EPICORMIC DEVELOPMENT IN POLE-SIZE WHITE OAK (*QUERCUS ALBA* L.) PROGENY TESTS THREE YEARS FOLLOWING CROWN RELEASE

Andrew Meier and Mike R. Saunders[1]

Abstract—Epicormic development has been traditionally thought to be a response to increased light and to varying vigor and genetics among individuals within a species, but epicormic ontogeny has increasingly been shown to be a more fundamental factor. Previous studies have quantified the impact of tree vigor on epicormic sprouting and epicormic branch size following silvicultural treatments, but few assessed the genetic component of development. In this study, data from a crop tree release treatment in a 25 year old white oak (*Quercus alba* L.) progeny test in Indiana was used to isolate the relative influences of tree vigor and progeny-level genetic variation on epicormic development. We found no significant difference in the total number of epicormic branches three years following crop tree release ($p = 0.940$), but a significant increase in epicormic branch size ($p < 0.001$). Variation explained by family effects was stronger for branch size than for branch numbers, but provenance did not improve fits for any model. Tree vigor-related variables were significant predictors in all models, but the epicormic response was driven most strongly by pre-treatment epicormic composition. Therefore, a major objective in the management of young oak stands should be to maintain tree vigor to avoid the initial sprouting of epicormics and to remove individuals with many epicormics early in the rotation.

INTRODUCTION

Epicormic branches in many trees sprout from buds that have either been dormant since initial shoot elongation or have descended from primary buds initiated on an annual shoot (Del Tredici 2001, Meier and others 2012). In the oaks (*Quercus* spp.), epicormic buds can be traced to an original primary bud on an expanding annual shoot (Fontaine and others 1999, Yokoi and Yamaguchi 1996, Meier and Saunders 2013). As shoots become older, single buds develop into complex epicormic structures consisting of numerous buds and sprouts. Diameter expansion of these structures over time can produce knots in the wood that reduce log value (Stubbs 1986, Meadows and Burkhardt 2001).

Environmental and genetic factors interact to influence the development of epicormics on individual trees (Meadows 1995, Colin and others 2010, Meier and others 2012). Genetic effects on the development of complex epicormic structures have not been widely studied (Meier and others 2012), though some level of genetic control over initial epicormic sprouting has been demonstrated (Bowersox and Ward 1968, Jensen and others 1997). In oaks, the strongest genetic variation in epicormics occurs at the species level (Meadows 1995), with the white oak group (section Quercus) more susceptible to sprouting than the red oak group (section Lobatae) (Meier and others 2012). Provenance level genetic effects are generally weak (Jensen and others 1997, Colin and others 2010), but progeny level heritability has been reported to be high for some species (Jensen and others 1997).

Silvicultural treatments manipulate environmental conditions, thereby potentially impacting epicormic trajectories. Treatments that increase individual tree vigor are sometimes associated with lower levels of epicormic branching (Miller 1996, Meadows and Goelz 2002, Lockhart and others 2006) compared to low vigor, overstocked stands (Evans 1987, Nicolini and others 2001). However, by increasing light levels below the main canopy, these treatments can also create an environment conducive to epicormic growth (Spiecker 1991, Meadows 1995, Yokoi and Yamaguchi 1996) and thinning stands with stressed or low vigor trees tends to exacerbate incipient epicormic problems (Devine and Harrington 2006, Dimov and others 2006).

This study compares the relative effects of tree vigor, progeny level genetic variation and epicormic ontogeny on the epicormic response to complete crown release in polesize white oak (*Q. alba* L.) plantations. We compared the epicormic response in both high and low

---

[1] Andrew Meier, Former HEE Project Coordinator, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907; and Mike R. Saunders, Associate Professor, same address, respectively.

Citation for proceedings: Schweitzer, Callie J.; Clatterbuck, Wayne K.; Oswalt, Christopher M., eds. 2016. Proceedings of the 18th biennial southern silvicultural research conference. e–Gen. Tech. Rep. SRS–212. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 614 p.

vigor trees from families with low, medium and high epicormic tendencies. To simulate vigor reduction, a subset of these trees was subject to partial crown removal. We hypothesized that: 1) branch size and persistence would increase in response to crown release, but the total number of branches would show only a minimal response; 2) crown removal through pruning would stimulate significant increases in branch numbers while significantly reducing tree diameter growth; 3) the overall number of epicormic branches on an individual tree would vary among white oak families, but the size and persistence of branches would be influenced more by tree vigor components; and 4) epicormic characteristics three years following treatment would be strongly influenced by pre-treatment characteristics.

METHODS

Sites

This study was implemented in two plantations that are part of a half-sib white oak progeny test in Indiana. They are located at the Jasper-Pulaski Fish and Wildlife Area (JP) (41˚ 09' N, 86˚ 54' W, 1.1 ha) and the Harrison-Crawford State Forest (HC) (38˚ 15' N, 86˚ 15' W, 1.5 ha). Acorns were collected in 1982 from stands in Indiana, Illinois and Missouri and grown for one year in Indiana's Vallonia State Tree Nursery. Seedlings were outplanted in the spring of 1984 in row plots of 4 trees per family; there were 6 replicates of each family at JP and 8 replicates at HC (Coggeshall 1993). Height data has been collected periodically, with the most recent comprehensive measurement of all plantations completed in the fall and winter of 2005-06. This measurement cycle also included diameter at breast height (dbh, at 1.37 m) and qualitative ratings for tree form and epicormic branching (S. Rogers, unpublished data). Immediately prior to the current study, dbh (cm) at JP and HC averaged 16.9 (sd [standard deviation] = 3.8) and 14.3 (sd = 3.3), respectively. Basal area (m^2 ha^{-1}) was slightly lower at JP (= 21.8, sd = 4.3) than at HC (= 22.2, sd = 2.9). Soil at HC is a Haymond silt loam and at JP a Maumee sandy loam (O'Connor and Coggeshall 2011); HC has a slightly higher site quality with a site index (height at age 50 years) of 21 m compared to 20 m at JP.

