

# Individual Tree and Stand Level Influences on the Growth, Vigor, and Decline of Red Oaks in the Ozarks

Steven L. Voelker, Rose-Marie Muzika, and Richard P. Guyette

**Abstract:** Repeated oak decline and mortality events have occurred in the Ozark region for decades and probably longer. We sampled an age sequence of 1,259 black and scarlet oaks (*Quercus velutina* Lam. and *Quercus coccinea* Muench.) to better describe the process of oak decline and mortality in the red oak group (subgenera *Erythrobalanus*). Trend in basal area increment (BAI) over the most recent 40 years was used to establish three vigor classes for trees with decreasing, stable, or increasing growth (*Declining*, *Stable*, or *Healthy*). We compared crown condition measures with absolute BAI and boundary line BAI, a measure of radial growth adjusted for tree size. A pulse of mortality was found to occur just subsequent to the most recent drought, although decline often started decades previously. Time series of individual tree BAI suggests that half of all oak decline events were incited by one or two drought-related step-changes in growth and variance. Predisposing factors to decline generally showed significant but weak relationships with crown conditions. Surviving oaks growing in high-mortality stands had poorer crown conditions and grew more slowly than trees in low-mortality stands. When recently dead trees were accounted for, the same high-mortality stands had significantly greater predecline basal area and stocking than low-mortality stands. Thus, a less competitive growth environment may afford some buffer to drought stress before oak decline but does not appear to help afflicted stands improve their growth and vigor. FOR. SCI. 54(1):8–20.

**Keywords:** oak decline, drought, shoot dieback, forest health, boundary line basal area increment.

NUMEROUS DECLINE AND MORTALITY EVENTS have been recorded in red oak forests (Hursh and Hassis 1931, Millers et al. 1989, Biocca et al. 1993, Clinton et al. 1993, Jenkins and Pallardy 1995, LeBlanc 1998, Oak et al. 2004, Starkey et al. 2004). The classic etiology of oak decline suggests that an inciting event causes physical injury (often shoot dieback or defoliation), which reduces whole tree photosynthetic potential and depletes energy reserves in the form of nonstructural carbohydrates. These afflicted trees are then more susceptible to opportunistic pathogens (Manion 1991, Wargo 1996, Marçais and Bréda 2006). Consequently, crown conditions, or a tree's pattern of branching and hydraulic architecture providing water from the soil to the leaves are closely tied to past and present capacity for photosynthesis and growth (Dwyer et al. 1995, Rust and Roloff 2002). Indeed stem growth can be interpreted as a fixed record of tree vigor because of the priorities for carbon allocation during the growing season (Waring 1987, Barbaroux et al. 2003). Therefore, the lower basal area growth of declining oaks before an inciting event is evidence that some combination of predisposing factors play an important role in the decline process (Pederson 1998). Despite continued oak decline events and their study, forest managers and silviculturists have been frustrated by a lack of fundamental knowledge that could prioritize treatable versus unavoidable influences to decline and mortality of mature red oaks. Inciting events such as drought are

unavoidable, but an improved knowledge of how trees respond to predisposing factors to oak decline may allow forest scientists to better focus and experimentally test preventative silvicultural approaches in maturing forests. To monitor forest health and vigor, crown condition measurements provide an immediate assessment (Zarnoch et al. 2004) whereas stem growth patterns determined from increment cores have often been viewed as too labor-intensive despite the detailed information they provide (Biondi 1999).

The need to assess forest declines with respect to potential predisposing factors such as stand composition, stand age, stand density, and site productivity has been acknowledged for some time (Hyink and Zedaker 1987), but few studies are designed within the context of evaluating these factors. Some research has suggested that certain site characteristics interacting with stand age predispose oaks to decline (Starkey and Oak 1988, Tainter et al. 1990, Biocca et al. 1993, Dwyer et al. 1995, Oak et al. 1986, 1996) or that declining oaks were more often located on xeric landforms or other site-specific conditions (Oak et al. 1986, 1996, Jenkins and Pallardy 1993, 1995). In the Missouri Ozarks, drought and *Armillaria* root disease are the most important inciting and contributing factors in the mortality of red oaks (Jenkins and Pallardy 1995, Bruhn et al. 2000). Our study builds on this knowledge by more thoroughly considering how predisposing factors at the stand level can affect tree

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growth and vigor as well as detailing individual tree variability in the temporal course of decline caused by the interaction of tree age and past droughts. Therefore, our objectives here are to verify which crown condition measure provided the best agreement with intertree variation in basal area increment (BAI) versus our novel method for determination of boundary line BAI, use the best crown condition measure and boundary line BAI to investigate predisposing factors to drought-induced shoot dieback and oak decline, and provide perspective on tree age and the timing of droughts as influences on the process of decline and tree death.

## Methods

### Study Area

The study area was centered near 37°N latitude and 91°W longitude and encompasses the upper Current River watershed, the most dissected and densely forested region of the Missouri Ozark highlands. The most important tree species in this region, as a percentage of basal area on Missouri Ozark Forest Ecosystem Project (MOFEP) control sites are black oak (28%), scarlet oak (24%), white oak (*Quercus alba* L.) (19%), shortleaf pine (9%), and post oak (*Quercus stellata* Wangenh.) (6%). Upland soils are highly weathered ultisols or alfisols with variable-to-high content of cherty-gravel (Kabrick et al. 2000). The upland soils overlying the ancient Ozark uplift are generally slightly acidic and have low N availability. Mean annual precipitation for the Missouri Ozarks is near 1,150 mm.

Before Euro-American settlement the relatively open forests of the Missouri Ozarks were maintained through intentional burning by Native Americans (Batek et al. 1999, Guyette et al. 2002). The period after Euro-American settlement was characterized by increased fire frequency along with large scale forest cutting followed by more recent efforts for fire suppression (Beilmann and Brenner 1951, Cunningham and Hauser 1989, Guyette and Larsen 2000, Guyette et al. 2002). The loss of seed trees from historic preferential cutting of shortleaf pines combined with later fire suppression allowed the red oaks to replace most pine forests of the region (Law and Gott 1987, Cunningham and Hauser 1989).

### Site Selection

During 2002 and 2003, two plot-selection techniques and sampling procedures were used. Access to preexisting data for vegetation monitoring plots on MOFEP sites provided an opportunity to exclude sites having had recent timber harvests or not containing >35% live and dead basal area in red oaks. This allowed for an intensive sample of randomly selected trees (up to 10 red oaks at each plot) while retaining the ability to use plot-level data collected the winter of 2002–2003 (by Randy Jensen and others at MOFEP). Across all nine MOFEP sites, 88 0.2-ha plots were sampled. The second plot selection included 59 0.083-ha plots randomly distributed across a wider portion of the watershed using GIS software (Arcview version 3.2; ESRI, Inc., Red-

lands, CA) and located with a handheld global positioning system. These sample plots were relocated to a nearby location if a considerable recent disturbance was evident. A more detailed description of plot selection and locations can be obtained from Voelker et al. (2006).

### Measures of Tree Vigor, Crown Size, and Condition

At each outlying plot, we measured the dbh of all live and recently dead trees. The only requirement for being classified as recently dead for these standing or down trees was that they have intact bark and sapwood. At each MOFEP plot, we updated mortality records for all newly dead trees. For all plots, we made absolute measures of crown size on living trees sampled: height, live crown ratio, and crown radius. We defined live crown ratio as the proportion of total height that live, leaf-bearing branches are distributed along. The crown condition measures *Dieback* and *Density* were also estimated for each living tree according to the descriptions provided in the US Forest Service 2002 Forest Inventory and Analysis/Forest Health Monitoring Phase 3 Field Guide. Details of how these measures are defined are available in Zarnoch et al. (2004). Briefly, *Dieback* is a visual estimate of the percentage of fine branches that are dead. *Density* is a visual estimate of the percent volume of intact crown remaining, compared with an optimal use of the growing space occupied by the crown. Functionally, these measures account for recent and past shoot dieback events as well as irregularities in potential crown volume as a result of competing neighbor trees.

