependent variable. QCS in these data resulted from the large number of clones that had dramatically different values for each of these variables (e.g. some clones had no incidence, others high incidence). As a result, no statistics are presented for inference for these three independent variables, only mean and frequency data with interpretations of meaningful differences left to the reader. Regressions described are simple linear models implemented in PROC REG.

Clonal repeatability was assessed for growth and crown traits as described in Eq. (1), where σ_c^2 is the clonal variance, and σ_ε^2 is the residual variance. This was implemented with an ANOVA modeling clone as a random effect. The standard error for repeatability was calculated according to Dickerson's approximation. Between and within trait correlations among clonal means at each annual time step were calculated between and within fertilizer treatments.

$$R^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_\varepsilon^2} \quad (1)$$

3. Results

3.1. Survival

Survival after six growing seasons in this trial was 88% (175 of 200 ramets) across all 25 clones. Most mortality occurred in the first growing season after planting, accounting for 16 of the eventual 25 deaths. Survival was greater than or equal to 75% in 21 of the 25 clones. With the exception of survival data, analyses in the remainder of this paper are based only on these 21 clones. Of the four clones that were excluded from further analyses due to excessive mortality reducing our ability to make statistical inferences, three had survival rates of 63%, while the fourth had a survival rate of only 50%. Mortality in these four clones accounted for 13 of 25 total tree deaths in this trial. All mortality in these four clones occurred in either the first or second growing seasons. For the remaining 21 clones on which analyses were performed, survival after the first growing season was 97% (163 of 168 ramets), which declined to 93% (156 of 168 ramets) by the end of the sixth growing season. No incidence of insect or disease damage was observed in this trial, and mortality was not attributed to any specific cause.

Table 1
p-Values for variables measured on a six-year-old *P. taeda*. Crown volume, crown width, and growth efficiency metrics were analyzed with repeated measures, while foliage per branch mass was only assessed after year 3. Significant *p*-values are shown in bold face.

Variable	Clone	Fertilizer	Clone × fertilizer	Year	Clone × year	Fertilizer × year	Clone × fertilizer × year
Height	**0.00**	**0.08**	**0.09**	**0.00**	**0.00**	**0.00**	0.10
dbh	**0.00**	**0.02**	0.23	**0.00**	**0.00**	0.88	1.00
Stem volume	**0.00**	**0.02**	0.11	**0.00**	**0.00**	**0.05**	0.89
Sinuosity score	**0.00**	0.11	0.99	0.25	1.00	0.49	1.00
Branch number	**0.00**	0.97	0.10	0.71	0.68	**0.02**	0.76
Branch diameter score	**0.00**	0.97	0.53	0.97	0.40	0.99	0.59
Branch angle score	**0.00**	0.99	**0.02**	**0.02**	0.46	0.92	0.80
Flush number	**0.00**	0.14	0.13	**0.00**	**0.00**	0.66	**0.09**
Crown volume	**0.03**	**0.05**	0.18	–	–	–	–
Crown width	**0.04**	**0.04**	**0.06**	–	–	–	–
Stem to crown volume ratio	**0.01**	**0.07**	0.21	–	–	–	–
Foliage per branch mass	**0.00**	0.27	**0.00**	–	–	–	–

3.2. Stem growth

Clones showed a dramatic range of stem growth over time. Height, dbh, and stem volume were all significantly influenced by the clonal main effect and the clone-by-year interaction ($p < 0.01$; Table 1). By the end of the sixth growing season, the smallest clone, clone E, had a mean dbh of 9.2 cm, a mean height of 5.4 m, and a mean stem volume of 11,453 cm^3 (Fig. 1). By contrast, the largest clone based on stem volume, clone I2, had a mean dbh of 13.0 cm, a mean height of 7.3 m, and a mean stem volume of 13,723 cm^3, differences of 41.2%, 35.5%, and 19.8%, respectively, compared to clone E. When the full-sib pairs in the trial were compared, some grew at similar rates. For instance, clones C1 and C2 showed less than 1% difference in dbh and stem volume, and only a 12.4% difference in height. However, other pairs of full-sib clones grew at dramatically different rates from one another. For example, after six growing seasons clone I2 had 30.0% greater mean dbh and 11.8% greater mean stem volume than clone I3 while showing a less than 1% difference in height. Trends among different clones presented in Fig. 1 reflect that clonal differences in stem volume and height increase in absolute magnitude over time.

Averaged across all clones, fertilizer had a small but statistically significant impact on stem growth by the end of the sixth growing season ($p < 0.05$). Height and stem volume showed significant fertilizer-by-time interactions, and dbh showed a significant fertilizer main effect ($p < 0.05$; Table 1). After the sixth growing season, trees in fertilizer plots had a mean dbh 6.1% greater than controls, a mean height 1.4% greater, and a mean stem volume 2.5% greater (Fig. 2). While these differences were small in magnitude averaged across all clones, fertilizer growth response varied among clones

