

Allometry of Constitutive Defense: A Model and a Comparative Test with Tree Bark and Fire Regime

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ABSTRACT: In a simulation model, the relative advantage of negative versus positive allometry of defense, that is, early versus delayed defensive investment, depends on the forms of the relationships between body size and growth, body size and mortality deterrence, and defense size and mortality deterrence. Positive allometry is favored by strongly sigmoidal growth, a strongly convex body-size/deterrence relationship, and a concave defense-size/deterrence relationship. Rapid early growth, a weakly convex body-size/deterrence relationship, and a convex defense-size/deterrence relationship favor negative allometry. The model is tested by comparing, among *Pinus* and *Quercus* species, measured intraspecific bark allometry with a predicted ranking of bark allometry along the negative-positive continuum. The ranking is based on the forms of body-size/deterrence and defense-size/deterrence relationships expected in each species' typical habitat given the fire regime and canopy type. This predicted ranking of bark allometry is significantly correlated with measured bark allometry. Negative bark allometry and thick sapling bark are associated with habitats characterized by frequent low-intensity fire and relatively open canopies. Fire-resilient *Pinus* spp. and species of infrequently burned, closed-canopy forests tend to have positive bark allometry and thin sapling bark.

Keywords: allometry, defense, tree bark, fire resistance, *Pinus*, *Quercus*.

Optimal defense theory, dealing mainly with defense by plants against herbivores, has often assumed that investment in defense is not a function of the ontogenetic stage of the whole organism (Herms and Mattson 1992). How-

ever, change in the rate of constitutive defensive investment, or change in the magnitude of induced defense, during the organism's life is certainly possible. Allometry of defense is an appropriate term for such changes. Perrin (1992) applied optimal control theory to defensive investment and showed that growth of defensive structures is likely to be allometric.

Here, our approach to allometry of defense combines a simulation model for generating qualitative predictions with an empirical system to test them. Because increased defense size involves a trade-off against body-size increase, we use the model to investigate how the relative effectiveness of body size and defense size in deterring mortality affect optimal allometry of defense. The empirical system that we employ is pine and oak bark as the defense and fire as the threat. This system provides many species over a wide range of fire tolerance (McCune 1988; Abrams 1992). For a comparative approach, its particularly useful feature is the abundance of natural history information with which to estimate the effect of habitat on the functional relationships between body size and mortality and between defense size (bark thickness) and mortality. In the empirical system, we assess whether major differences in allometry of defense exist among closely related species and whether such differences are consistent with a hypothesis of adaptation.

Because this work proceeded by means of several discrete but related steps, we list them here as a guide to the subsequent presentation. First, we defined a set of functions to encompass the possibilities for relationships between mortality deterrence and both body size and defense size. Mortality deterrence refers to the survival probability that is associated with a given body size or defense size. These functions are applicable to trees and their bark but are abstract enough to apply to other taxa. Second, we performed Monte Carlo simulations to determine how optimal allometry is affected by different combinations of body-size/deterrence function, defense-size/deterrence function, and growth function. Third, we subsequently used natural history information regarding fire frequency, fire intensity, canopy type, and recruitment mode to hy-

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pothesize which forms of the deterrence relationships of body size and bark thickness (e.g., convex and concave upward) putatively co-occur in natural habitats, and by this process we recognized seven habitat types for *Pinus*, and six for *Quercus*. Fourth, we predicted, in terms of selective regimes for adaptive bark allometry, how the habitat types would be ordered along a continuum of negative to positive allometry. This was done by comparing the simulation results with the forms of deterrence relationships that putatively apply to the habitat type. Fifth, based on the dendrology and forest ecology literature we assigned each of 32 *Pinus* and 23 *Quercus* species to its typical habitat type. Finally, we measured intraspecific allometry of bark in the 55 tree species and, using the method of phylogenetically independent contrasts, tested the correlations between predicted allometry rank and actual allometry.

The Simulation Model

Model Structure

For intraspecific allometry, the equation $y = bx^\alpha$ often provides an adequate description of the growth of an organ (y) relative to growth of the whole organism (x). When it does,

$$\frac{dy}{dt} = \alpha \frac{dx}{dt} \frac{y}{x},$$

and the share of increase in size of the whole organism that is allocated to y is proportional to the ratio y/x , with the proportionality defined by α . Thus, the allometric coefficient, α , can be interpreted as an allocation coefficient that indicates the share of the total increase in x that constitutes an increase in y (Calow and Townsend 1981). An allometric coefficient greater than one defines positive allometry, that is, disproportionately greater investment in y at large body sizes, in effect representing postponement of investment in y . When there is disproportionately greater investment in y at small body sizes, the allometry is termed negative, and the allometric coefficient is less than one. Precisely proportionate investment in y with increasing body size is isometry.