By comparison of increment cores paired with crown conditions in the field, it was noted that a few years after a drought and shoot dieback event, dead shoots that might have initially characterized decline had largely decayed away leaving a smaller and ragged-looking crown without much shoot dieback as strictly defined by the presence of dead fine branches. Therefore, we thought *Dieback* may be an unsatisfactory measure with which to interpret tree vigor. The most conspicuous characteristics of dying red oaks was that their leaf area was greatly reduced compared with the size of the tree, and this leaf area was largely displayed by epicormic sprouts along the stem and primary branches. Trees with little leaf area in which to fix carbon but large fixed carbon costs due to woody tissue respiration must have relatively less carbon capital to spend on branch regrowth after shoot dieback or for defenses that could ward off contributing pathogens such as *Armillaria* root disease (Wargo 1996). Therefore, we hypothesized that, given such a large range of leaf area displayed on trees of similar size, measurements of the exposed crown surface area and its distribution, held proportional to the stem surface area (SSA) (*sensu* Whittaker and Woodwell 1967), would represent an index more closely tied to the carbon economy and long-term vigor of oak trees. For clarity we list this index of tree vigor, TVI, and other potential measures of tree vigor we considered (Table 1). For the calculation of TVI, we estimated crown surface area (CS) as the area of the trans-

**Table 1. Potential individual tree measures considered as surrogates of tree vigor for this study**

Measures of growth	
BAI	Absolute measure of xylem radial growth, useful as time-series data to identify the timing of step-changes in growth and variance
BAI trend	Significant time-related trends ( $P < 0.01$ ) were determined by $t$ -tests between periods
Boundary line BAI	BAI held relative to the range in BAI for a certain tree size
Measures of crown condition and tree size	
Dieback	An estimate of percentage of fine branches recently dead, unrelated to tree size
Crown surface area (CS):	An estimate of crown size
Weighted crown surface area (CS <sub>w</sub> )	CS inversely weighted by crown length to help account for intertree variation in the proportion of increasingly shaded lower leaves
TVI	CS <sub>w</sub> held relative to stem surface area to help account for intertree variation in sapwood respiratory costs

verse and lateral surface of a cylinder as

$$CS = ((\pi \times CR^2) + (2 \times \pi \times CR \times H \times LCR \times D)), \quad (1)$$

where  $\pi = 3.14159$ , CR is crown radius, H is height, LCR is live crown ratio (scaled to range from 0 to 1) and D is *Density* (scaled to range from 0 to 1).

We hypothesized that lower photosynthetic capacity and light attenuation would cause leaves lower in the canopy to have a poorer carbon balance (i.e., less carbon return for that invested in leaf construction and respiratory costs). To roughly account for this intertree variation we weighted the CS of each tree by the inverse of its LCR. This weighted crown surface (CS<sub>w</sub>) was calculated as

$$CS_w = CS \times (1/LCR). \quad (2)$$

Maintenance respiration of woody tissue can account for more than half of the total annual respiration for oaks (Edwards and Hanson 1996) and consequently must impinge on the levels of stored nonstructural carbohydrates outside of the growing season. This constraint on total stored carbohydrates must also be proportionally greater during drought years when gas exchange is limited yet temperatures result in greater respiration rates of woody and leaf tissues. Thus, when leaf area is very low compared with tree size, carbohydrate stores must at some point limit the necessary and relatively fixed costs of earlywood formation, shoot growth, and early leaf expansion each spring (Barbaroux et al. 2003). Furthermore, a tree's annual carbon balance may depend on other costs outside of the "growing season," such as allocation to fine root growth (Teskey and Hinckley 1981) and exudation, as well as the synthesis of secondary compounds laid down during heartwood formation and those used to ward off opportunistic pathogens (Wargo 1996). To calculate TVI we used CS<sub>w</sub> as the numerator of this tree-level carbon balance and held it proportional to SSA as a denominator. In turn, we hypothesize SSA to be proportional to the carbon allocated to the maintenance and protection of woody tissues. Hence, TVI is calculated solely from simple forest health inventory measures.

$$TVI = CS_w/SSA, \quad (3)$$

where

$$SSA = \pi \times DBH \times Height/2 \times a, \quad (4)$$

and  $a = 1.268$ , an adjustment to the lateral surface area of a cone to estimate the regression-derived SSA of scarlet oaks (Whittaker and Woodwell 1967). We used conic surface area because it should take tree height and stem taper into account, whereas allometric models associated with dbh alone internalize this variation. The adjustment factor,  $a$ , is simplistic but helps account for variation in SSA owing to the decurrent growth form of hardwoods. To assess the efficacy of this adjustment factor, we compared SSA values calculated as above with that provided by Martin et al. (1998) for scarlet oaks. The SSA calculation by Martin et al. is based only on dbh and predicted 46 and 48% of the variation in CS and CS<sub>w</sub>, whereas the SSA calculation by Whittaker and Woodwell predicted 60 and 65% of the variation in CS and CS<sub>w</sub>, respectively. Each of the above four relationships was best fit by linear relationships indicating no tree size-related biases. When directly compared, the two calculations of SSA showed only slight differences for the smallest and largest trees. There were also no apparent differences when black oaks were compared with scarlet oaks or between canopy positions. However, variation in site productivity showed a potential for differences between the two estimates. The adjustment factor that best matched the two estimates of SSA was near 1.8 for trees on the lowest productivity sites and near 1 for trees on the highest productivity sites (data not shown). This result suggests that the dbh-derived equation from Martin et al. overestimates tree height and SSA of shorter, stouter trees on low-productivity sites, whereas the equation provided by Whittaker and Woodwell overestimates SSA to some degree for trees on the highest productivity sites. We decided to keep the original equation and adjustment factor for all trees and acknowledge that TVI is slightly underestimated for trees on the highest site productivities where severe drought stress and oak decline events are rare.

### ***Preparation and Analysis of Radial Increment and Crown Condition Data***

Increment cores were taken from each tree at dbh (1.3 m), perpendicular to the aspect of the slope. Although more

than one core was often taken, only the first core judged close enough to the pith for age determination was kept for analysis. All age-related data are in reference to age at dbh. Only cores containing >35 annual rings that were free from physical disturbance (e.g., fire scar, wood-boring insect damage, or rot) were analyzed. Once mounted on a wooden stove, cores were sanded with progressively finer sandpaper. Tree-rings were measured to the nearest 0.01 mm using an electronic transducer and binocular microscope fixed over a moving stage (model 1; John Roberts, Columbia, MO). All cores were aged and visually cross-dated using two or more known wet and dry signature periods and then statistically cross-dated using the program COFECHA (Holmes et al. 1986). No detrending or standardization procedures were used on the tree-ring data presented here. For BAI, we report data up to the last full tree-ring formed for all increment cores collected in 2001.

To identify vigor classes of individual red oaks we used a method similar to that proposed by LeBlanc (1996). Raw ring-widths were converted to BAI from an estimate of DBH inside bark to avoid distortion of the most recent patterns in stem growth. Using a relationship from increment cores with fully intact bark, we created a regression model of bark width as a function of tree diameter for those increment cores without fully intact bark (Voelker 2004). Each tree was classified as *Healthy*, *Stable*, or *Declining* using a *t*-test to determine whether mean BAI between adjacent 20-year periods (1962–1981 versus 1982–2001) was significantly different. Although this method probably violates the assumption of independence in the often auto-correlated ring-width values, we believe it is warranted because of our use of a conservative *P* value ( $P < 0.01$ ) to minimize type I error in the determination of significant differences in BAI.

To determine a standard means for classifying each crown condition measure we plotted the cumulative frequencies for each CS, CS<sub>w</sub>, TVI, and *Dieback* (Figure 1). These patterns derive from a frequency distribution of TVI that nears normality, whereas those of the other three variables are quite skewed. Although these distributions varied widely, the inner 50%, or central two quartiles seemed to best isolate the portions of each plot where each step of increase or decrease in a crown condition measure added trees to the distribution at a nonconstant rate. To isolate the tails of each frequency distribution we deemed trees in the upper and lower quartiles for each crown condition measure as *Healthy* and *Declining*, whereas trees in the two central quartiles were classified as *Stable*.