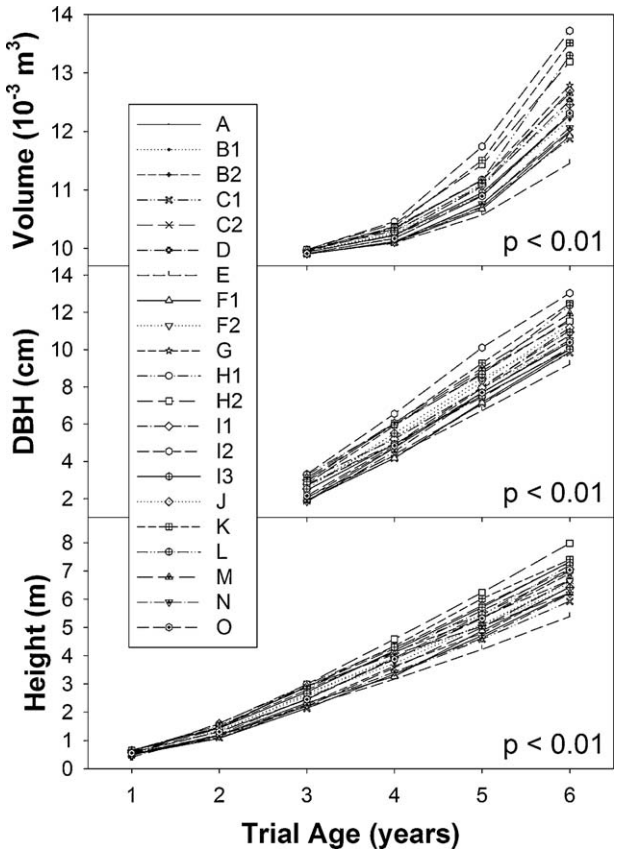

Fig. 1. Mean stem growth of 21 clones of *P. taeda*. Full-sib clones are named with the same letter (e.g. B1, B2). Stem volume was calculated based on the empirical formula found in Burkhart (1977).

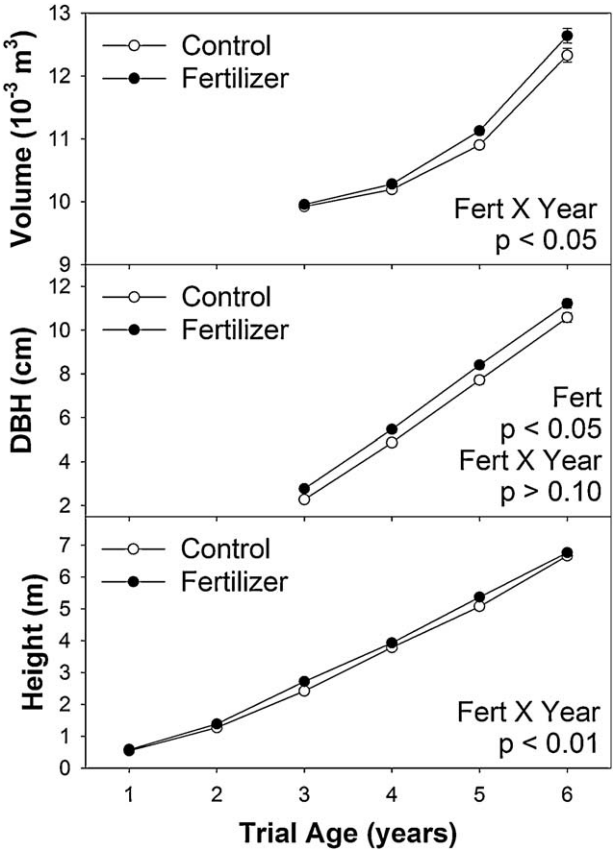

Fig. 2. Stem growth of fertilized and unfertilized ramets averaged across 21 clones of *P. taeda*. Stem volume was calculated based on the empirical formula found in Burkhart (1977). Standard error bars are shown.

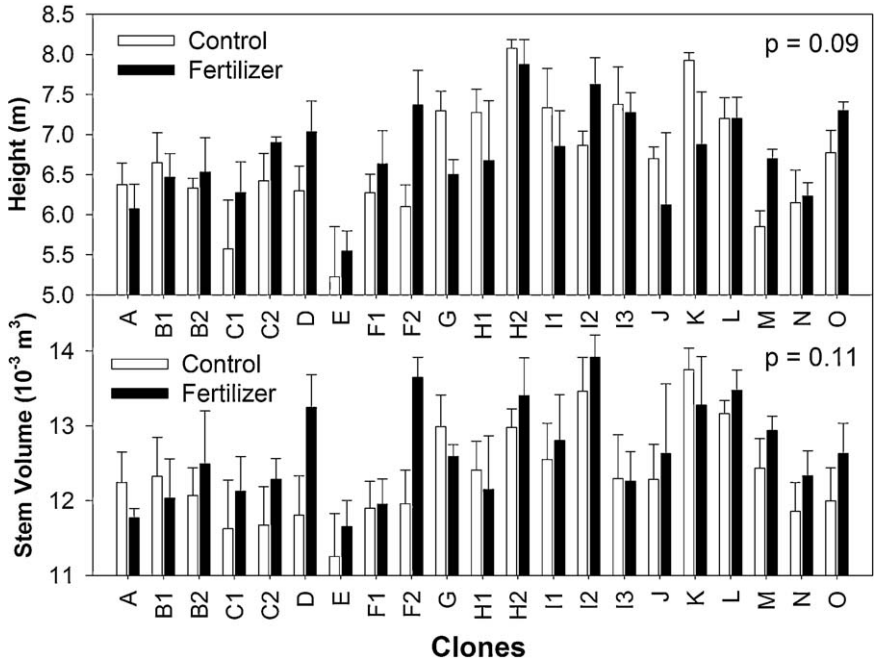

Fig. 3. Clone-by-fertilizer interactions at age six for stem growth of 21 clones of *P. taeda*. Stem volume was calculated based on the empirical formula found in Burkhart (1977). Standard error bars are shown, and *p*-values are presented for the interactions depicted.

for height ($p < 0.10$; Fig. 3). Although the clone-by-fertilizer interaction was not statistically significant for stem volume ($p = 0.11$), data are presented in Fig. 3. A small number of clones displayed greater growth responses to fertilizer application versus the mean of all clones in this trial. For example, clone D had 12.2% greater stem volume in fertilizer plots, and clone F2 had 14.2% greater volume. By contrast, other clones like clones F1 or I3 showed almost no fertilizer growth response. Still others, like clones A and K actually had reduced mean stem volume in fertilizer plots, although the reductions in stem volume were small compared to the magnitude of variability observed. While some full-sib pairs of clones showed similar fertilizer growth responses (e.g. clones C1 and C2), others were markedly different in their response to fertilizer application (e.g. clones F1 and F2).