We use a simulation model to examine how optimal allometry of defense is affected by the form of functional relationships between body size and growth, between body size and mortality deterrence, and between defense size and mortality deterrence. In the model, body size refers to the cumulative result of organismal growth, except for growth of components that defend against a specific threat. Defense size refers to the cumulative result of growth of these latter components. Mortality deterrence refers to the

organism's probability of surviving any potentially lethal threat. The reasons for using a simulation are several: (1) to constrain the defense/body-size ratio to be equal at initiation and cessation of growth so that only the allometric pathway differs among experimental units, (2) to hold growth function and onset of maturity constant while assessing the effects on optimal allometry of the forms of body-size/deterrence and defense-size/deterrence relationships, and (3) for each combination of functional relationships to compare a measure of fitness across a range of allometric coefficients to assess whether the optimum is broadly or narrowly peaked.

The experimental unit of the simulation is a cohort of 10^5 individuals that grow in body size and defense size and that are exposed to successive episodes of potential mortality, against which both body size and defense are potentially protective. Each individual passes through a series of age units, the length of the series depending on death of the individual or attainment of maximum age. At the beginning of an age unit, the total size of an individual is incremented according to a growth function in which the increment is based on the body size. The increment generated by the growth function is distributed between body size and the defensive component by an allocation procedure that insures the relationship between the two remains as defined by an allometric equation of the traditional form, $y = bx^\alpha$. Such an approach provides relationships as in figure 1A and allows one to consider the effects of varying allometric coefficients while all else is held constant. Both initial body size and initial defense size are 2% of their final sizes; initial and final defense sizes are 20% of initial and final body sizes, respectively. One of two equations is used to define growth as a function of current body size (fig. 1B). The maximal growth per age unit is the same in both functions but is positioned differently relative to final body size. With the logistic equation, growth is maximal at one-half of the final body size, whereas growth is maximal at 0.3 of final body size when growth is defined by the von Bertalanffy equation (Andrews 1982). After growth occurs in each age unit, the individual is tested probabilistically for survival because of the deterrence capability of body size, with probability of deterrence ranging from 0.6 to 0.8 as a function of body size. If body size does not deter death, the defense is tested probabilistically for deterrence using the same probability range as for body size/deterrence. An individual leaves the cohort when both deterrences fail in an age unit or when it completes the final age unit. The probability that an individual survives a given age unit is $P(B) + P(D)[1 - P(B)]$, where $P(B)$ and $P(D)$ are probabilities of deterrence by body size and defense size, respectively. Because $P(B) + P(D)[1 - P(B)] = P(D) + P(B)[1 - P(D)]$, the or-