Although time series of BAI are useful for identifying significant drought-related step-changes in growth and variance, this variable should generally not be used as a surrogate for vigor when trees or stands are compared because there is great potential for error owing to tree size alone. Tree vigor should be approximately linked to time-related trends in BAI (LeBlanc 1996). However, trend in BAI of individual trees should not be preferred as a continuous measure of tree vigor because larger trees have greater potential BAI and can decrease at a much faster rate, whereas small trees can increase at a much faster rate. For most trees and ring-porous species such as oaks in particu-

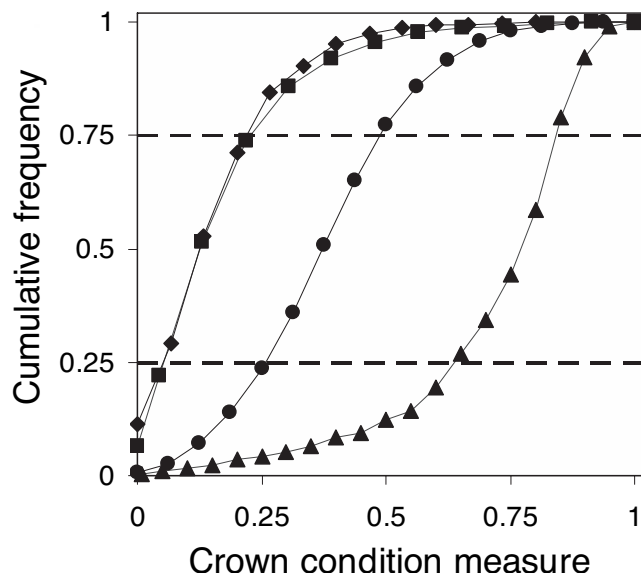


Figure 1. Cumulative frequencies plotted against crown condition values for each oak tree having all four crown condition measures in common ( $n = 1,294$ ); CS (■), CS<sub>w</sub> (◆), TVI (●), and *Dieback* (▲). Dashed lines indicate quartile boundaries. Note that both axes were plotted on a relative scale, so for each variable a lower crown condition measure is considered less vigorous (i.e., 0.1 on the *x* axis corresponds to a tree with 90% *Dieback* of fine branches CS equal to 10% of the maximum value recorded).

lar, two key nonlinear relationships can define the size-related upper and lower potentials of radial growth. The upper limit of BAI growth would be defined by some optimal combination of genotype, soil, site, and competitive conditions a tree experiences within a regional growing season length, temperature, and precipitation regime. The lower limit would often be defined by species tolerances to various minimal resource combinations while still adding at least enough earlywood xylem conduits around the perimeter of the tree to effectively conduct water to expanding shoots each spring. With our large sample size, we defined these boundaries to more accurately compare radial growth in relation to its size-related potential among tree groupings that might differ in size distributions. To define the upper and lower boundaries of radial growth per unit tree size we identified those trees in the 91st–100th percentile and the 1st–10th percentile away from a power regression relating BAI to dbh of all trees sampled (Figure 2). Power regressions were then fit to these upper and lower subsets to predict the size-related boundaries for any group of red oaks sampled from our region. This “boundary line BAI,” was calculated as  $[(BAI - Pred_{Lo}) / (Pred_{Hi} - Pred_{Lo})] \times 100$ , where BAI is the mean for the calendar years 1982–2001,  $Pred_{Lo}$  is the BAI predicted for a given dbh from trees in the lowest percentile range and  $Pred_{Hi}$  is the BAI predicted for a given dbh from trees in the highest percentile range. Individual trees, of course, may have BAI growth that is greater or lesser than boundary lines (i.e., >100% or <0%), but mean values of boundary line BAI from a stand or other tree grouping should nearly always fall somewhere between 0 and 100% of the boundary lines. Other similar boundary line techniques have been developed, including the identification of historic growth releases due to stand dynamics

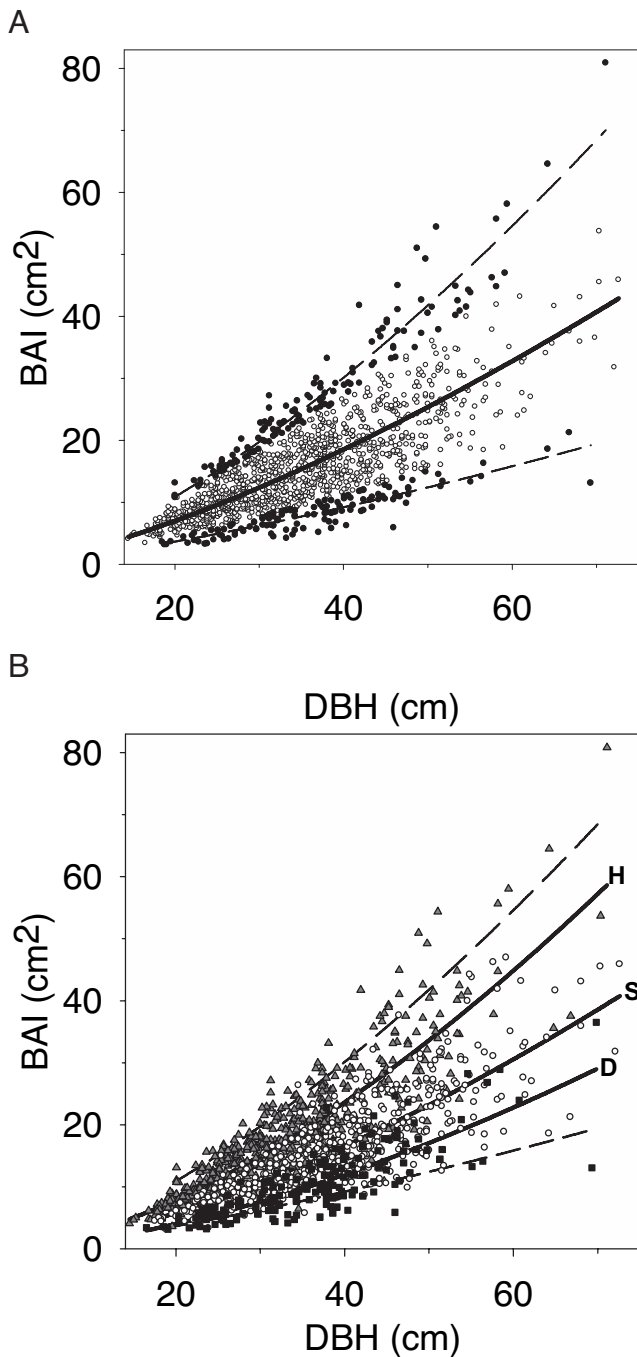


Figure 2. Top panel: Tree size-dependent variation in BAI for each tree sampled. The bold regression line,  $BAI = 0.1194 \times dbh^{1.3518}$  describes the mean response across all trees, whereas the upper and lower 10 percentile boundaries (black circles and dashed regression lines) are described by  $BAI = 0.1508 \times dbh^{1.4339}$  and  $BAI = 0.0572 \times dbh^{1.3737}$ , respectively. All regression lines were significant ( $P < 0.0001$ ). Bottom panel: The boundary lines from the upper panel are still shown (dashed lines), but the three bold regression lines labeled *H*, *S*, and *D* are for *Healthy* (gray triangles,  $R^2 = 0.77$ ), *Stable* (white circles,  $R^2 = 0.69$ ), and *Declining* (black squares,  $R^2 = 0.64$ ) red oaks. All regression lines were significant ( $P < 0.0001$ ).

(Black and Abrams 2003), but this is the first application we are aware of that helps determine tree vigor and growth potential.