3.3. Stem form

By the end of the sixth growing season, some degree of stem sinuosity affected 25% of the surviving ramets in the trial. However, only 6% of surviving ramets were categorized in the worst sinuosity category, indicating that sinuosity was so severe that it would likely still be present at the end of a 20 year rotation. Neither height growth the year before quantifying sinuosity, nor height growth the year after were significantly correlated with the severity of sinuosity observed ($p > 0.10$). However, there were differences among clones in the frequency and severity of sinuosity observed ($p < 0.01$; Fig. 4). For example, at age six 75% of the ramets of clone I2 were affected with sinuosity of a mean score of 3, indicating severe sinuosity that may still be observed at the end of a 20 year rotation. However, clone I3, full-sib to clone I2, showed no observable sinuosity in any ramet at age six.

Overall the incidence of forking observed in this trial, only 7% at age six, was very low. Only 5% of ramets in control plots (4 ramets) and 9% of ramets in fertilizer plots (7 ramets) were forked after six growing season. Only one clone had more than one forked ramet. Clone J had two forked ramets, one in a fertilizer plot and the other in a control plot. Ramicorns were observed at a much greater frequency, affecting 24% of all ramets after the sixth growing season. Ramicorns were nearly twice as common in fertilizer plots versus controls; while only 18% of control ramets had at least one ramicorn, 30% of ramets in fertilizer plots did. Ramicorn incidence also varied among clones (Fig. 5). For example, clone H2 had no incidence of ramicorns at age six, while clone H1, full-sib to H2, had at least one ramicorn present on five of eight ramets. Fertilizer response in terms of ramets also varied among clones. For example, in clone A ramicorn incidence increased from 25% in control plots to 75% in fertilizer plots. Other clones showed little effect of fertilizer, such as clone I2 which had incidence rates of 33% and 25% in control and fertilizer plots, respectively. Still other clones showed no ramicorns in fertilized plots despite a high incidence in control plots, such as clone F2 (Fig. 5). Again, no statistics are available for forking or ramicorn data due to issues with quasi-complete separation of data points among such a large number of clones.

3.4. Cold damage and height growth

Cold damage affected 18% of ramets in the winter of 2005–2006, after the third growing season. Table 2 displays the relationship

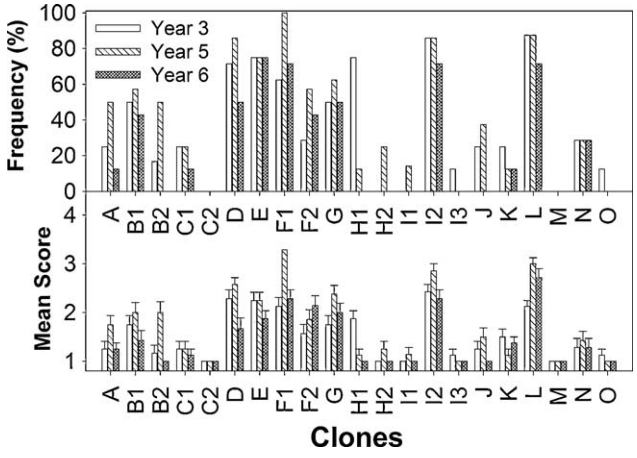

Fig. 4. Sinuosity over three different years of 21 clones of *P. taeda*. Standard error bars are shown. Sinuosity increases in severity as the score increases. Specific detail on scoring may be found in the methods section.

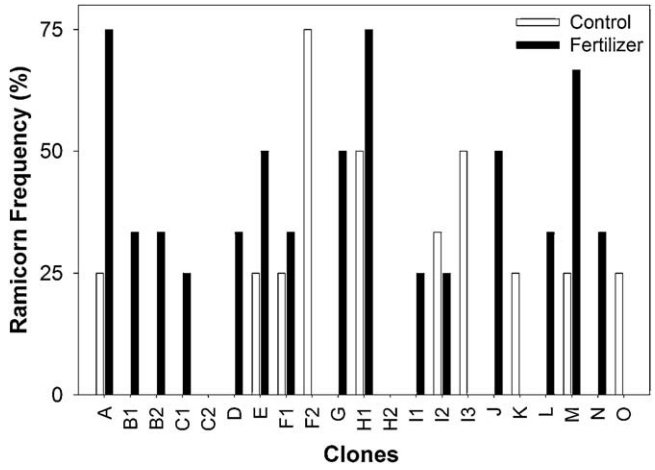

Fig. 5. Ramicorn frequency at age six in fertilized and unfertilized ramets of 21 clones of *P. taeda* replicated four times in the Virginia Piedmont.

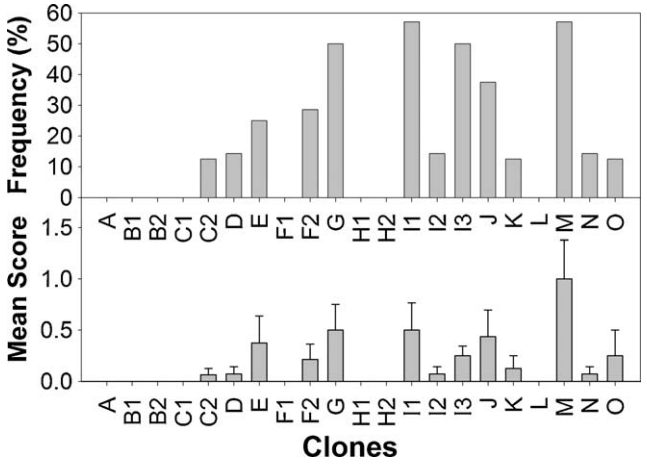

Fig. 6. Cold damage from the 2005 to 2006 winter of 21 clones of *P. taeda*. Standard error bars are shown. Cold damage increases in severity as the score increases. Specific detail on scoring may be found in the methods section.