Treatments

Based on family mean epicormic ratings from 2005-06, we randomly selected six individual families with high (in top quartile), medium (in mid two quartiles), and low (in bottom quartile) epicormic tendencies. Within each resulting epicormic class (epiC) individual trees were stratified into upper (dominant and codominant) and lower (intermediate and suppressed) pre-treatment crown classes (cc) to capture within family variation in tree vigor. An approximately equal number of trees were then randomly selected as study trees from within each combination of epiC and cc at each site. Full details of the study tree selection protocols, as well as a list of study families, can be found in Meier (2012).

Study trees were given a full crown-touching release (Miller and others 2007) requiring the removal of 1 to 8 trees in the immediately adjacent planting locations. Trees were randomly assigned to one of three pruning treatments: no crown removal, one-third (= low) or two-thirds (=high) live crown removal. Crowns were pruned from the bottom of the crown upward. Because of the variation in crown structure for individual trees, we reclassified trees into quantitative pruning classes following treatment (prC, table 1); these classes were similar to the initial pruning treatment assignments though there was some variation (data not shown).

Data Collection

Initial data collection occurred prior to the installation of treatments from January to March 2010 and was repeated in both late spring and early fall of 2010-12, a total of seven measurement cycles. Variables measured are shown in Table 1. Growth related variables were measured prior to treatment and only during fall measurement cycles; epicormic branch counts were taken at every cycle. Branches were counted on the trunk section from 0.15-3.81 m in height, allowing for a 0.15 m stump height. This corresponds to approximately a 3.66 m butt log, which is a common merchantable log length in Indiana. Epicormic branches were distinguished from sequential branches by their generally large branch angles, weak trunk attachment, small size and highly variable branch structure (Spiecker 1991), though only rarely were live sequential branches encountered in this section of any bole. Epicormic branches were considered dead if they were brittle or easily broken off the tree. New branches were tallied separately for each of the post-treatment measurement cycles. Only branches with a single green growth unit were considered to be new branches; we had no way of distinguishing between growth units resulting from multiple flushes within a single growing season and growth units developing over multiple years (Spiecker 1991). Epicormic branches were tallied by branch diameter classes (brDC), as measured at the base of the branch just above the basal swell. These classes were: brDC1: <0.64 cm, brDC2: 0.64-1.27 cm, brDC3: 1.27-2.54 cm, brDC4: 2.54-3.81 cm and brDC5 >3.81 cm. The threshold between brDC1 and brDC2 corresponds to the size at which an epicormic must in all cases be considered a defect in US Forest Service log grading (Rast and others 1973). When multiple epicormic branches emanated from the same underlying epicormic structure, they were counted as a single branch (Spiecker 1991) and the diameter of the cluster was recorded. The number of clusters was not tallied.

Table 1—Descriptions and mean values for predictor variables and factors that were included in the full models. Variables that were significant in either the br12 or the brBA12 models are listed in bold; variables that were removed from br12 or brBA12 because of high collinearity are shown in italics. Note that response variables are for the total log length, not the per meter average

Variable	Description	Mean value (±SD) or distribution of factors
Response		
br10t[†]	Total number of epicormic branches in 2010 to 3.81 m	53.7 (±25.7)
brBA10t[†]	Total epicormic branch basal area in 2010 (cm^2)	8.6 (±5.0)
br12t	Total number of epicormic branches in 2012 to 3.81 m	50.6 (±26.3)
brBA12t	Total epicormic branch basal area in 2012 (cm^2)	20.1 (±9.9)
Factors		
epiC	Epicormic class (L = low, M = medium, H = high)	L (26), M (27), H (28)
prC	Crown pruning classes (N = none, L = low, H = high)	N (27), L (27), H (27)
cc	Crown class (L = intermediate and suppressed, U = dominant and codominant)	L (39), U (42)
ftg12	The free to grow rating of the tree in 2012, ranging from 0 (no lighted faces) to 4 (all faces receiving sunlight)	0 (2), 1(5), 2(12), 3(31), 4(31)
site	One of two plantation locations, either JP or HC	HC (50), JP (31)
Covariates		
brNewM	Mean number of new branches for all measurement cycles (2010-2012)	12.7 (±8.8)
dbh10	Tree diameter (cm) prior to the 2010 growing season	14.8 (±3.9)
dbh06	Tree diameter (cm) prior to the 2006 growing season	13.3 (±3.2)
dbhincP	Annualized pre-treatment dbh increment (cm) for 2006-2009 growing seasons	0.4 (±0.3)
dbhinc	Mean annual dbh increment (cm) for 2010-2012 growing seasons	0.5 (±0.2)
hgt94	Total height (m) in 1994	3.0 (±0.9)
hgtincP	Annualized pre-treatment height increment (m) for 2006-2009 growing seasons	0.4 (±0.2)
hgtinc	Mean annualized height increment for 2010-2012 growing seasons	0.4 (±0.6)
lcrinc	Mean live crown radius for 2010-2012 growing seasons	1.9 (±0.7)
lcr	Average pre-treatment live crown radius (m)	1.9 (±0.6)
pctlc	Pre-treatment percent live crown	50.5 (±12.5)
ci	Pre-treatment competition index, calculated $\sum_{j=1}^{n} D_j/D_i$ where n is the number of competitors, D_j is dbh of an individual competitor and D_i is dbh of the study tree (from Lorimer 1983)	5.9 (±2.6)

[†] Also a covariate in br12t and brBA12t models.