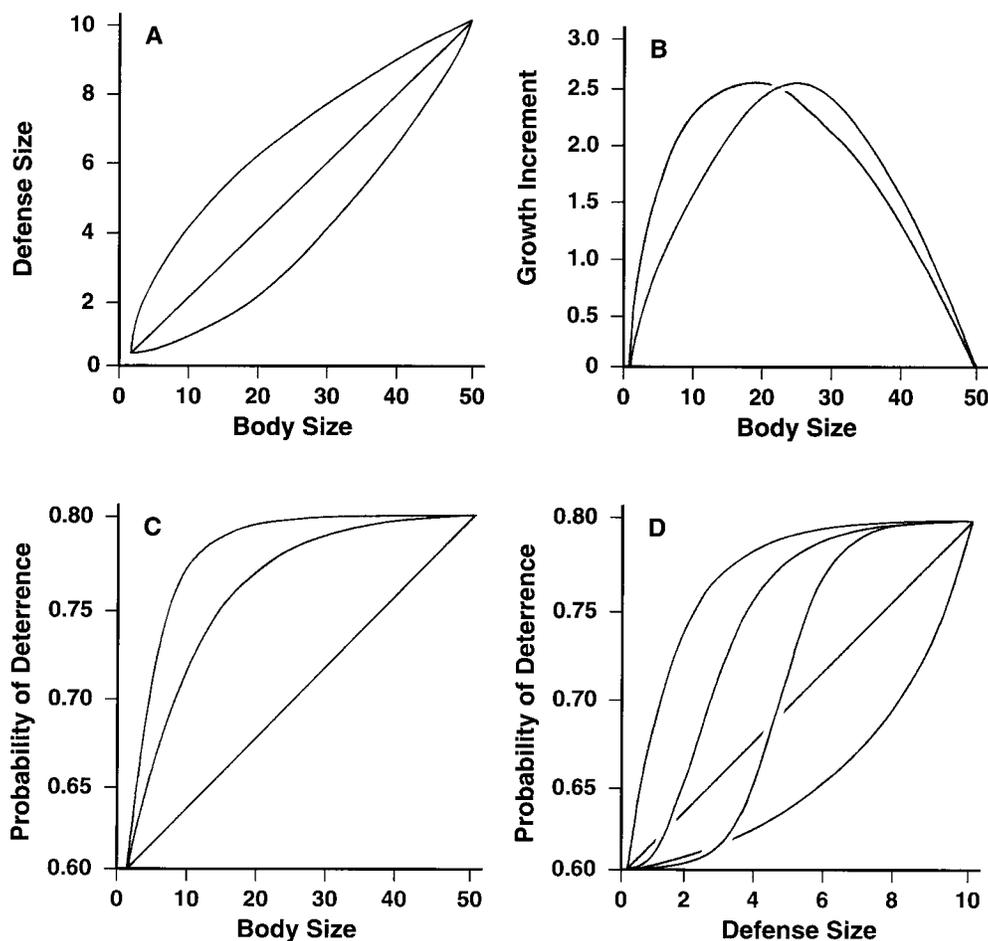


Figure 1: Relationships within the simulation model. *A*, Range of allometric trajectories. From left: allometric coefficients are 0.55, 1.0, and 1.82. *B*, Two growth functions. From left: von Bertalanffy and logistic. *C*, Body-size/deterrence relationships. From left: fast asymptotic, slow asymptotic, and linear. *D*, Defense-size/deterrence relationships. From left at probability of 0.75: moderate asymptotic, Gompertz, logistic, linear, and concave upward.

der of testing for mortality deterrence is computationally irrelevant.

Three functions relating body size to the probability of mortality deterrence are considered (fig. 1C). Although a few studies (e.g., Travis et al. 1985; Glitzenstein et al. 1995) have shown that larger body size deters mortality, such data are not available for large sets of species. However, survivorship curves implicitly relate deterrence to body size. The probability of deterrence can be approximated as $1 - q_x$, that is, one minus the differential of the survivorship curve at any body size. For organisms that increase body size substantially without parental care, Hutchinson (1978) concluded that the typical survivorship curve is the strongly concave Type III; that is, juvenile mortality is much higher than, and declines toward, pre-senile adult mortality. This curve applies to trees before

senescence (Harcombe 1987), and, replotted as probability of deterrence ($1 - q_x$) against body size, it yields a convex body-size/deterrence curve. Two body-size/deterrence functions are employed to model different degrees of this typical situation: fast asymptotic function and slow asymptotic function. In both, minor increases in body size are initially associated with major increases in the probability of deterrence, but, as body size increases further, the probability of deterrence approaches an asymptote. In the third function employed, the probability of deterrence increases linearly with body size; this would apply to a weakly concave survivorship curve whose slope diminishes linearly.

Five functions were chosen to span the range of reasonable possibilities for defense-size/deterrence relationships (fig. 1D). With the moderate asymptotic function,

small increases beyond the initial defense size provide large improvements in deterrence. The Gompertz and logistic functions display the greatest rate of improvement in deterrence when the defense is 25%–50% of its final size and show little increase in deterrence for early increments in defense size. In the concave upward function, deterrence increases exponentially when the defense is large but exhibits slow improvement at small defense sizes.

Each cohort is simulated with a combination of one growth function, one of the three body-size/deterrence functions, one of the five defense-size/deterrence functions, and one allometric coefficient defining allocation to defense over the ontogeny. The simulation is restricted to the survivorship component of fitness and does not vary size at maturity nor model the allocation of resources to reproduction after maturity. Reproductive maturity is set at 70% of maximum body size, and all mature individuals reproduce at equal rates. The criterion of fitness, obtained from a cohort simulation, for each defense allocation strategy is the expected reproductive life span (ERL), defined as the total number of age units of reproductive maturity actually occupied by the individuals of a cohort divided by the total number of age units of reproductive maturity that would have been occupied if all individuals had reached the final age unit. If all mature individuals are assumed to reproduce at equal rates, ERL is the expectation of reproductive output for an individual entering the simulation subject to the particular functional relationships. For each combination of functional relationships, 50 cohorts were simulated, each with a different allometric coefficient. These coefficients covered the range from 0.55 to 1.82 in equal increments. To ascertain how different allometries of defense affect fitness (as estimated by ERL) for a given combination of functional relationships, ERLs from the simulations were regressed on the 50 allometric coefficients by a fifth-degree polynomial.