between cold damage score and height growth in both the previous and subsequent growing seasons. Cold damage preferentially affected ramets that had displayed greater height growth in the previous growing season. Ramets affected by cold damage had grown an average of 1.44 m in the previous growing season, compared to mean height growth of only 1.20 m for unaffected ramets. Data were of insufficient temporal resolution to determine whether these ramets grew more rapidly or whether they continued to produce flushes later in the growing season. While ramets in the least severe cold damage category (score = 0.5) again showed the greatest height gains the following growing season, ramets that received the most severe cold damage showed significantly reduced height growth in 2006 ($p < 0.10$; Table 2). Cold damage appears to have been more severe for some clones compared to others (Fig. 6). While some clones showed no cold damage in any ramet (e.g. clones B1, B2, H1, and H2). Other clones showed a high incidence of relatively minor cold damage (e.g. clones G, I1), while still others showed a high incidence of relatively major cold damage (e.g. clone M). This was despite all clones having been derived from Florida or Atlantic Coastal Plain provenances, two or more USDA plant hardiness zones away from this trial's location in the Virginia Piedmont. As with forking and ramicorn data, issues with quasi-complete separation of these data resulted in spurious statistical results, so no statistics are presented for inference.

3.5. Crown morphology and growth efficiency

Clones varied in their branch morphology, and in the response of branch morphology to fertilizer application. Branch number and branch diameter varied among clones, but not in response to fertilizer application (Table 1; Fig. 7). Branch number ranged from a mean of 2.6 branches per whorl in clone N to a mean of 4.0 in clone F2. Branch diameter score ranged from a category mean of 2.1 in clone H1 up to 3.8 in clone B2. While branch number and diameter did not vary in their fertilizer response among clones ($p > 0.10$), branch angle and crown width both showed significant clone-by-fertilizer interactions ($p < 0.10$; Fig. 7). Some clones did not respond to fertilizer application in terms of branch angle (e.g. clones E and I3), while others responded by reducing branch angle (e.g. clones F2 and K). Crown widths varied among clones, ranging from 119 cm in clone H1 to 166 cm in clone G. While crown width generally

Table 2
Cold damage data from the 2005to 2006 winter measured on a four-year-old *P. taeda* trial. Means are shown with one standard error in parentheses. Letters denote significantly different means based on Tukey's HSD test with $\alpha = 0.10$. Cold damage increases in severity as the score increases. Specific detail on scoring may be found in Section 2.

Cold damage score	*N*	Height growth previous growing season (m)	Height growth next growing season (m)
0	131	1.20 (0.03) A	1.29 (0.03) AB
0.5	15	1.44 (0.07) AB	1.42 (0.07) A
1	6	1.45 (0.08) B	1.17 (0.13) AB
2	8	1.44 (0.07) AB	1.03 (0.12) B

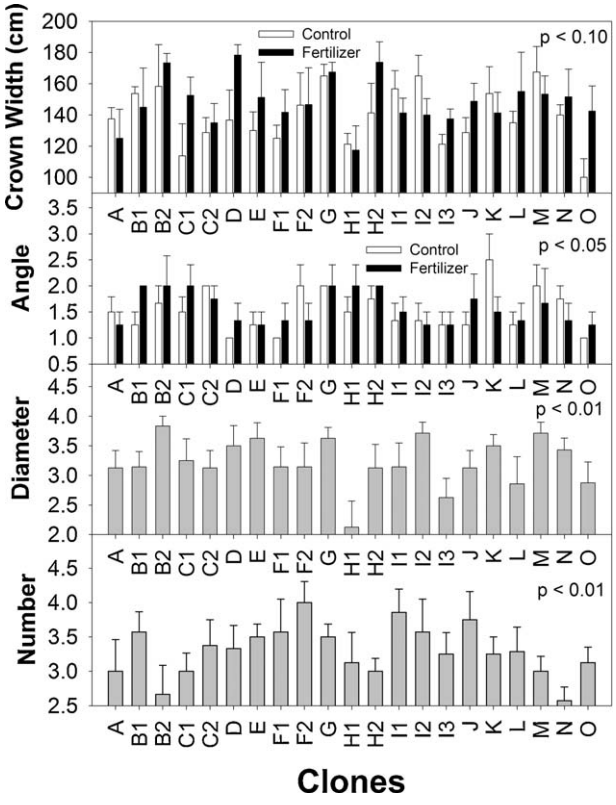

Fig. 7. Branch morphology metrics at age six of 21 clones of *P. taeda*. The upper two panels show clone-by-fertilizer interactions, while the lower two depict only the clonal effect. *p*-Values presented are for the effects shown (interaction upper two panels, clonal effect lower two panels). Standard error bars are shown. Branch diameter increases in size and branch angle becomes increasingly vertical as scores increase. Specific detail on scoring may be found in the methods section.

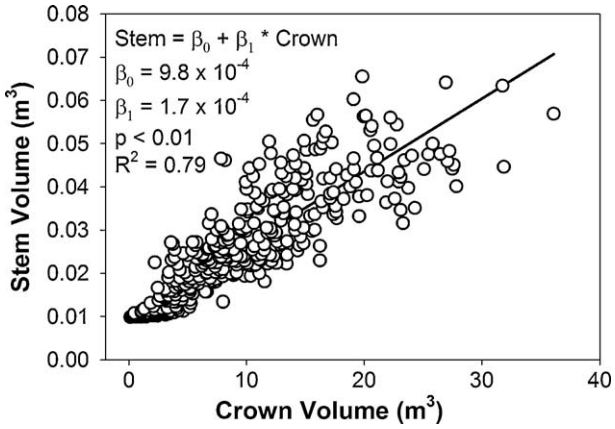

Fig. 8. Simple linear regression of crown volume to stem volume of individual trees with data from three different years from 21 clones of fertilized and unfertilized ramets of *P. taeda*. $N = 468$, regression statistics are shown.