Later we show that the BAI trend method for vigor classification provides a more effective differentiation of boundary line BAI than any of the crown condition classi-

fications. However, besides the possibility for random error introduced by having only one increment core per tree, type II error could also be introduced because BAI trends are loosely correlated with absolute BAI ( $R^2 = 0.17$ ,  $P < 0.05$ ). Because BAI trends upward with greater tree size (Figure 2) and age, a *Stable* tree with no significant trend would more probably be better classified as though it were in decline. Therefore, for our final determination of vigor classes we sought to minimize this potential bias by reclassifying *Stable* trees (as per BAI trend) but still in the lowest 10% of TVI values as *Declining*. This resulted in the final proportion of overstory red oaks classified as *Declining*, *Stable*, and *Healthy* as approximately 20, 35, and 45% of the sample population.

Using six known droughts we visually identified step-changes in BAI growth and variance, presumably initiated by shoot dieback events, by inspection of graphs of BAI series (see example in Figure 3). These were subsequently verified with a test of adjacent 20-year periods of BAI as described above. An inciting drought event was recorded for a tree if the BAI pattern declined or stabilized at a significantly lower level, after a known severe drought (e.g., the drought year tree-ring was included in the predrought test period to make the test more conservative in the assessment of the long-term effect of an inciting event). For the 1988 and 1999 droughts, means from the most recent 13 and 2

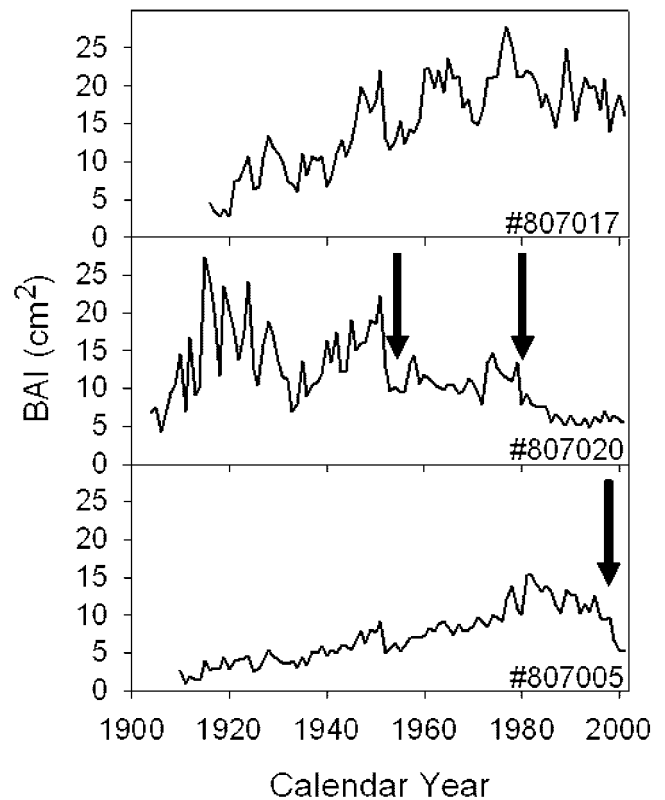


Figure 3. BAI series from three representative trees growing on the same sample plot. Tree 807017 was classified as *Stable* whereas trees 807020 and 807005 were classified as *Declining*. Drought-induced shoot dieback events were assigned (black arrows) to calendar years of known droughts corresponding to step-changes in growth and variance. These were later verified with *t*-tests that compared BAI before and after each drought. Arrows point to severe droughts in 1952–1954 and 1980 as they affected tree 807020 and 1999 for tree 807005.

years were used for comparison with the previous 20-year mean BAI. If BAI declined monotonically after a drought, only that drought was recorded as the inciting event. If a tree stabilized following a drought and then declined again after a second drought, both inciting events were recorded (Figure 3).

Stand-level predisposing factors include soil parent material, site index, “current” stand basal area when sampled, and basal area difference in relation to recent tree mortality estimates. Soil parent material was determined at each plot by observing the local elevation, landscape position, and soil characteristics as well as the types of exposed rocks at the soil surface. Stand basal area and basal area differences were determined from summed dbh measurements of all live and recently dead trees at each plot. Site index or species-specific height growth over a certain time period has long been used by silviculturists to estimate forest site productivity because of the relative invariance of height growth of dominant trees to stand density (Gingrich 1967). Site index values reported are in meters at base age 50 years based on the averages of total height and age of the three tallest red oaks sampled at each plot. A within-stand predisposing factor we investigated was relative height. Relative height was calculated as the total height of each tree divided by the mean height of all red oaks sampled at a plot. Analysis of variance (ANOVA) for unbalanced designs (PROC GLM, SAS Institute 2002) was used to test for differences in TVI for stand-level predisposing factor classes with age group as a blocking factor. TVI values within the six age groups we identified were sufficient to conform to the assumptions of ANOVA.

## Results

### Crown Condition, Tree Growth, and Vigor

Crown condition measures described mean 1982–2001 BAI better in *Healthy* > *Stable* > *Declining* red oaks (Table 2). Within each vigor class, the weighting of CS by the inverse of LCR to calculate CS<sub>w</sub> (equation 2) explained more variation in BAI (Table 2). As hypothesized, this weighting by the inverse of LCR explained more variation in the growth of *Healthy* trees for which lower branches were probably more self-shaded. Less improvement was seen for *Declining* oaks characterized by leaf area largely

displayed by epicormic branches in light-rich canopy gaps (Table 2). TVI did not predict mean BAI as well as CS and CS<sub>w</sub>, whereas *Dieback* explained surprisingly little variation in BAI. The variables CS and CS<sub>w</sub> were better predictors of absolute BAI because of their positive correlation with tree size. Across a range in tree sizes then, the better correlations of CS and CS<sub>w</sub> with BAI tell us more about crown size and less about oak decline and tree vigor. To compare these crown condition measures and test this hypothesis we classified each tree by its trend in BAI, a measure of radial growth that is better than absolute BAI for the epidemiological classification of tree vigor (LeBlanc 1996). Our tests for such BAI trends found that 17% of red oaks were *Declining*, having significantly lower BAI ( $P < 0.01$ ) over the most recent 20 years than over the previous 20 years.

We used boundary line BAI (Figure 2) for further comparisons with crown condition measures because as a continuous comparison of growth, even the trend in BAI among tree groupings could be confounded by differing tree size distributions. Not surprisingly, the BAI trend method for vigor class determination most effectively separated oaks in terms of boundary line BAI than vigor classes determined by the crown condition measures we tested (Table 3). As determined by the BAI trend method, *Declining* and *Healthy* trees captured 12% versus 66% of their size-related growth potential. Of the four crown condition measures, TVI was best at separating oaks into vigor classes in terms of boundary line BAI. Although *Dieback* showed no significant relationships with BAI, it did discriminate between *Declining* and *Stable* trees as well as TVI. Both CS and CS<sub>w</sub> were less effective than TVI for differentiating boundary line BAI among vigor classes (Table 3).

### Stand Dynamics in Relation to Oak Decline

Greater than 95% of trees judged to be recently dead had died within 5 years of the sampling date, with a maximum of 11 years previously (Figure 4A). The frequency of mortality before 1998 is underrepresented owing to sapwood decay. Nevertheless, red oak mortality increased substantially after the 1999 drought and then decreased by 2003. Consistent with the notion that younger trees may be more resilient to drought, there were proportionally more *Declining* and recently dead trees sampled for the ages 75–100

**Table 2.** Coefficients of determination,  $R^2$ , for simple linear regression models relating mean 1982–2001 BAI to four measures of crown condition