Data Preparation and Analysis

We modeled the pre-treatment epicormics and post-treatment epicormic response based on two epicormic branch variables: the total number of epicormic branches (br) and the total basal area of epicormic branches (brBA, cm^2) as calculated using the midpoint diameter of each brDC. We chose to use absolute measures for both because relative values in regards to initial conditions would have the potential to disproportionally amplify effects in individuals with small initial values. We elected to analyze responses using only the spring 2010 and fall 2012 data and avoided a complex time series analysis; Meier (2012) found little variation in epicormic characteristics in the intervening measurement cycles. We were also interested in the magnitude of new epicormic sprouting across all years rather than only the number of new epicormic branches present in fall 2012, so we calculated the mean number of new epicormic branches per year (brNewM) and included this in the br and brBA models. Though our branch variables were based on count data, there were no trees with counts of zero for br or brBA. Therefore, these variables were transformed to approximately normal distribution using square root transformations.

We utilized linear mixed effects models to analyze our data and assessed family (fam) variation as a random effect. Site was included as a fixed effect in all models because we did not have a sufficient number of sites to calculate meaningful random effect parameters. Full models for br and brBA included growth, stocking and prior epicormic characteristics (table 1). In all models, when pairs of variables showed high Pearson's correlations ($|r| > 0.7$) one of the pair was removed (table 1, italics) prior to stepwise model reduction. Generally, variables retained had the strongest pairwise relationships with the response variable and were correlated with the fewest other predictors.

Linear mixed effects models of the transformed response variables were fit using restricted maximum likelihood estimation. The significance of variables ($\alpha = 0.05$) in the full models was tested with marginal F-tests and the least significant variable was removed in a stepwise manner (Pinheiro and Bates 2000). Relative AIC was calculated subsequent to each stepwise model reduction and variables were retained if their removal caused a large increase (>5) in the AIC. In some instances, non-significant terms remained in the model when AIC was minimized; these were also removed in the interest of model parsimony. In the reduced models, we used likelihood ratio tests to test the significance of the family random effect by comparing models with identical fixed effects, but with and without family random effects (Pinheiro and Bates 2000). The magnitude of the family effect was assessed using the estimated standard deviation of the random intercept ($\hat{d}$) (Zuur and others 2009). Diagnostic plots of the final models were used to identify variation from the normality assumption and heteroscedasticity of the models. Model fit was further evaluated by calculating lme R^2 (Maj 2011).

In addition to the models described above, absolute differences between transformed br and brBA in spring 2010 and fall 2012 values were assessed with paired t-tests. A Mann-Whitney test was used to test whether there was a difference in the proportion of branches that were new in 2010 to the proportion that were new in 2012. All analyses were performed using the R statistical computing program, version 2.15.0 (R Development Core Team 2012), using the packages stats, nlme (Pinheiro and others 2012), bbmle (Bolker 2012), and lmmfit (Maj 2011).

RESULTS

Diameter Growth

Diameter growth (dbhinc, cm yr^{-1}) across all classes was greater following treatment (= 0.47, sd = 0.21) than prior to treatment (= 0.39, sd = 0.28), and it did not differ significantly by site. Diameter growth varied little by epiC (low: = 0.47, sd = 0.22; medium: = 0.46, sd = 0.22; high: = 0.46, sd = 0.20) and decreased slightly with prC (none: = 0.50, sd = 0.24; low: = 0.46, sd = 0.22; high: = 0.44, sd = 0.16). There was a significant influence of crown class (cc) on diameter increment ($p < 0.001$), with upper crown classes (= 0.58, sd = 0.19) growing faster than lower (= 0.34, sd = 0.17). Trees with initially larger crowns had higher growth rates; unpruned trees in the upper crown class (fig. 1, white circles) had the highest average growth rates, while the most heavily pruned lower crown class trees (fig. 1, gray triangles) had the lowest.

Pre-treatment Epicormic Dynamics

The mean number of epicormic branches prior to treatment (br10) was 14.7 m^{-1} (sd = 7.0). There were no distinct pretreatment differences between the study sites (fig. 2a). Strong pretreatment differences were also not evident between epicormic classes or pruning classes, though there was some separation between crown classes (fig. 3a-c). A large proportion (= 0.37, sd = 0.24) of pre-treatment epicormic branches were newly formed in the prior year. The best model for br10 included only cc as a significant effect; variation attributable to different families was minimal. However, the model had a very low predictive value (R^2 = 0.08, table 2).