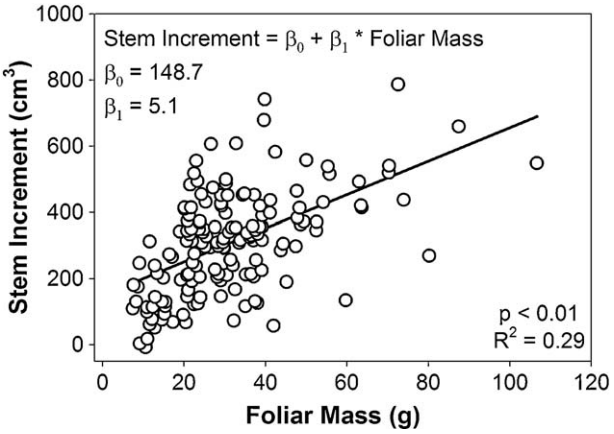

Fig. 10. Simple linear regression of foliar mass per branch mass from a single representative branch harvested in January 2006 to stem volume increment the following growing season from 21 clones of fertilized and unfertilized ramets of *P. taeda*. $N = 159$, regression statistics are shown.

increased with fertilizer application, the magnitude of increase varied among clones. The number of flushes per year also significantly varied among clones, ranging in the sixth growing season from a low mean of 2.0 in clone K to a high mean of 3.8 in clone B2. Flush number across the three growing seasons assessed showed a small but significant negative correlation to height growth ($p < 0.01$, $R^2 = 0.21$, data not shown), with fewer flushes corresponding to greater height growth.

There was a strong positive correlation between stem volume and crown volume across all individual trees from years three, five, and six ($p < 0.01$, $R^2 = 0.79$; Fig. 8). Despite this correlation, there was significant clonal variability in the stem to crown volume ratio, which we are interpreting as a growth efficiency ideotype ($p < 0.01$; Fig. 9). The ratio ranged from a low of 2.1×10^{-3} in clone B2 to a high of 3.8×10^{-3} in clone O. While some full-sib pairs had similar ratios (e.g. clones B1 and B2), others contrasted in their ratios (e.g. clones H1 and H2). A positive correlation was observed between the foliar mass from a single representative branch harvested after the third growing season and stem volume increment in the fourth growing season ($p < 0.10$, $R^2 = 0.29$; Fig. 10). When foliar mass was standardized to the mass of the branch from which it was harvested, a significant clone-by-fertilizer interaction emerged ($p < 0.01$; Fig. 11). While a number of clones showed little response to fertilizer application (e.g. clones I2 and K), others showed increases (e.g. clones B2 and H1) while still others showed decreases (e.g. clones C2 and O). As with other clonal comparisons, some full-sib pairs showed similar fertilizer responses (e.g. clones F1 and F2) while others showed dissimilar responses (e.g. clones I1 and I2).

Clonal repeatability values for height and dbh were significant ($p < 0.05$) and varied from 0.15 to 0.49 for height, and from 0.26 to 0.36 for dbh (Table 3). For height, the repeatability was consistently lower for the fertilizer treatment when compared to the control. Similarly, correlations between stem and crown traits were generally lower in the fertilizer treatment (Table 4). These results reflect that fertilizer plots were more heterogeneous than control plots at ages 3, 4, 5, and 6. Stem dimensions (height, dbh, and volume) showed low to moderate ($0.35 < R^2 < 0.68$) correlations between the clonal means in fertilizer versus control plots (Table 5). This is consistent with results depicted in Fig. 3, and corroborates that while most clones showed similar responses to fertilizer application, several did respond considerably more or less than average. Crown traits were not significantly correlated between fertilizer and control plots in years 5 or 6, indicating a greater effect of fertilizer application on crown morphology than on stem dimensions in this trial.

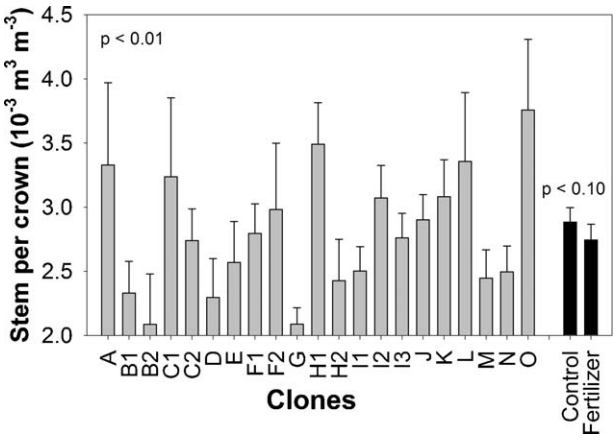

Fig. 9. Clone and fertilizer main effects at age six for stem volume per crown volume from fertilized and unfertilized ramets of 21 clones of *P. taeda*. Stem to crown volume ratio can be interpreted as an approximation of growth efficiency, or stem produced per unit foliage. Standard error bars are shown.

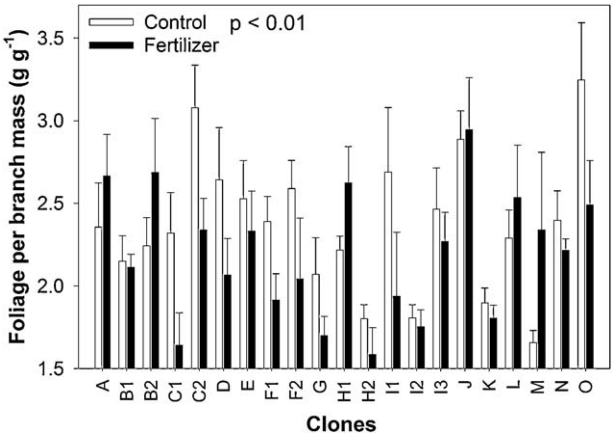

Fig. 11. Clone-by-fertilizer interactions for foliar mass per branch mass from a single representative branch harvested in January 2006 from fertilized and unfertilized ramets of 21 clones of *P. taeda*. Standard error bars are shown.