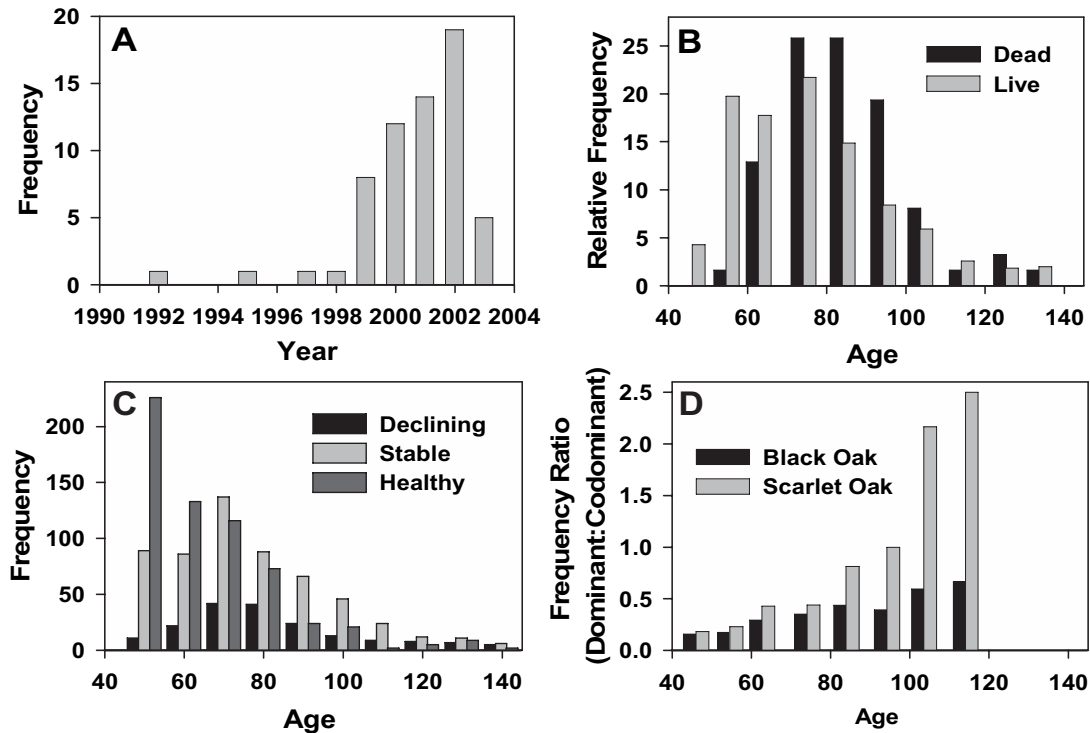
	<i>Declining</i> $R^2$ (n)	<i>Stable</i> $R^2$ (n)	<i>Healthy</i> $R^2$ (n)	All vigor classes $R^2$ (n)
Crown surface (CS); both species	0.34	0.51	0.58	0.55
<i>Q. velutina</i>	0.33 (122)	0.42 (330)	0.59 (207)	0.46
<i>Q. coccinea</i>	0.29 (40)	0.55 (193)	0.64 (271)	0.58
Weighted crown surface (CS <sub>w</sub> ); both species	0.39	0.55	0.65	0.60
<i>Q. velutina</i>	0.34 (122)	0.46 (329)	0.60 (206)	0.52
<i>Q. coccinea</i>	0.39 (40)	0.60 (193)	0.69 (270)	0.64
Index of tree vigor (TVI); both species	0.09	0.14	0.14	0.19
<i>Q. velutina</i>	0.07 (122)	0.08 (329)	0.16 (206)	0.13
<i>Q. coccinea</i>	0.02 (40)*	0.17 (193)	0.13 (270)	0.16
<i>Dieback</i> ; both species	0.02*	0.01*	0.00*	0.04*
<i>Q. velutina</i>	0.01 (122)*	0.01 (330)*	0.00 (207)*	0.01*
<i>Q. coccinea</i>	0.06 (40)*	0.04 (193)*	0.00 (271)*	0.02*

\*Relationship was not significant ( $P < 0.05$ ).

**Table 3. Mean boundary line BAI values ( $\pm 1$  SD) for *Declining*, *Stable*, and *Healthy* red oaks**

	BAI trend vigor classes	TVI vigor classes	Dieback vigor classes	CS <sub>w</sub> vigor classes	CS vigor classes
<i>Declining</i>	12.2 ( $\pm 15.6$ )	27.2 ( $\pm 24.2$ )a	29.9 ( $\pm 25.0$ )a	34.2 ( $\pm 26.0$ )b	35.1 ( $\pm 26.4$ )b
<i>Stable</i>	35.0 ( $\pm 19.0$ )	46.7 ( $\pm 25.9$ )a	48.6 ( $\pm 28.0$ )a	46.7 ( $\pm 28.3$ )a	46.1 ( $\pm 28.1$ )a
<i>Healthy</i>	65.7 ( $\pm 24.4$ )a	62.6 ( $\pm 28.2$ )a	56.5 ( $\pm 27.5$ )b	55.4 ( $\pm 28.6$ )b	55.2 ( $\pm 28.8$ )b

Data are shown within the five vigor classification methods investigated (BAI trend method and four crown condition classifications). Within vigor classes, values followed by the same letter are not significantly different ( $P < 0.05$ ).



**Figure 4.** (A) Frequency of year of last full tree-ring formed for recently dead trees that were cored and cross-dated. (B) Relative frequencies of live and dead red oaks indicate that living trees were sampled more frequently in the youngest three age groups 45, 55, and 65 whereas dead trees were sampled more frequently in the next oldest age groups 75, 85, and 95. (C) Age-related frequency of red oaks within vigor classes. (D) Ratios of the number of trees tallied in dominant:codominant canopy classes for black and scarlet oaks by age class. Data in D are only shown through age 120 because small sample sizes made the ratio highly variable.

years (Figure 3B and C). Although scarlet oak is known to be very shade intolerant, the proportional change in dominance with tree age was amazingly consistent for each species (Figure 4D). This species comparison suggests that scarlet oak is unlikely to survive for very long as a codomi-

nant, whereas black oak is more tolerant to multiple stresses such as drought and shading.

Many tree attributes were significantly different among vigor classes, especially in how *Declining* trees contrasted with the other two groups (Table 4). Notable were the

**Table 4. Mean attributes ( $\pm 1$  SD) of overstory red oak trees by vigor class**

	<i>Healthy</i>	<i>Stable</i>	<i>Declining</i> and dead*
Age (years)	67 ( $\pm 18$ )	80 ( $\pm 21$ )	87 ( $\pm 22$ )*
dbh (cm)	32.6 ( $\pm 3.8$ )	38.3 ( $\pm 4.1$ )	36.2 ( $\pm 3.6$ )*
Crown aspect ratio	1.0 ( $\pm 0.4$ )a	1.0 ( $\pm 0.5$ )a	1.5 ( $\pm 0.7$ )
Height (m)	20.4 ( $\pm 3.9$ )	21.1 ( $\pm 3.6$ )	19.5 ( $\pm 3.6$ )
TVI	7.4 ( $\pm 2.5$ )	6.6 ( $\pm 2.2$ )	3.4 ( $\pm 1.7$ )
Dieback (%)	20 ( $\pm 14$ )a	27 ( $\pm 16$ )a	47 ( $\pm 27$ )
Density (%)	59 ( $\pm 14$ )a	54 ( $\pm 14$ )a	38 ( $\pm 15$ )
Transparency (%)	35 ( $\pm 7$ )	37 ( $\pm 7$ )	39 ( $\pm 9$ )
1962–1981 BAI (cm <sup>2</sup> )	12.2 ( $\pm 7.0$ )	16.4 ( $\pm 8.2$ )	11.6 ( $\pm 7.0$ )*
1982–2001 BAI (cm <sup>2</sup> )	17.7 ( $\pm 9.5$ )	16.0 ( $\pm 7.9$ )	9.9 ( $\pm 2.5$ )*
1997–2001 BAI (cm <sup>2</sup> )	20.1 ( $\pm 11.3$ )	16.1 ( $\pm 8.9$ )	8.2 ( $\pm 4.6$ )*

Means with the same letter are not significantly different among vigor classes. Values followed by \* are column means.

\*Means include data from *Declining* and recently dead trees.

differences in tree age, crown aspect ratio (crown length/crown width), and TVI. Differences in BAI among vigor classes between the 20-year growth periods is to be expected because that is largely how vigor classes were ultimately defined, but the most recent 5-year period of BAI showed a continuation of the overall BAI trends: increases in *Healthy* trees and continued growth decreases for *Declining* red oaks (Table 4).