Means for total branch basal area per meter prior to treatment (brBA10, cm^2) were similar, but significantly different ($p = 0.005$) between HC and JP (fig. 2b). For all other grouping variables, differences were small, variability was high (fig. 3d-f), and none were significant

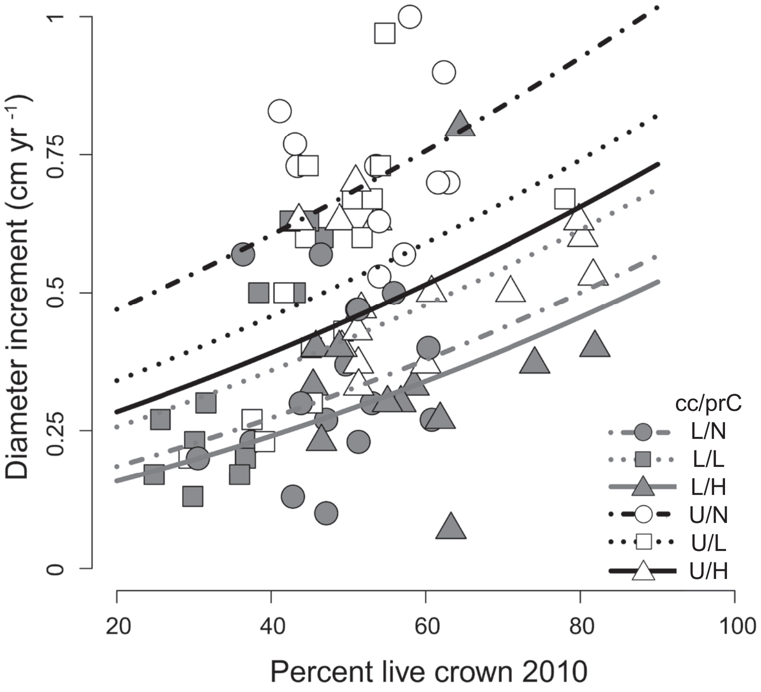

Figure 1—Annual diameter increment following treatment by pre-treatment percent live crown for individual combinations of crown class (cc) and pruning class (prC). Grouping codes are defined in Table 1.

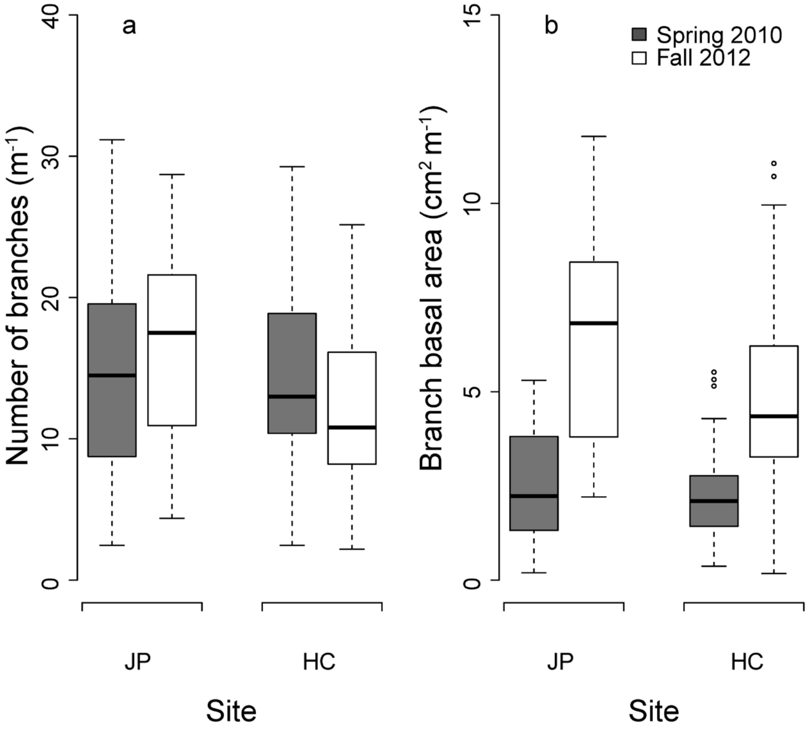

Figure 2—Boxplots indicating the variation in number of epicormic branches per meter (br; a) and branch basal area per meter (brBA; b) by site prior to the first growing season following treatment (br10 or brBA10; gray boxplots) and after three full growing seasons (br12 or brBA12; white boxplots).

in the final model (table 2). Instead, dbh increment prior to treatment (dbhincP) was negatively correlated and tree height in 1986 (hgt86) was weakly positively correlated with brBA10 in the final model (table 2). Family random effects were greater in this model than for br10, but still non-significant (p = 0.578), and model fit was somewhat better (R^2 = 0.20).

Post-treatment Epicormic Dynamics

The number of epicormic branches per meter in fall of 2012 (br12) declined slightly (= 13.9, sd = 7.2) from br10, but was not significantly different (V = 1203, p = 0.968). Branch numbers at JP were higher than at HC (fig. 2a). The proportion of branches that were new was significantly lower three years after treatment (= 0.15, sd = 0.12; V = 301.5, p <0.001). For the various grouping classes, br12 was similar and not significantly different (Fig. 3a-c). Average branch size generally increased for all families (data not shown; see Meier 2012). Four covariates were significant in the final br12 model (table 2); these included pretreatment epicormic composition (br10), competition (ci), pre-treatment heigh increment (hgtIncP), and the average annual production of new shoots (brNewM). Family effects were minimal, and this model explained overall variation well (R^2 = 0.71) (table 2).

In contrast to the total number of branches, there was a significant increase in total branch basal area per meter (V = 3294, p < 0.001) three years following treatment (brBA12, = 5.5, sd = 2.7); this increase was evident across all groups and at both sites (fig. 2, fig. 3). Of the 81 study trees, only 3 had lower brBA in 2012 than 2010; the average increase in brBA of the 3.66 m butt log was 11.1 cm^2 (sd = 8.4), equivalent to about 15 branches transitioning from brDC1 to a defect-causing brDC2. The brBA12 per meter was higher at JP than at HC (fig. 2b) and also differed by epiC (fig. 3d). There was little variation between cc (fig. 3e), but pruning stimulated an increase in brBA in respect to initial levels (fig. 4). The final brBA12 model included brBA10, site and prC table 2). Family effects were stronger than for other models, but still insignificant; variation explained was moderate (R^2 = 0.40).