Table 3
Clonal repeatability for growth traits by year for fertilizer and control treatments among 21 *P. taeda* clones. Standard errors are presented in parentheses. All values were statistically significant ($p < 0.05$).

Year	Control treatment		Fertilizer treatment	
	Height	dbh	Height	dbh
3	0.41 (0.20)	0.31 (0.16)	0.32 (0.16)	0.28 (0.15)
4	0.34 (0.17)	0.28 (0.16)	0.15 (0.13)	0.36 (0.18)
5	0.49 (0.20)	0.35 (0.17)	0.18 (0.14)	0.28 (0.15)
6	0.49 (0.21)	0.37 (0.17)	0.37 (0.17)	0.24 (0.15)

Table 4
Correlation of clonal means of stem and crown dimensions for 21 *P. taeda* clones within fertilizer and control treatments in different years, with *p*-values in parentheses.

	Control treatment					Fertilizer treatment				
	Height	dbh	Stem volume	Crown width	Crown volume	Height	dbh	Stem volume	Crown width	Crown volume
Year 3										
Height	1	0.93 (<0.0001)	0.97 (<0.0001)	0.62 (0.0027)	0.76 (<0.0001)	1	0.93 (<0.0001)	0.74 (0.0001)	0.55 (0.0094)	0.70 (0.0004)
dbh		1	0.94 (<0.0001)	0.60 (0.0041)	0.72 (0.0002)		1	0.82 (<0.0001)	0.45 (0.0416)	0.58 (0.0061)
Stem volume			1	0.66 (0.0011)	0.80 (<0.0001)			1	0.21 (0.3568)	0.28 (0.2193)
Crown width				1	0.96 (<0.0001)				1	0.96 (<0.0001)
Crown volume					1					1
Year 4										
Height	1	0.86 (<0.0001)	0.94 (<0.0001)			1	0.75 (<0.0001)	0.83 (<0.0001)		
dbh		1	0.92 (0.9225)				1	0.85 (<0.0001)		
Stem volume			1					1		
Year 5										
Height	1	0.60 (0.0037)	0.80 (<0.0001)	0.20 (0.3774)	0.52 (0.0159)	1	0.62 (0.0028)	0.67 (0.001)	−0.01 (0.9562)	0.41 (0.062)
dbh		1	0.95 (<0.0001)	0.65 (0.0015)	0.78 (<0.0001)		1	0.95 (<0.0001)	0.57 (0.0068)	0.77 (<0.0001)
Stem volume			1	0.55 (0.009)	0.77 (<0.0001)			1	0.61 (0.0035)	0.85 (<0.0001)
Crown width				1	0.93 (<0.0001)				1	0.89 (<0.0001)
Crown volume					1					1
Year 6										
Height	1	0.49 (0.0228)	0.77 (<0.0001)	0.10 (0.6567)	0.46 (0.0381)	1	0.58 (0.006)	0.71 (0.0003)	−0.01 (0.9761)	0.32 (0.1522)
dbh		1	0.91 (<0.0001)	0.59 (0.0053)	0.72 (0.0003)		1	0.96 (<0.0001)	0.32 (0.1535)	0.48 (0.0275)
Stem volume			1	0.51 (0.0173)	0.74 (0.0001)			1	0.34 (0.1326)	0.55 (0.0102)
Crown width				1	0.92 (<0.0001)				1	0.93 (<0.0001)
Crown volume					1					1

Table 5
Correlation of clonal means of stem and crown dimensions of 21 *P. taeda* clones between fertilizer treatments in different years, with *p*-values in parentheses.

	Control treatment				
	Height	dbh	Stem volume	Crown width	Crown volume
Fertilizer treatment					
Year 3					
Height	**0.62 (0.0025)**	**0.67 (0.0009)**	**0.65 (0.0013)**	0.29 (0.1967)	**0.47 (0.0303)**
dbh	**0.55 (0.0101)**	**0.62 (0.0029)**	**0.57 (0.0069)**	0.26 (0.2631)	**0.40 (0.0758)**
Stem volume	0.37 (0.1005)	**0.46 (0.0375)**	0.36 (0.1088)	0.03 (0.9039)	0.10 (0.6705)
Crown width	0.25 (0.2700)	0.25 (0.2724)	0.29 (0.2056)	0.07 (0.7787)	0.26 (0.2620)
Crown volume	**0.044 (0.0474)**	**0.43 (0.0546)**	**0.49 (0.0245)**	0.24 (0.2939)	**0.45 (0.0422)**
Year 4					
Height	**0.65 (0.0014)**	**0.41 (0.0643)**	**0.53 (0.0130)**		
dbh	**0.50 (0.0221)**	**0.43 (0.0517)**	**0.44 (0.0457)**		
Stem volume	**0.52 (0.0166)**	**0.49 (0.0236)**	**0.49 (0.0241)**		
Year 5					
Height	**0.67 (0.0009)**	0.33 (0.1475)	**0.49 (0.0227)**	0.10 (0.6654)	**0.37 (0.0996)**
dbh	0.33 (0.1409)	**0.52 (0.0149)**	**0.54 (0.0114)**	0.28 (0.2249)	**0.41 (0.0626)**
Stem volume	0.35 (0.1237)	**0.42 (0.0568)**	**0.48 (0.0279)**	0.17 (0.4490)	0.32 (0.1524)
Crown width	−0.32 (0.1572)	−0.02 (0.9338)	−0.06 (0.7922)	0.08 (0.7261)	0.00 (0.9924)
Crown volume	0.03 (0.9084)	0.11 (0.6220)	0.16 (0.4854)	0.09 (0.7002)	0.14 (0.5389)
Year 6					
Height	**0.61 (0.0032)**	0.37 (0.1010)	**0.50 (0.0208)**	−0.03 (0.8807)	0.20 (0.3809)
dbh	0.29 (0.2031)	**0.65 (0.0015)**	**0.61 (0.0032)**	**0.49 (0.0233)**	**0.57 (0.0068)**
Stem volume	**0.38 (0.0915)**	**0.62 (0.0027)**	**0.62 (0.0025)**	**0.41 (0.0616)**	**0.54 (0.0113)**
Crown width	−0.04 (0.8544)	0.03 (0.8863)	−0.01 (0.9721)	0.30 (0.1864)	0.28 (0.2138)
Crown volume	0.20 (0.3786)	0.15 (0.5163)	0.18 (0.4422)	0.25 (0.2744)	0.33 (0.1500)