An alternative version of the simulation allowed variable reduction of the inhibitory effect of defensive investment on body-size growth without reducing the deterrence capability of the defense. This amounts to having a cheaper defense, and we expected that it would result in more negative optimal coefficients.

Results from the Simulation

Optimal Allometry. Four replicate simulations were run for each combination of the two growth functions, the three body-size deterrence functions, the five defense-size/deterrence functions, and 50 allometric coefficients ranging from 0.55 to 1.82. Averaged over all combinations of functional relationships, the mean body size at death was 18% of maximum body size, 8% of the individuals reached the 70% of maximum body size required for reproduction,

and ERL was 0.023. The effects of changes in the functional relationships of the model were examined by Model I ANOVA of ERL. All functional relationships had significant effects ($P < .001$), and all first-order interactions were significant. Judged by the magnitude of its standardized partial regression coefficient, the growth function was the most influential factor in determining ERL, and the factor with the weakest effect was the allometric coefficient. Judged by the relative magnitudes of F statistics, allometric coefficient had its strongest interaction with the growth function, not with the body-size or defense-size/deterrence functions.

Figure 2 shows the relation, as defined by polynomial

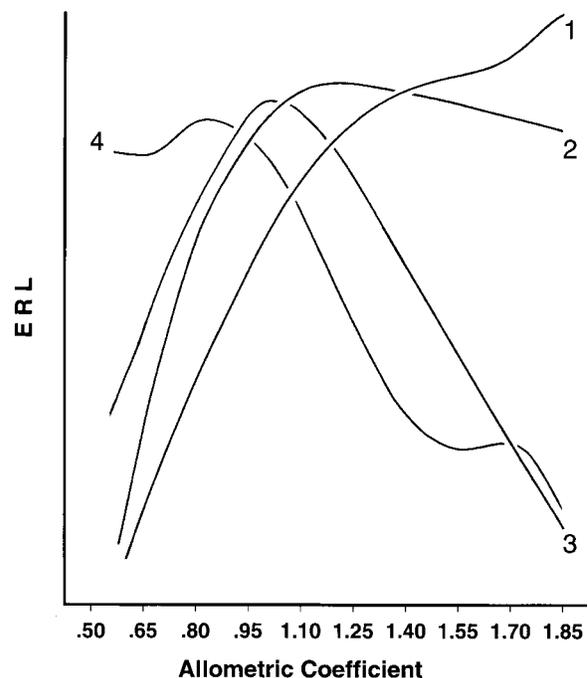


Figure 2: Effects of functional relationships and allometric coefficient on expected reproductive life span (ERL). Each curve is the polynomial regression of ERL on allometric coefficient for 50 simulations, each using a different coefficient between 0.55 and 1.82. In simulations of curves 1–3, the growth function was logistic and the body-size/deterrence function was linear; defense-size/deterrence functions were 1 = concave upward, 2 = Gompertz, and 3 = moderate asymptotic. Curve 4 represents a set of simulations that used the von Bertalanffy growth function, the fast asymptotic body-size/deterrence function, and the Gompertz defense-size/deterrence function. Each curve has a different scale on the ERL axis. Extremities of the ERL axis specific to each are 1 = 0.0014, 0.0044; 2 = 0.0044, 0.0062; 3 = 0.0078, 0.0100; and 4 = 0.0516, 0.0626. A particular combination of functional relationships is conceived as a taxon-specific attribute. Thus, within-curve ERL differences are relevant to selection on defense allometry, but between-curve ERL differences are not relevant because genotypes that control the allometric coefficients on separate curves are expected to occur in different taxa exposed to different selective regimes.

regression, between ERL and allometric coefficient for several combinations of functions that illustrate opposite extremes of optimal allometry of defense. The regression lines shown account for >85% of variation in ERL. With logistic growth and a linear body-size/deterrence relationship, the extent to which a clearly optimal allometric coefficient can be defined depends on the defense-size/deterrence function. When the defense-size/deterrence function is concave upward, the most extreme positive allometry ($\alpha > 1.8$) is optimal (curve 1). The logistic and linear defense-size/deterrence functions give their highest ERL values (not shown) over a wide range of allometric coefficients that define strongly positive allometry ($\alpha > 1.4$). The Gompertz defense-size/deterrence function leads to a broadly peaked curve (curve 2) in the region of allometric coefficients that define moderately positive allometry of the defense ($1.1 < \alpha < 1.2$). The moderate asymptotic defense-size/deterrence function provides a sharp peak (curve 3) in ERL near isometric growth ($\alpha \approx 1.0$). Upward convexity of the defense-size/deterrence functions, judged by their relative elevations at midontogeny, is inversely correlated with the magnitude of the optimal allometric coefficient (Spearman's rank test; $P < .05$). When a von Bertalanffy growth function is combined with a fast asymptotic function defining body-size/deterrence and a Gompertz defense-size/deterrence function, the optimal allometry (curve 4) is negative ($\alpha = 0.8$). A shift to extremely negative optimal allometry occurs whenever the growth function is changed from logistic to von Bertalanffy, hence the significant interaction between the allometric coefficients and growth functions found in the ANOVA. Earlier occurrence of the maximal growth increment in the von Bertalanffy function favors negative allometry because it mitigates the drag of defensive investment on body size: there are more resources early in ontogeny that can support body growth as well as investment in defense. The alternative simulations that reduced the drag of defensive investment on body-size growth always produced more negative optimal allometric coefficients than did the standard simulations.