DISCUSSION

Growth and Vigor

In this study, we considered higher than average diameter growth rates to be indicative of high vigor. Overall, we observed a significant increase in growth rates in this study following crop tree release compared to pre-treatment growth. The growth rate was similar to that for other studies of pole-sized oaks following release (Minckler 1967, Schlesinger 1978). Pre-treatment crown characteristics significantly influenced growth rate and crown pruning caused variation in growth both among and within crown classes (fig. 1). The heavily

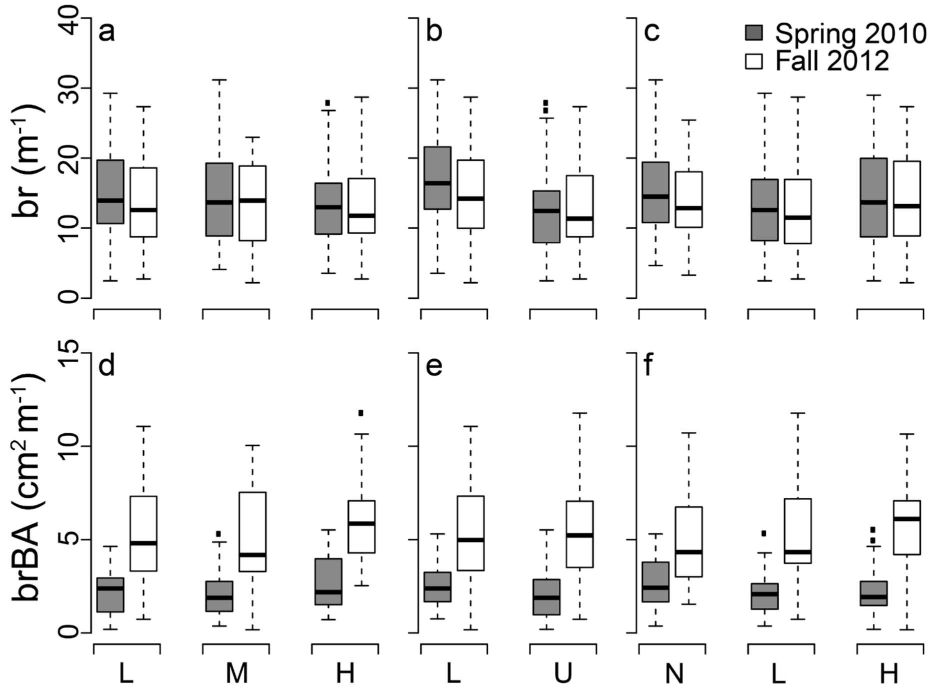

Figure 3—Boxplots for number of epicormic branches per meter (a-c) and branch basal area per meter (d-f) for three grouping factors, epicormic class (epiC: a, d), crown class (cc: b, e) and pruning class (prC: c, f), prior to the first growing season following treatment (gray bars) and after three full growing seasons (white bars). Grouping codes are defined in Table 1. Thick black bars represent sample medians.

Table 2—Parameter estimates for linear mixed effects models of the various response variables. The family effect was calculated with a likelihood ratio test of models with and without the family random effect included; the associated *P* value indicates whether there was significant variation between models. Significance in all cases was assessed at α = 0.05

Response variable	Family random effect		lmm $R^{2\dagger}$	Parameters			
	$\hat{d}$	*P* value		Fixed effects	Estimate	SE	*P* value
sqrt(br10t)	<0.001	0.999	0.08	intercept	7.631	<0.001	<0.001
				ccU	-1.015	0.387	0.011
sqrt(brBA10t)	0.200	0.578	0.20	intercept	2.634	0.304	<0.001
				siteJP	0.583	0.198	0.005
				dbhincP	-1.605	0.364	<0.001
				hgt86	1.587	0.726	0.033
sqrt(br12t)	<0.001	0.999	0.71	intercept	0.521	0.703	0.462
				ccU	0.658	0.271	0.018
				siteJP	1.342	0.293	<0.001
				sqrt(br10)	0.538	0.085	<0.001
				brNewM	0.078	0.018	<0.001
				hgtincP	-1.347	0.610	0.031
				ci	0.196	0.055	<0.001
sqrt(brBA12t)	0.228	0.440	0.40	intercept	1.454	0.401	0.001
				prC1	0.730	0.250	0.005
				prC2	0.555	0.240	0.024
				siteJP	0.705	0.213	0.002
				sqrt(brBA10)	0.781	0.117	<0.001

$^{\dagger}R^2$ values were calculated as adjusted R^2 when multiple fixed effects remained in the final model.

pruned upper canopy trees had growth rates that were close to the growth rates of the most vigorous lower canopy trees, fulfilling our objective of simulating the development of low vigor trees in the upper crown classes.

Branch Number and Size

We confirmed our first hypothesis that the increase in size of epicormic branches is a much more important component of the response to crop tree release than increases in the overall number of branches. We observed no changes in br three growing seasons after thinning (fig. 3a-c), but did observe significant increases in brBA (fig. 3d-f). These brBA increases were driven by increased diameters of extant branches. Transitions from the smallest, more ephemeral branches in brDC1 to more persistent, larger branches in brDC2 accounted for most of the increase in brBA. Trees with the highest number of large branches prior to treatment were those with the highest brBA subsequent to treatment (fig. 4).