4. Discussion

4.1. Growth, growth efficiency, and implications for clonal testing

The range of growth rates observed in this trial among different clones was consistent with previous reports in the literature (Paul et al., 1997). The 19.8% difference in stem volume observed between the best and worst performing clones would likely increase by rotation age if growth trends observed by age six continued. The nearly continuous distribution of different clones within this range reflects the high degree of within-species genetic diversity in *P. taeda* breeding populations and the complex polygenic nature of growth (Williams et al., 1995; Kaya et al., 1999). While the clone-by-time interaction was significant, it appears that this was largely the result of scale-effect rather than rank-shift interactions. For example, between the fifth and sixth years, no clone changed stem volume rank by more than three places out of 21 clones. These data support that clonal selection at any time within years three to six will likely yield similar results in terms of identifying the top performing clones based on growth. However, whether these clones remain top performers at full rotation age is a distinct question not addressed by these data, although other evidence suggests that early selection based on growth data is likely predictive at rotation age (Foster, 1986; McKeand, 1988; Gwaze et al., 1998).

The fertilizer growth response observed in this trial, while statistically significant, was small in magnitude (<15% for all clones). The average growth response for *P. taeda* plantations in the southeast is 25% when fertilizer is applied midrotation (Fox et al., 2007b). It is possible that this site had sufficient nutrient availability for a newly initiated stand prior to crown closure, based on the model of stand nutrition over the length of a rotation described in Fox et al. (2007a). However, prior to crown closure at approximately age 8 to 12, many plantations are not limited primarily by nutrients due to the small size of the trees relative to the large nutrient pool available from decomposing slash from the previous rotation (Switzer and Nelson, 1972; Piatek and Allen, 1999). While there was no slash on our site at planting, this experiment may still not have yet developed nutrient deficiencies substantial enough to result in a large fertilizer growth response. Further evidence to support this hypothesis includes relatively high foliar nitrogen content at age two as was reported in King et al. (2008) in eight of these clones. Levels were generally greater than 1.2%, the established critical limit for nitrogen limitation in *P. taeda* (Comerford and Fisher, 1984). While foliar nitrogen content is not as strong a predictor of fertilizer growth response as leaf area index (Vose and Allen, 1988; Albaugh et al., 1998), we do not have leaf area index data for this trial.

The lack of a significant clone-by-fertilizer interaction for stem volume indicates that widespread clonal screening for these interactions may be unnecessary. However, we should note that a small number of clones did show substantial growth responses to fertilizer application compared to the trial average. The consistently higher repeatability values observed for height in control versus fertilizer plots is also indicative of the potential need to screen for clonal fertilizer response, as is further corroborated by the low to moderate within trait clonal mean correlations between fertilizer treatments. While the 12–14% stem volume responses observed in the highly responsive clones is considerably less than average midrotation fertilizer growth responses in *P. taeda* as discussed above, a similar growth increase in a high performing clone may represent a substantial increase in both yield and value at harvest if single genotype stands are deployed. It is also possible that fertilizer response in these highly responsive genotypes might have been much more substantial on a site with lower native nutrition. There do appear to be opportunities to realize substantial growth increases with appropriate nutrient management in a small number of genotypes, while other genotypes may be less sensitive to nutrient additions and require lower intensity, and thus lower cost, inputs. One potential solution suggested by our results is to test the fertilizer response of clones produced in large numbers as they are deployed on a site with minimal native nutrition over the first several years after planting to establish midrotation fertilizer recommendations for those same genotypes in operational plantations. This approach would likely provide adequate information for the management of deployed clones in a timely fashion, while eliminating the expense of testing clones that have not been operationally deployed for responsiveness to fertilizer application.

Clonal selection requires knowledge of heritability, or clonal repeatabilities. The repeatability values we observed for height and dbh in this trial were somewhat low, given the high degree of genetic control expected in clones. However, our values were greater than those obtained by Emhart et al. (2006) for similar growth variables in full-sib families, as would be expected since there is a lesser degree of genetic control in families compared to clones. A lack of uniform growing conditions on this site may partially explain the low values we observed. It is also possible, given the significance of the covariate of initial height ($p < 0.01$), that taller trees at the time of fertilizer application may have been more capable to responded to fertilizer since they likely had more significant root systems and greater leaf area. A differential fertilizer response among individuals based on initial size could potentially enlarge the error variance compared to the clonal variance, reducing the magnitude of repeatability values (see Eq. (1)). This hypothesis is supported by the within-treatment clonal mean correlations, which tended to be higher in control versus fertilizer plots, indicating less uniformity following fertilizer application.