### ***Predisposing Factors to Oak Decline***

TVI of red oaks was significantly different among the Roubidoux, upper Gasconade and lower Gasconade soil parent materials (ANOVA,  $F = 4.37$ ,  $P = 0.0128$ ). A significant interaction term was present between parent material and age group (ANOVA,  $F = 6.27$ ,  $P < 0.0001$ ). This nonlinear relationship is due to the significantly greater TVI values ( $t$ -test,  $P < 0.05$ ) of trees that grew on the lower Gasconade parent material. Soils derived from the lower Gasconade parent material are consistently located on lower slope positions, and those trees are likely to have incurred less drought stress. Within vigor classes very little variation in TVI or boundary line BAI occurred compared with variation among vigor classes (Figure 5A).

Site productivity or site index often varies locally with aspect and slope position in the Ozarks, consistent with differences in soil-water availability during the growing season (Kabrick et al. 2004). The species-specific nature of this estimate of productivity thus confers different information than parent material or directly observed soil characteristics. The peaking patterns within a vigor class for TVI are due in part to an overestimate of stem surface area of trees on the highest productivity site boundary line BAI (Figure 5B). However, this variation among site index classes is small compared with the variation among vigor classes, so a significant effect of site index on TVI was still found, (ANOVA,  $F = 5.20$ ,  $P = 0.0014$ ) owing to *Declining* trees being sampled more frequently on plots with lower site indices. The expected linear effect of site index on boundary line BAI was still evident (Figure 5B).

As a testament to the importance of competition for light as a predisposing factor, only four *Declining* trees were found to have a total height 10% greater than average. Trees with lower relative height (and thus lower irradiance per crown size or leaf area) tend to have lower TVI and boundary line BAI values (Figure 5C). This pattern of TVI is important to note because red oaks with lower height relative to competitors are often characterized by leaves only near the very top of their crown. The weighting of the crown surface area by the inverse of the LCR (equation 2) would tend to proportionally increase TVI of these shaded trees with leaves just at the top. However, TVI was robust enough not to be unduly influenced by this particular situation (Figure 5C).

Given the same developmental state for these red oak forests, the live basal area of a stand can be used as a surrogate for site occupancy or average competition for resources that the trees incur from each other. There was

no overall effect of the plot-level live basal area (when sampled) on TVI (ANOVA,  $F = 1.18$ ,  $P = 0.3161$ ). However, basal area difference, a measure of recent mortality, was found to be a significant influence on TVI (ANOVA,  $F = 4.45$ ,  $P < 0.0001$ ). Trends in overall mean TVI and boundary line BAI with respect to recent mortality indicate that growth and vigor of surviving trees on high-mortality stands were unimproved despite the resources made available around decline-related canopy gaps (Figure 5D).

To more closely examine how competition may have influenced oak decline we calculated predecline stand characteristics of high- and low-mortality plots by adding recently dead trees to all plots. Basal area on high-mortality plots changed an average of  $-7.7 \text{ m}^2 \text{ ha}^{-1}$ , whereas low-mortality plots increased slightly ( $+0.4 \text{ m}^2 \text{ ha}^{-1}$ ). The predecline basal area and stocking of high-mortality plots ( $27.0 \text{ m}^2 \text{ ha}^{-1}$  and 98.8%, respectively) were both significantly greater ( $t$ -tests,  $P < 0.002$ ) than the basal area and stocking of low-mortality plots ( $19.3 \text{ m}^2 \text{ ha}^{-1}$  and 89.7%, respectively). Decreased current stocking levels versus previous stocking levels on high-mortality plots are largely due to basal area rather than tree density (Figure 6) because trees died across all size classes on high-mortality plots whereas on low-mortality plots, tree deaths predominately occurred in intermediate and suppressed individuals.

### ***Drought, Tree Age, and the Decline Response***

We used an epidemiological approach (*sensu* Leblanc 1996), to detail the complex individual growth responses of *Declining* red oaks to drought. Of the 243 dead or *Declining* trees with adequate BAI series for testing, 51.3% showed no statistically detectable inciting event, 40.2% declined monotonically after a single inciting event, and the remaining 8.4% of red oaks incurred an initial step-decrease in growth, partially recovered, and then declined further after a second drought (Table 5). Because some step-decreases in growth surely occurred during past moderate drought years we did not investigate, droughts were probably responsible for inciting oak decline in more than half of the trees in this region. Because of past mortality, more recent droughts have caused more secondary step-decreases in growth. No dead or *Declining* individuals were observed to recover from more than one step-decrease in growth. In rare cases, the decline process has taken nearly 70 years, with two trees that showed a step-decrease associated with the 1936 drought. However, these trees were both located on low-productivity sites where the severe shoot dieback that probably accompanied the growth decrease was not such a hindrance to competition for light. Between species, the longer-lived black oaks tended to not only survive for more years after a step-decrease in growth but survived proportionally longer than scarlet oaks. By dividing the time since an inciting event by total tree age it was found that black oaks survived about  $30 \pm 2\%$  of their longer lives in decline whereas scarlet oaks survived only  $21 \pm 3\%$  of their shorter lives in a state of decline (data not shown).



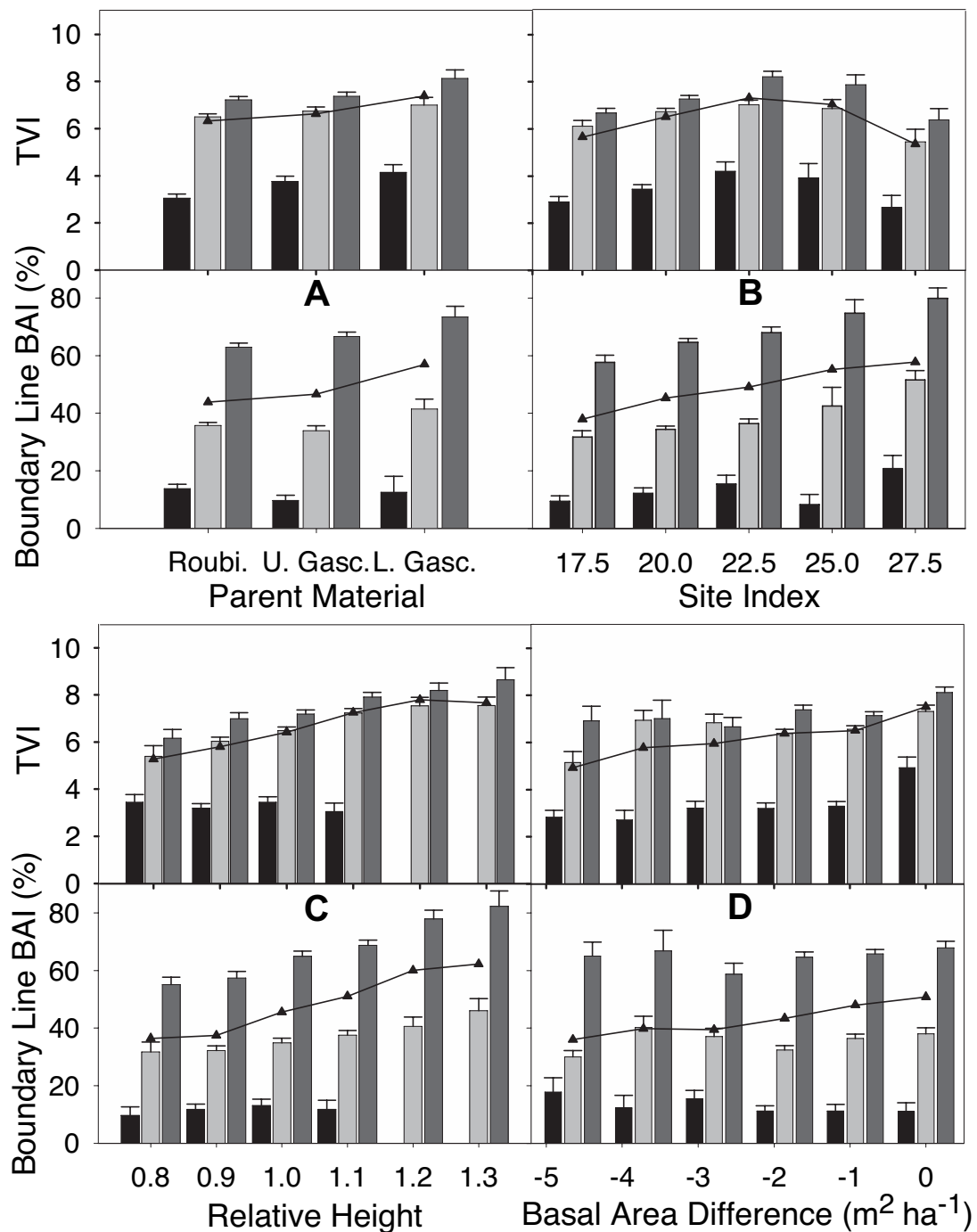


Figure 5. Mean TVI and boundary line BAI values ( $\pm$ SE) indicate trends in tree vigor and growth among potential predisposing factors: (A) parent materials in the region, (B) site index classes, (C) relative height classes, and (D) basal area difference classes. Black bars are *Declining*, light gray bars are *Stable*, and dark gray bars are *Healthy* red oaks. Triangles with connecting lines indicate the trend in the overall mean, which accounts for the relative frequencies of each vigor class. More negative basal area differences indicate greater recent mortality.