Our observed br and brBA dynamics have been reported in other oak thinning studies (Minckler 1967, Yokoi and Yamaguchi 1996), though some authors have reported significant increases in branch numbers (Stubbs 1986, McDonald and Ritchie 1994). The lack of a response in branch numbers is often attributed to vigor increases in released trees (Lockhart and others 2006) or the removal of low vigor trees (Meadows and Goelz 2002), while branch stimulation often occurs following the release of very low vigor trees (Devine and Harrington 2006, Dimov and others 2006). Though we did observe increased diameter growth at the tree level, and therefore increased vigor in this study, vigor following release was not a significant covariate in the br model. Rather, the epicormic impact we observed may have occurred as a result of release at the level of individual branches. Since epicormic branches were numerous on most trees in this study prior to treatment, we suggest that increased light levels following treatment promoted increased vigor of the

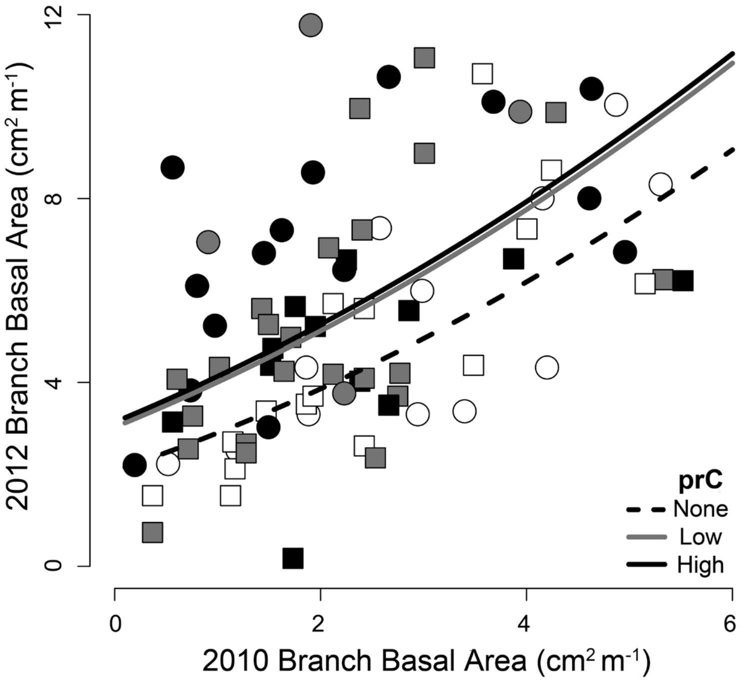

Figure 4—Relationship between branch basal area per meter in 2010 and 2012 for sites JP (circles) and HC (squares). Regression lines and symbol colors represent pruning classes (prC) at each site. Model parameters for the full mixed model are shown in Table 2.

dominant meristems of these extant branches, thus increasing the physiological control by these meristems over dormant buds in the subtending bud cluster (Chen and others 1996, Meier and others 2012). Our finding that the proportion of branches that were less than one year old was halved between the initial 2010 measurement and the final 2012 measurement further indicates CTR actually limited new sprouting by favoring existing sprouts. Apical dominance is a well-established concept in the literature (Brown and others 1967, Kormanik and Brown 1969), and there is no reason to assume that this concept should not apply in the same way at the level of an individual epicormic structure as it does at the level of the entire tree. In trees with few epicormic sprouts prior to canopy release, prolific sprouting may occur initially, as observed in other studies, followed by a period of branch development similar to our study.

Crown Pruning

Crown pruning and the associated reduction in vigor had surprisingly no significant impact on branch sprouting (fig. 2, 3c), which was contrary to our second hypothesis. In a number of species, branch pruning has been shown to stimulate epicormic sprouting (Evans 1987, Springmann and others 2011), but it commonly occurs from the buds nearest to the point of damage (Kormanik and Brown 1969, Wignall and Browning 1987). Therefore, it is possible that crown pruning did indeed stimulate epicormic sprouting in this study, but since crowns in most cases were pruned well above our 3.81 m counting limit, the resulting new branches would not have been tallied.

Although crown pruning did not stimulate the sprouting on the lower bole, it did influence development of extant branches (fig. 4). The brBA response is probably the result of two factors. The first relates to reduction in self-shading on the bole after the partial crown removal. This would allow for higher photosynthetic rates in epicormic branches lower on the tree, which in turn, would lead to increased branch size. The second factor could be related to nutrient sink dynamics. With the removal of branches in the live crown during the dormant season, the amount of potential leaf area in the crown would have been substantially less at the time of bud flush than the nutrient base that had supported leaf area in the previous growing season. Therefore, previously low vigor epicormic branches on the bole could have become stronger nutrient sinks and benefited from an influx of nutrients that would otherwise not have been available (Ishii and others 2007, Meier and others 2012).

Genetics and Ontogeny

In general, family effects on epicormic development after either pruning or crop tree release were weak or even nonexistent (table 2). Somewhat contrary to our third hypothesis, progeny level genetic variation was higher for branch size than branch numbers, though the effect was still negligible. In contrast to genetic effects, epicormic characteristics prior to treatment had a significant effect on epicormic characteristics three years following treatment, confirming our final hypothesis. Many studies have alluded to ontogenic effects on epicormic development (e.g. Ward 1966, Minckler 1967, Miller 1996), but only recently has ontogeny become an important line of study (Fontaine and others 1999, Colin and others 2010).