Clonal variability in growth efficiency or crown metrics that affect growth efficiency has been previously reported among clones of *P. taeda* (Emhart et al., 2007; Tyree et al., 2009b). These results are consistent with the clonal main effect we observed in the stem volume per crown volume ratio. The clone-by-fertilizer interaction observed for foliage mass per branch mass indicated differences in foliar display in response to fertilizer application similar to previous reports (Tang et al., 1999; Maier et al., 2008). However, our results point toward foliar display response to fertilizer application varying among genotypes, demonstrating that results reported for two clones in Tyree et al. (2009b) are likely applicable across a greater population of clones. The fact that foliar mass per branch mass only accounted for 29% of the variability in stem growth in the following growing season indicates that photosynthetic rates, foliar morphology, and other traits that we did not assess likely varied among clones in response to fertilizer application, as has previously been reported for this and other studies (King et al., 2008; Tyree et al., 2009b). Variability in branch metrics among clones and in response to fertilizer application has been previously observed, and is another source of fertilizer and clonal variability in crown and foliar display (Maier et al., 2002; Albaugh et al., 2006; Tyree et al., 2009a). The extent of variation in crown traits and growth efficiency offers numerous opportunities for ideotype-based clonal selection, as has been previously discussed in Emhart et al. (2007).

4.2. Stem form defects

Stem form defects were found only at relatively low incidence rates in this trial, although their incidence did vary significantly among clones in some cases. While sinuosity was not severe in this trial when averaged across clones, we did find that some clones displayed a high incidence of severe sinuosity, indicating that clonal screening for severe cases of sinuosity may be advisable. Similar to our findings, sinuosity has previously been shown to vary among both open-pollinated families and clones in the *Pinaceae* family (Schermann et al., 1997; Espinoza, 2009). Also consistent with our results, sinuosity in *Pseudotsuga menziesii* (Mirb.) Franco showed

little correlation between leader height growth and sinuosity class (Gartner and Johnson, 2006). Due to the extremely low incidence of forking in this trial, we can make no inference on treatment effects, although previous work has shown both genotypic variability in forking frequency and increased incidence forking as a result of fertilizer application (Schermann et al., 1997; McKeand et al., 2006; Espinoza, 2009). Ramicorns were a more common defect present in this trial. While ramicorn incidence almost doubled with fertilizer application, clones did vary widely in their ramicorn fertilizer response. Past studies have found conflicting results with regard to genetic variation in ramicorns, with some studies finding little variability among open-pollinated families (Codesido and Fernandez-Lopez, 2008), while others observed different family means (Schermann et al., 1997). As with some of our genotypes, *P. taeda* has previously shown worsening of stem form defects with fertilizer application in some provenances (Espinoza, 2009).

4.3. Cold damage and survival

While we did find differences among genotypes in the frequency and severity of cold damage occurrence, overall incidence was low in this trial. There was no mortality that could be directly attributed to cold damage, and only eight ramets were assigned the worst cold damage score that was correlated with significantly reduced growth in the subsequent growing season. Our results are consistent with the literature in terms of genotypic variability in cold damage, which has previously been shown to vary among different open-pollinated families of *P. taeda* (Kolb et al., 1985). Our ability to infer that cold damage will not be a problem for genotypes deployed far from their recommended hardiness zone (see Schmidtling, 2001) is very limited based on this dataset from a single site over a single severe winter. However, the fact that some genotypes of Atlantic Coastal Plain and Florida provenances had no incidence of cold damage is promising for specific clones with regards to moving seed sources large distances from their origin. While inference space based on these data is similarly limited for survival, mortality was higher in four genotypes than the rest. The fact that all of this mortality occurred prior to the third growing season in these clones suggests that the seedlings may have had varying levels of fitness across clones, but we cannot attribute this mortality to a more specific cause. Genotype-by-environment interactions for survival across a number of sites are already implicitly considered in clonal testing, since dead trees cannot be selected for favorable traits, so little change in current practices is suggested by these data.

5. Conclusions

Differences in clonal traits offer a number of different opportunities for precision silvicultural systems targeted to specific clones planted in single-genotype blocks. For instance, clones with rapid stem volume growth rates and narrow crowns might be planted at a wide spacing if they do not have problems with ramicorns, allowing for the production of a high percentage of sawtimber without necessitating intermediate treatments beyond fertilizer application and possibly pruning. Even if pruning becomes necessary, selecting clones with a lower number of smaller diameter branches may reduce effort and thus costs involved with pruning operations. Clones with lower foliage per branch mass ratios may allow more light to reach the understory through their more diffuse crowns, and thus be more appropriate for inter-row planting with biomass crops such as switchgrass. Alternatively, clones with high foliage per branch mass ratios may create a more heavily shaded understory, possibly reducing requirements for competition control earlier in the rotation. These examples highlight only a few of the possibilities for clone-specific silvicultural systems that depend on the specific traits of individual clones that are selected for deployment over large acreages. These results also suggest that companies practicing clonal forestry could select a number of similarly performing clones in order to eliminate unnecessary complications that might arise from multiple clone-specific silvicultural regimes. Further work to optimize the management of individual genotypes produced in large numbers for specific product classes may greatly increase the value of clonal plantations in the coming decades.

Our results also indicate that clone-by-fertilizer interactions for a number of traits, such as height growth, branch traits, and foliage per branch mass may offer specific silvicultural opportunities in the management of clonal plantations. Genotypes with growth rates that are known to be more responsive to fertilizer application can be managed with maximal nutrient inputs in order to take full advantage of their responsiveness. By contrast, genotypes that are less responsive to fertilizer application may be fertilized at lower rates, thus reducing costs without substantially reducing potential growth. Minimizing fertilizer rates in these genotypes may also reduce the incidence of stem quality defects that have been associated with greater nutrient additions in other studies (e.g. Espinoza, 2009). While clone-by-fertilizer interactions can create management opportunities, lacking information on the fertilizer response of specific genotypes may make it difficult to optimize the management of clonal plantations. Fertilizer applied to non-responsive genotypes could be an unnecessary expense, while on the other end of the spectrum insufficient fertilizer application for clones that are highly responsive could result in yields substantially below what might be economically achieved. While further research is necessary on fertilizer interactions with a greater number of clones on a greater number of sites, the results from this trial suggest that opportunities do exist for the design and application of clone-specific silvicultural systems for widely deployed *P. taeda* genotypes.

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