## Discussion

### *Crown Conditions, Tree Growth, and Vigor*

The reactions of crown conditions to environmental stresses are exceedingly complex, but across numerous and widespread samples such measures may inform us of important spatial or temporal trends not readily detected at large scales by satellite imagery nor at fine scales by detailed physiological measurements. One problem with mea-

suring crown conditions has been defining standard measures of “tree health” or vigor. This task has long been perplexing if not occasionally arbitrary without careful consideration of what tree characteristics have the most merit as proxies for the physiological measures that cannot be sampled extensively.

Other studies have shown that increment core data may be a valuable addition to forest inventory data (Biondi 1999, Bigler and Bugmann 2004). In addition to these methods,

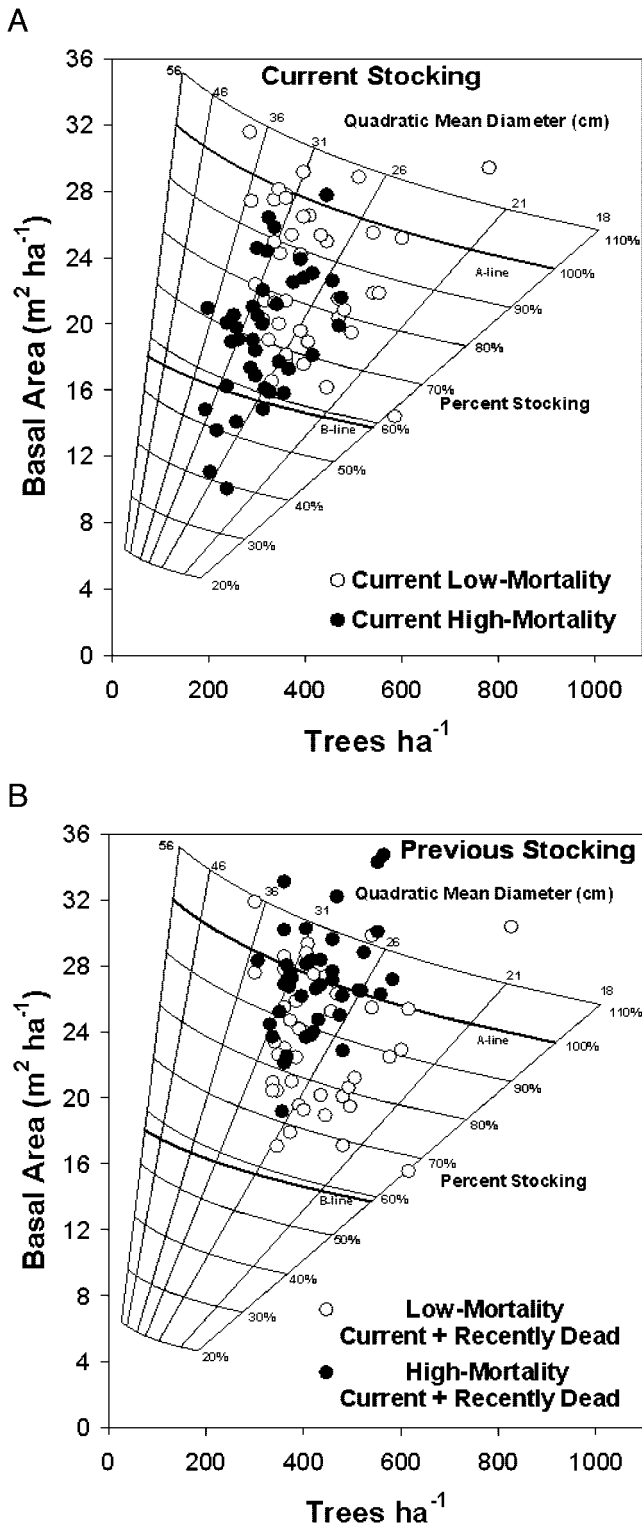


Figure 6. Current and previous estimates of basal area and stand density indicate the percent stocking on declining, high-mortality plots versus healthy, low-mortality plots. Data were plotted after Larsen (2002), modified to metric units with data from Rogers (1980).

boundary line BAI, as an indicator of growth potential is a promising quantitative technique that could help standardize how tree growth and vigor are compared. However, processing tree-ring data correctly requires expertise that is not accessible to most forest inventories considered to be the standard for forest health monitoring. Therefore, we have detailed relationships between four crown condition mea-

asures and absolute tree growth (BAI) and tree growth potential (boundary line BAI). The dependence of BAI on tree size is clear (Figure 2), so it is not surprising that the crown condition measures CS and  $CS_w$  were better at describing intertree variation in BAI than TVI or *Dieback* (Table 2). If the objective behind measuring crown conditions is to clearly identify and separate groups of trees by their growth potential, or boundary line BAI values, then TVI and *Dieback* were better than CS and  $CS_w$  (Table 3). Considering their relative strengths and weaknesses, forest health monitoring efforts would probably benefit from the mutual use of *Dieback* and TVI. For the Missouri Ozarks, most oaks displayed 15–40% *Dieback* of fine branches (Figure 1). The very skewed distribution of *Dieback* made it more difficult to identify healthy versus declining oak stands or significant predisposing factors to oak decline because of the great potential influence and seemingly stochastic occurrence of the minority of trees that displayed severe dieback, >50%. TVI, with its more normal frequency distribution was more influenced by the preponderance of moderately symptomatic or asymptomatic trees.

TVI is a simple empirical ratio that only applies to the aboveground portions of a tree and is yet to be validated with detailed physiological data. Nevertheless, since respiration of woody tissue can be nearly half the total annual carbon use for oaks (Edwards and Hanson 1996), there is reason to believe that this rough estimate of the potential fixed/respired carbon ratio should prove to be a useful measure with which to predict long-term tree vigor. In contrast, *Dieback* may immediately identify where drought-induced injury has been most severe, but it is a more temporally inconsistent crown condition measure considering that most fine branches decay in a few years, but the time between an inciting dieback and death takes most oaks >20 years.