Predictions. The simulation results lead to several predictions. First, negative allometry of defense will be found in taxa in which the growth rate of the whole organism is most rapid very early in ontogeny. Second, negative allometry of defense will be found in taxa whose habitat or trophic position results in a weakly convex upward body-size/deterrence relationship, and whose habitat or particular defense results in a convex upward defense-size/deterrence relationship. Third, positive allometry of defense will be found in taxa whose habitat or trophic position results in a strongly convex upward body-size/deterrence relationship, and whose habitat or particular defense re-

sults in a concave upward defense-size/deterrence relationship. In the next section, we use interspecific comparisons to test these predictions for investment in tree bark.

The Comparative Tests

General Approach

Tree bark is composed of an external largely nonliving layer, rhytidome, and an internal living layer of phloem and parenchymal phloem rays. The rhytidome contains nonliving phloem but mainly consists of a series of periderms in which adventitious cambia termed phellogen have produced phellem, or cork. The primary function of phloem is the transport of organic compounds, although the thickness of phloem may influence conduction of heat to the vascular cambium (Vines 1968). Rhytidome undoubtedly has multiple functions, for example, reducing water loss, providing a barrier against insect and fungal invasion, and defending the vascular cambium against fire. We focused on the fire-resisting function of thick bark on the lower bole because clear connections exist between the defense size and its likelihood of success. Thicker rhytidome better insulates against high temperatures (Spalt and Reifsnnyder 1962; Martin 1963; Fahnestock and Hare 1964; Bond and van Wilgen 1996) and has been shown to affect survival probability during surface fire (Harmon 1984; Ryan and Reinhardt 1988; Uhl and Kaufmann 1990). Body size, particularly crown height, influences the probability of surviving surface fire as well, survival being lower at smaller body sizes because of crown scorch (Rebertus et al. 1989; Agee 1993; Glitzenstein et al. 1995). In most tree species, whether of fire-prone or infrequently burned habitat, annual survival probability increases with size between the seedling stage and small adult sizes; the greatest improvement in survival probability occurs at sapling sizes (Harcombe 1987). This suggests that, besides increasing the probability of surviving fire, larger body size deters mortality from such hazards as competition and falling woody debris.

As in the model, bark thickness and tree size may act sequentially against threats. Failure of the bark defense and rescue by body size would occur when a surface fire creates a bole scar that is susceptible to microbial infection, but the tree's height prevents crown scorch and sufficiently avoids shading by neighboring trees so that resources are available to heal the fire scar. The opposite temporal order could also occur: when the tree is small, fire scorches the crown, but, if bark is thick enough, the cambium is not killed; and resprouting high on the bole reduces the likelihood of mortality from over-topping by neighbors. Such resprouting is common in savanna oaks of southeastern