More specifically, our results suggest that the numbers of epicormics are more strongly controlled by intrinsic developmental processes and are less responsive to environmental and genetic factors in pole-sized white oaks (table 2). The importance of these ontogenic factors is demonstrated by the substantially stronger fit of the br12 model (lme $R^2 = 0.77$) than the br10 model (lme $R^2 = 0.08$); in the br12 model we were able to include br10 and brNewM as predictors while there was no quantitative data available to include in the br10 model describing epicormic ontogeny. In another study at these sites, it was found that the number of epicormic structures on a tree is heavily influenced by the per meter density of non-epicormic branches, a factor that is set at a very young age (Meier and Saunders 2013). Therefore, selection of individuals that show greater apical dominance at an early age could lead to a decrease epicormic numbers later.

On the other hand, variations in brBA among groups became more accentuated following CTR and there was a significant brBA increase in response to release. The stronger family random effect suggests that there may be more potential for selection of superior genotypes by considering the cumulative size of branches rather than the absolute number of branches (sensu Meier 2012). Further research seems merited, both for thinned and unthinned stands. Additionally, with half-sib plantations, some of the family variation is introduced by the genetics of the paternal tree; a stronger understanding of the genetic effect could be gained from studying either controlled crosses or clones, or by conducting parentage analysis on individual half-sibs to identify which share the same parent.

CONCLUSIONS

Colin and others (2010) defined a research framework in which the relative impacts of genetics and environment should be studied in terms of their effect on epicormic ontogeny. In this study, we focused on the contribution of family history and tree vigor to total branch numbers and branch size following crop tree release. The family effect on total branch numbers was negligible, but the family effect on branch size was slightly more important. Vigor was an important influence on the number and size of branches present prior to treatment, with higher vigor trees having fewer, smaller branches than less vigorous trees. However, epicormic response to crop tree release was most strongly influenced by the epicormic composition prior to treatment. This suggests that a better understanding is needed of the ontogenic factors that influence epicormic development early in a tree's life.

ACKNOWLEDGMENTS

This project would also not have been possible without the invaluable cooperation of the Indiana Department of Natural Resources. Special thanks go Phil O'Connor, Dwayne Sieg and John Karstens for access to the white oak progeny tests. Individuals that helped with data collection include: Jake Dyer, Daniel Moscoso, Sebastian Saenz, Aaron Forgey, Orianna Rueda-Krauss, Caleb Brown, Phil Crystal, Chris Zellers, Travis Swaim and Ethan Belair. Finally, we would like to thank the Fred M. van Eck Foundation for Purdue University and the US Forest Service, Northern Research Station for funding this project.

LITERATURE CITED

Bolker, B. 2012. Package 'bbmle': tools for general maximum likelihood estimation. R package version 1.0.4.1. http://cran.r-project.org/web/packages/bbmle/index.html [Date accessed: May 10, 2015].

Bowersox, T.W.; Ward, W.W. 1968. Auxin inhibition of epicormic shoots in white oak. Forest Science. 14: 192-196.

Brown, C.L.; McAlpine, R.G.; Kormanik, P.P. 1967. Apical dominance and form in woody plants: a reappraisal. American Journal of Botany. 54: 153-162.

Chen, H.-J.; Bollmark, M.; Eliasson, L. 1996. Evidence that cytokinin controls bud size and branch form in Norway spruce. Physiologia Plantarum. 98: 612-618.

Coggeshall, M.V. 1993. Oak tree improvement in Indiana. Annales des Science Forestières. 50: 416s-419s.

Colin, F.; Ducousso, A.; Fontaine, F. 2010. Epicormics in 13-year-old *Quercus petraea*: small effect of provenance and large influence of branches and growth unit limits. Annals of Forest Science. 67: 312.

Del Tredici, P. 2001. Sprouting in temperate trees: a morphological and ecological review. Botantical Reviews. 67: 121-140.

Devine, W.D.; Harrington, C.A. 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. Trees–Structure and Function. 20: 747-756.

Dimov, L.D.; Stelzer, E., Wharton, K. [and others]. 2006. Effects of thinning intensity and crown class on cherrybark oak epicormic branching five years after treatment. In: Conner, K.F., ed. Proceedings of the 13th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-92. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 606-610.

Evans, J. 1987. The control of epicormic branches. In: Patch, D., ed. Advances in practical arboriculture. Bull. 65. London, England: Forestry Commission: 115-120.

Fontaine, F.; Kiefer, E.; Clement, C. [and others]. 1999. Ontogeny of the proventitious epicormic buds in *Quercus petraea*. II. From 6 to 40 years of the tree's life. Trees–Structure and Function. 14:83-90.

Ishii, H.T.; Ford, E.D.; Kennedy, M.C. 2007. Physiological and ecological implications of adaptive reiteration as a mechanism for crown maintenance and longevity. Tree Physiology. 27: 455-462.

Jensen, J.S.; Wellendorf, H.; Jager, K. [and othrs]. 1997. Analysis of a 17-year old Dutch open-pollinated progeny trial with *Quercus robur* (L.). Forest Genetics. 4: 139-147.

Kormanik, P.P.; Brown, C.L. 1969. Origin and development of epicormic branches in sweetgum. Res. Pap. SE-54. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station. 17 p.