### Stand Dynamics in Relation to Oak Decline

In evidence by the greater relative dominance of scarlet oak in older age groups (Figure 4D), this species has been qualified as intolerant to shade and is generally known to be the fastest growing upland tree species in the Ozarks (Burns and Honkala 1990). During stand development of intolerant species, the midpoint of dominant tree crowns tends to shift proportionally higher, ultimately leading to a change in crown aspect ratio as trees near their potential maximum height and lateral growth becomes a greater priority (Oliver and Larson 1996). Although quite variable, shoot dieback and re-growth of epicormic sprouts along the bole has resulted in a trend opposite to that expected for crown aspect ratio (Table 4). Increased competition for light should decrease crown length relative to tree size during the former phase and tend to lead to differentiation in dominance among a cohort as the trees reach their maximum height. This phase of even-aged stand development needs to be attained before a considerable change in stand structure can be caused by the drought and oak decline-induced canopy gaps. Previous to this phase, even substantial mortality would not change stand structure for long because of rapid vertical and lateral ingrowth by surviving competitors

**Table 5. Responses of *Declining* and dead red oaks to six shoot dieback-inciting droughts**

	Drought calendar years and Palmer Drought Severity Index										Inciting events				
	1936, -5.1 (n = 198)		1952–1954, -5.8 (n = 229)		1971–1972, -2.3 (n = 243)		1980, -3.1 (n = 243)		1988, -1.9 (n = 243)		1999–2000, -2.5 (n = 233)		0	1	2
	1°	2°	1°	2°	1°	2°	1°	2°	1°	2°	1°	2°			
Age group 50	—	—	—	—	0.4	—	0.8	—	0.4	—	1.3	0.9	50	35.7	14.3
Age group 65	—	—	0.9	—	0.4	—	1.2	—	1.2	—	3	0.4	48.4	48.4	3.2
Age group 75	0.5	—	1.3	—	2.1	—	3.3	0.4	2.9	0.4	4.3	3	45.2	40.3	14.5
Age group 85	0.5	—	1.7	—	2.1	—	4.1	—	2.1	0.4	3.4	1.7	45	46.7	8.3
Age group 100	—	—	0.9	—	1.6	—	1.2	—	1.2	—	3	0.9	56.8	38.6	4.5
Age group 120	—	—	0.9	—	1.2	—	0.8	0.4	—	0.4	2.1	0	62.5	31.3	6.3
Grand total or mean*	1.0		5.7		7.8		12.3		9.1		24		51.3*	40.2*	8.5*

Examples of how decline inciting droughts were identified are shown in Figure 3. For each age group row the percentage of trees where a primary (1°) or secondary (2°) inciting drought was tallied is indicated. The three rightmost columns indicate the relative percent of trees that displayed two or fewer step-change growth responses indicative of a shoot dieback event. Dashes indicate where too few trees were alive during the drought to assess growth responses. The Palmer Drought Severity Index (Palmer 1965) values listed are the minimum values for June, July, or August in the nearest climatic division for the drought period listed.

and smaller mid-story trees. These stand dynamics may in part be the reason that mortality was observed to be the greatest in trees 70–100 years old (Figure 4B). The oaks that may have succumbed to oak decline before this age were probably sampled to a lesser extent because they never reached the minimum diameter and crown size required by our methods.

### ***Predisposing Factors to Oak Decline***

Our investigation of predisposing factors was predicated on the ability of crown conditions to correctly differentiate between *Healthy* and *Declining* trees. Secondly, we had to assume that the relative frequency of *Declining* trees would be positively correlated with the degree that predisposing factors can affect crown conditions of those trees that survived to be sampled. Because mortality related to oak decline was already greater on sites with the greatest predisposition to poor crown conditions, our investigation of predisposing factors using TVI were inherently conservative. The relatively small variation of TVI within vigor classes compared with that among vigor classes was promising (Figure 5). This characteristic of TVI allows the frequency with which *Declining* or *Healthy* trees occurred to most affect the overall trend across the range of predisposing factors investigated.

The importance of parent material and resulting soil conditions for forest community organization is apparent from the relationship between historic shortleaf pine dominance and the Roubidoux parent material (Fletcher and McDermott 1957, Batek et al. 1999). On these same sites, red oaks have commonly replaced the extensive pines forests of the Ozarks known from the 1800s (Cunningham and Hauser 1989). The TVI and boundary line BAI of red oaks growing on Roubidoux parent material was lowest, indicating that below-ground conditions on this parent material have significantly predisposed trees to drought and oak decline. These conditions probably include the indirect effects of *Armillaria* root disease (Bruhn et al. 2000) as well as the prevalence of these soils on drought-prone upper slope positions.

Stand density has been implicated but not shown to be a significant predisposing factor of oak decline and mortality (Starkey and Oak 1989, Oak et al. 1996). A strong relationship between these variables would not be expected because few if any studies were initiated before considerable mortality had already occurred. Consequently, as oak decline and mortality progressed, increased symptoms of the surviving trees have had little relationship with the lower stand densities after mortality. Potentially adding to the confusing interpretations of stand density as a predisposing factor to oak decline is site productivity. Higher rates of shoot dieback might be initially found on xeric, lower productivity sites, whereas oak mortality may have substantially lagged because the additional stress of competition for light is lesser on these sites. By keeping track of all recently dead trees, we were able to better estimate predecline site occupancies for each plot. When recently dead trees were added to current stand conditions, the higher stocking and basal area apparent on high-mortality sites suggests that stand density may be a predisposing factor to oak decline (Figure 6). We can only speculate that stands with greater stocking may have incurred relatively greater drought stress or promoted the spread of virulent *Armillaria* spp. Symptoms of *Armillaria* root disease were found to be present on nearly every one of more than 100 dead red oak trees where we excavated a primary root near the root crown (S. L. Voelker, unpublished data). This observation lends further support to the findings of Bruhn et al. (2000) and, in conjunction with the recent experiments by Marçais and Bréda (2006), solidifies how important *Armillaria* root disease is in keeping declining oak trees from improving their growth and crown conditions.

### ***Drought, Tree Age, and the Decline Response***

Many hardwood species abscise leaves to avoid severe drought stress. The oak species we investigated do not regularly abscise leaves during the growing season, but they do undergo regular shoot dieback. Although shoot dieback has been associated with droughts, the physiological process of shoot dieback probably occurs mainly outside of the

growing season because “flagging” branches were rarely observed unless a tree incurred physical disturbance.

Despite the negative connotation of shoot dieback, in an evolutionary context, it has been argued to be adaptive for other woody species that incur severe droughts irregularly (Thomas and Hartmann 1996, Rood et al. 2000, Davis et al. 2002). The tree-ring record for oaks in this region spans at least 350 years and indicates that the return interval for the intensity of droughts that have recently caused pulses of severe dieback and mortality of red oaks is less than 10 years (S. Voelker, unpublished data). Intuitively one would think that more severe droughts should tend to incite more oak decline. However, such severe events should also eventually kill more trees, creating discordance in our interpretation of the relevance of historic drought severity (Table 5). Because of increased mortality after accumulated drought stresses it is impossible to sample the many oaks long dead from earlier droughts. Adding to the difficulty of assessing how drought severity affects oak growth and demography is the fact that Ozark forests in general (and the oaks we sampled) were comparatively young during the severe droughts of the 1930s and 1950s. Few trees in which decline was incited by these long past droughts are still alive, so the tallies of drought-related step-changes in growth and variance for these older droughts are vastly underrepresented. One consistent pattern we found is that when *Declining* trees were able to stabilize basal area growth, the process occurred so slowly that another drought followed to further the decline process (Table 5). That none of the 243 BAI series inspected included a second recovery suggests that the trees we classified as *Declining* were indeed closing in quickly on death.

### ***Implications for Management of Red Oak Stands with Potential for Oak Decline***

Given the variation among stands in tree age, species composition, predisposing factors, and the patchy occurrence of virulent *Armillaria* spp., it is no wonder that forest scientists have been able to provide few broadly applicable lessons for land managers. Our data suggest that scarlet oaks not growing in a dominant canopy position can be assumed to have a much lower probability of survival. Whereas scarlet oaks are increasingly unlikely to live longer after 70 years of age, we found the age of black oaks to regularly exceed 120 years (the oldest individual we found was >210 years of age). This difference in tree age distributions means that black oaks may be managed for longer with less risk of mortality. We found that crown conditions of residual trees did not improve on high-mortality sites, suggesting that removal of *Declining* trees after a severe shoot dieback event is unlikely to increase the vigor of the remaining red oaks unless a much younger cohort is already in place. If most trees on a site are *Declining*, harvest and regeneration may be the best option, considering that the declining trees we sampled only captured 12% of their growth potential. As a preventative measure, our stand stocking charts suggest that lower stand densities maintained through early and repeated thinning may help some stands from experiencing undue drought stress and decline. This is a preliminary

hypothesis and is yet to be experimentally tested. In addition, the degree that intermediate harvests may increase root disease problems in future stands is as yet unknown. Nevertheless, any shift away from red oak dominance will be sure to incur fewer oak decline-related losses.

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