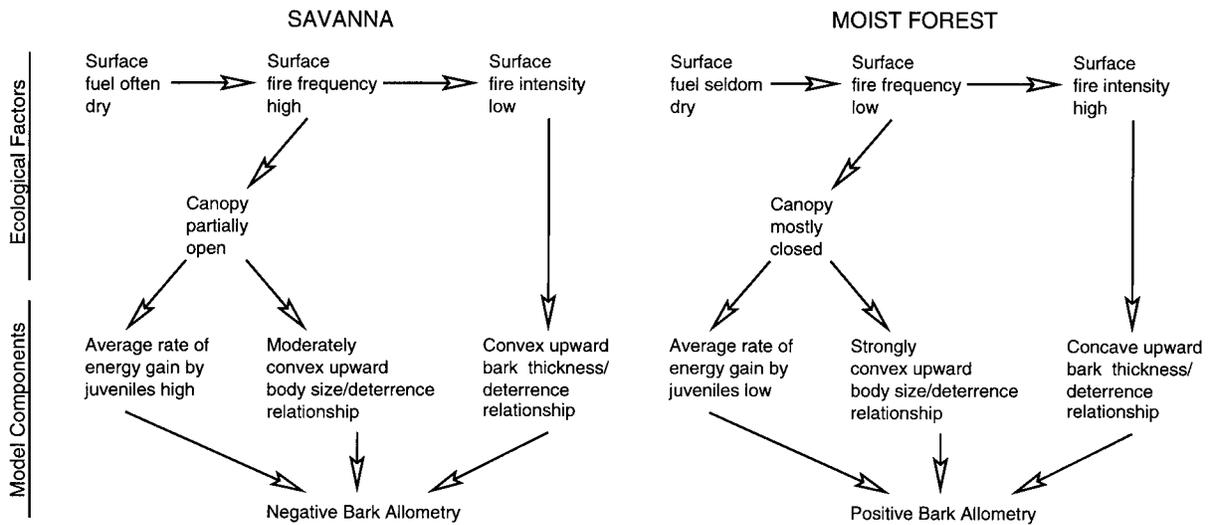


Figure 3: Hypothesized causal connections between ecological factors and adaptive bark allometry in trees of savanna and moist forest as mediated through relationships analogous to the components of the simulation model. Relative occurrence of low moisture content in surface fuels is hypothesized as the initial causal factor.

North America (Rebertus et al. 1993). Although species differences in resprouting ability (e.g., Gignoux et al. 1997) may be relevant to an evolutionary explanation of bark allometry, we did not include resprouting in our analysis because the literature does not provide sufficient information on resprouting ability among pines and oaks, that is, species differences in resprouting frequency and in morphological site of resprouting, and how the probability of deterring mortality by resprouting high on the bole may differ from that associated with basal resprouting.

Several conceivable measures of tree size differ in practicality for field measurement and in how relevant they are to mortality deterrence. Mass or total caloric content are the purest measures of body size but are impractical and not as clearly connected to mortality deterrence as height, bole diameter, or canopy size. Greater height and canopy size reduce the probability of competitively induced mortality; greater height and bole diameter generally reduce the probability of mortality from surface fire and from falling woody debris. Although height may be the most ecologically relevant aspect of tree body size, we chose to employ bole diameter because it is highly correlated with height and can be measured more readily and accurately.

To predict bark allometry quantitatively, the model would require age-specific data on natural growth rate and on probabilities of death caused by fire damage on the bole, by crown scorch, by competition, by herbivory, and by abiotic stress. In the absence of such data, we test whether measured bark allometry is correlated with a rank-

ing of bark allometry that we predict from qualitative habitat differences. We reason that such differences probably cause between-habitat disparities in functional relationships for tree size and survivorship and for bark thickness and surface fire protection. The set of putative within-habitat functional relationships, compared with the simulation results for similarly shaped curves, gave the predicted ranking across habitat types. Each species was assigned to the habitat type where it typically grows, and all species in that type received the same predicted rank. The two groups of species employed in separate tests were 32 *Pinus* species within the United States and 23 tree-sized *Quercus* species of the eastern United States.

Ranking of Habitat Types as Putative Selective Regimes for Bark Allometry

The ranking of habitats as selective regimes along the negative-positive bark allometry continuum is based on the functional relationships expected to result from habitat differences in fire frequency, fire intensity, canopy type (open or closed), and recruitment mode (continual or episodic). The prediction is that between-habitat differences in the above characteristics, mediated through dissimilar functional relationships between body size and mortality deterrence and/or between bark thickness and mortality deterrence, affect the distribution of bark allometry across habitat types. The hypothesized causal relationships are shown in figure 3, and the next several paragraphs discuss them in reference to this figure.

For the climatic range that supports trees, a valid generalization is that habitats whose surface litter is often dry, usually because of steep topography or sandy soil, experience more frequent surface fire than mesic or hydric habitats (Bonnicksen and Christensen 1981; Swetnam and Baisan 1994). We therefore used subdivision of the moisture spectrum as the primary means of defining habitat types both for *Pinus* and for *Quercus*. Data on primeval fire-return intervals for *Pinus* (table 1) confirm a gradient of surface fire frequency across the habitat types we recognize. Absence of data in a cell may reflect the extreme infrequency of such a fire event; for example, crown fire in *Pinus palustris* savanna is virtually impossible when surface fire occurs every few years. Alternatively, empty cells reflect lack of information; frequency of moderate-severity fire in eastern dry mixed-species forest is unknown because these forests were almost completely cut before the advent of research in fire ecology. For this reason, fire-return data for eastern *Quercus* are few but, when present, support a fire frequency gradient across the habitat types that we recognize (Christensen 1981).