Lockhart, B.R.; Michalek, A.J.; Lowe, M.W. 2006. Epicormic branching in red oak crop trees five years after thinning and fertilizer application in a bottomland hardwood stand. In: Conner, K.F., ed. Proceedings of the 13th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-92. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 595-598.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. Forest Ecology and Management. 6: 343-360.

Maj, A. 2011. Package 'lmmFIT': goodness-of-fit measures for linear mixed models with one-level-grouping. R package version 1.0. http://cran.r-project.org/web/packages/lmmfit/index.html [Date accessed: May 10, 2015].

McDonald, P.M.; Ritchie, M.W. 1994. Epicormic branching of California black oak: effect of stand and tree characteristics. Northwest Science. 68: 6-10.

Meadows, J.S. 1995. Epicormic branches and lumber grade of bottomland oak. In: Lowery, G.; Meyer, D., eds. Proceedings of the 23rd annual hardwood symposium: advances in hardwood utilization: following profitability from the woods through rough dimension. Memphis, TN: National Hardwood Lumberman's Association: 19-25.

Meadows, J.S.; Burkhardt, E.C. 2001. Epicormic branches affect lumber grade and value in willow oak. Southern Journal Applied Forestry. 25: 136-141.

Meadows, J.S. and J.C.G. Goelz. 2002. Fourth-year effects of thinning on growth and epicormic branching in a red oak-sweetgum stand on a minor stream bottom site in west-central Alabama. In: Outcalt, K.W., ed. Proceedings of the 11th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-48. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 201-208.

Meier, A.R. 2012. Aspects of epicormic development in *Quercus alba* (L.) and other eastern North American oak species in relation to genetics, tree vigor and silvicultural treatments. West Lafayette, IN: Purdue University. 244 p. M.S. thesis.

Meier, A.R.; Saunders, M.R.; Michler, C.H. 2012. Epicormic buds in trees: a review of bud establishment, development and dormancy release. Tree Physiology. 32: 565-584.

Meier, A.R.; Saunders, M.R. 2013. Assessing internal epicormic dynamics in *Quercus alba* L. using CT scanning: the strong effects of shoot development and tree growth relative to progeny level genetic variation. Trees–Structure and Function. 27: 865-877.

Miller, G.W. 1996. Epicormic branching on central Appalachian hardwoods 10 years after deferment cutting. Res. Pap. NE-702. Radnor, PA: U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station. 9 p.

Miller, G.W.; Stringer, J.W.; Mercker, D.C. 2007. Technical guide to crop tree release in hardwood forests. Pub. PB1774. Knoxville, TN: University of Tennessee Extension. 23 p.

Minckler, L.S. 1967. Release and pruning can improve growth and quality of white oak. Journal of Forestry. 65: 654-655.

Nicolini, E.; Chanson, B.; Bonne, F. 2001. Stem growth and epicormic branch formation in understorey beech trees *(Fagus sylvatica* L.). Annals of Botany. 87: 737-750.

O'Connor, P.A; Coggeshall, M.V. 2011. White oak seed source performance across multiple sites in Indiana through age 16. In: Fei, S.; Lhotka, J.M.; Stringer, J.W. [and others], eds. Proceedings of the 17th central hardwood forest conference. Gen. Tech. Rep. P-78. Newtown Square, PA: U.S. Department of Agriculture Forest Service, Northern Research Station: 358-363.

Pinheiro, J.C.; Bates, D.M. 2000. Mixed-effects models in S and S-plus. New York: Springer-Verlag. 528 p.

Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; R Core Team. 2012. Package 'nlme': linear and nonlinear mixed effects models. R package version 3.1-104. http://cran.r-project.org/web/packages/nlme/index.html [Date accessed May 10, 2015].

R Development Core Team. 2012. R: A language and environment for statistical computing, version 2.15.0. Vienna, Austria: R Foundation for Statistical Computing.

Rast, E.D.; Sonderman, D.L.; Gammon, G.L. 1973. A guide to hardwood log grading (revised). Gen. Tech. Rep. NE-GTR-1. Upper Darby, PA: U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station. 32 p.

Schlesinger, R.C. 1978. Increased growth of released white oak poles continues through two decades. Journal of Forestry. 76: 726-727.

Spiecker, H. 1991. Controlling the diameter growth and the natural pruning of sessile and pedunculate oaks. Schriftenreihe der Landesforstverwaltung. Stuttgart, Germany: Baden-Württemberg Band 72. 135 p.

Springmann, S.; Rogers, R.; Spiecker, H. 2011. Impact of artificial pruning on growth and secondary shoot development of wild cherry (*Prunus avium* L.). Forest Ecology and Management. 261: 764-769.

Stubbs, J. 1986. Hardwood epicormic branching – small knots but large losses. Southern Journal of Applied Forestry. 10: 217-220.

Ward, W.W. 1966. Epicormic branching of black and white oaks. Forest Science. 12: 290-296.

Yokoi, S.; Yamaguchi, K. 1996. Origin of epicormic branches and effect of thinning on their development in *Quercus mongolic* var. *grosserrata*. Journal of the Japanese Forest Society. 78: 169-174.

Wignall, T.A.; Browning, G.; Mackenzie, K.A.D. 1987. The physiology of epicormic bud emergence in pedunculate oak (*Quercus robur* L.). Responses to partial notch girdling in thinned and unthinned stands. Forestry. 60: 45-56.

Zuur, A.; Ieno, E.; Walker, N.; Saveliev, A.; Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. New York: Springer. 574 p.