The second generalization from fire ecology invoked in figure 3 is that frequent surface fires keep the fuel load low and consequently are of low intensity, releasing little energy per unit of fireline length (Kaufmann and Martin 1989; Gibson et al. 1990). Their effects on trees are of low severity (Agee 1993). Infrequent fires tend to be more intense and have more severe effects (table 1). Exceptions to this generalization usually occur within a given habitat

type and relate to differences in fuel pyrogenicity (Platt et al. 1991) or burning season (Glitzenstein et al. 1995). We assume that fire intensity affects the relationship between bark thickness and the probability of surviving the fire. If intensity is low, we expect this relationship to be convex upward because of the manner in which bark serves as fire protection. Bark acts as insulation that slows heat conduction toward the vascular cambium (Spalt and Reifsnnyder 1962). Thicker insulation increases the fire exposure time necessary to cause a lethal cambial temperature (Vines 1968; Uhl and Kaufmann 1990) and thus increases the chance that a low-intensity surface fire will have exhausted the fuel near the tree before the cambium experiences a lethal temperature. However, because thicker bark would eventually exceed the insulating capacity necessary for protection, a convex relationship is expected (fig. 4, curve 1) and has been documented for low-intensity fires (Harmon 1984; Ryan and Reinhardt 1988). For moderate-intensity fire, the relationship of bark thickness to probability of bole protection is expected to be sigmoidal or concave upward (fig. 4, curve 2) because only thick bark successfully insulates against the higher temperatures and longer durations of high temperature. In crown fire, destruction of the tree's photosynthetic apparatus should render insulation of the lower bole largely irrelevant and produce a bark-thickness/mortality deterrence curve of low slope near the abscissa (fig. 4, curve 3). Ryan and Reinhardt (1988) present a response surface for probability of mortality as a function of bark thickness and percentage

Table 1: Estimates of presettlement fire-return intervals (yr) by *Pinus* habitat type and fire type

Habitat type	Low-severity surface fire	Moderate-severity surface and crown fire	High-severity surface and crown fire
Western park-like forest/savanna	1.9–6.4, ^a 5–9, ^b 5–25, ^c 8 ^d
Eastern park-like forest/savanna	2–8 ^e
Western dry mixed-species forest	11–18, ^f 16 ^g	18–37, ^h 20–40, ⁱ 40–65, ^j 80 ^k	...
Eastern dry mixed-species forest	3–30, ^l 10 ^m
Woodland	100–300, ⁿ 800 ^o
Moist mixed-species forest	...	20–40 ^p	150–200, ^p 129–172, ^q 250, ^r 300–500, ^s 1389 ^t
Fire-resilient monospecific forest	15 ^u	25 ^u	50–100, ^u 30–60, ^v 33–50, ^w 83 ^x

Note: The categorization of fire types follows Agee (1990). Severity expresses the effect on the vegetation and is correlated with fire intensity. Species and sources are as follows: a, *P. ponderosa* (Savage and Swetnam 1990); b, *P. ponderosa* (Kilgore and Taylor 1979); c, *P. ponderosa* (Agee 1993); d, *P. jeffreyi* (Barbour 1988); e, *P. palustris* (Christensen 1981); f, *P. lambertiana* (Kilgore and Taylor 1979); g, *P. lambertiana* (Barbour 1988); h, *P. lambertiana* (Agee 1991); i, *P. radiata* and *P. muricata* (Keeley 1981); j, *P. contorta* subsp. *murrayana* (Pitcher 1987; Taylor and Halpern 1991); k, *P. contorta* subsp. *murrayana* (Agee 1993); l, *P. echinata* (Cutter and Guyette 1994); m, *P. taeda* (Chapman 1942); n, *P. edulis* (Keeley 1981); o, *P. albicaulis* (Agee 1990); p, *P. resinosa* (Heinselman 1981); q, *P. resinosa* (Whitney 1986); r, *P. strobus* (Henry and Swan 1974); s, *P. monticola* (Hemstrom and Franklin 1982); t, *P. strobus* (Whitney 1986); u, *P. banksiana* (Heinselman 1981); v, *P. clausa* (Harper 1915); w, *P. attenuata* (Vogl et al. 1977); x, *P. banksiana* (Whitney 1986).

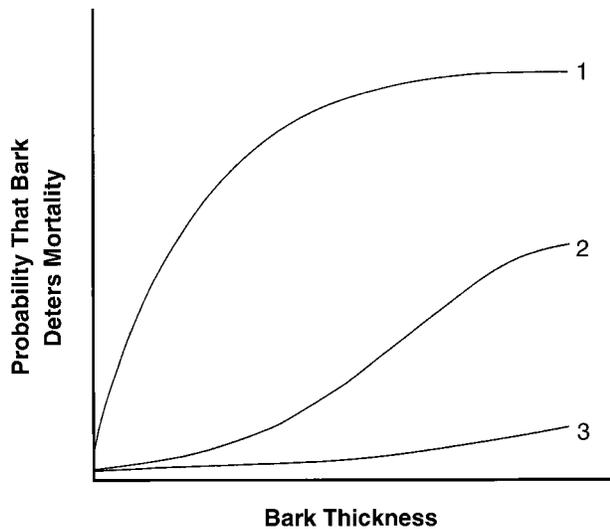


Figure 4: Expected relationship between bark thickness and mortality deterrence for fires of different intensity. 1 = low-intensity surface fire; 2 = moderate-intensity surface and crown fire; and 3 = high-intensity crown fire. These curves represent sections through the response surface of Ryan and Reinhardt (1988) at 0%, 60%–80%, and 100% of crown killed, respectively.

of the crown killed. Sections through this surface at 0%, 60%–80%, and 100% of crown killed correspond, respectively, to low-intensity surface fire, moderate-intensity surface and crown fire, and high-intensity crown fire; when replotted as probability of survival, these sections document the effect of fire intensity on the shape of the bark-thickness/deterrence relationship as represented in figure 4. The relationships of figure 4 are on a per fire basis. If adjusted to a per-unit-time basis to express both the probability of the threat occurring and the probability of surviving it, the curves would be farther separated.

Studies of how fire behavior is influenced by synoptic weather patterns (Swetnam and Betancourt 1990; Bessie and Johnson 1995) and by fuel pyrogenicity (Platt et al. 1991) may be relevant to future quantitative predictions of bark allometry but do not appear applicable to the qualitative predictions of our model. Although both types of study have increased understanding of variation in fire behavior (temporal variation caused by synoptic weather pattern and spatial variation caused by differences in fuel pyrogenicity), they primarily treat within-habitat variation in fire intensity. Our approach is based on the between-habitat differences in fire intensity that are associated with between-habitat differences in fire frequency (table 1).

As indicated in figure 3, we infer convex upward body-size/deterrence relationships for both dry and moist habitats as the inverse of the concave relationship between bole diameter and annual mortality rate in presenescent

trees (Harcombe 1987; Platt et al. 1988). Ranking of habitats for degree of convexity in the body-size/deterrence relationship is based on probable levels of competition faced by juveniles. Competition for light has been regarded as a selective factor in the evolution of tree life histories (Stearns and Crandall 1981; Govindaraju 1984; Loehle 1988) because of the inverse relation between tree growth rate and the size of closely neighboring trees (Weiner 1984) and because low growth rate is a good predictor of death (Buchman et al. 1983). Franklin et al. (1987) reported higher mortality rates both in mature second-growth forest compared with old growth and in moist sites compared with dry sites, pointing to higher mortality with denser canopies. Two situations should lead to strong convexity in a tree body-size/deterrence curve: (1) juveniles in closed-canopy forest, and (2) extremely high density of juveniles. Juveniles of species that occur in closed-canopy, multispecies forests inhabit a shady understory and may reach the canopy only if they survive on a low energy input until a light gap opens around them (Hirsh and Platt 1981). In *Pinus* spp. that seed from serotinous cones after a stand-replacing fire (fire-resilient category of McCune [1988]; type A of Clark [1991]) there may be several hundred thousand seedlings per hectare (Cooper et al. 1959), and high mortality caused by intraspecific competition subsequently results in uniform spacing of adults (Laessle 1965; Peet and Christensen 1987; Kenkel 1988).

Of course, competition occurs in savanna species as well. In *P. palustris*, growth rates are lower in trees close to large numbers of conspecifics (Rathbun and Cressie 1994), and juvenile growth is suppressed by larger trees (Platt and Rathbun 1993). However, two aspects of recruitment in park-like forest/savanna species suggest that their juveniles may experience less competition for light than juveniles of fire-resilient or closed-canopy forest species and that body-size increase for over-topping competitors may be less crucial. First, juvenile densities may be as much as an order of magnitude lower than in regenerating fire-resilient species; after a mast year in old-growth *P. palustris* savanna, there were 24,200 seedlings per hectare (Grace and Platt 1995), and in a frequently burned site, *Pinus ponderosa* had 1,800–2,100 seedlings and saplings per hectare (Cooper 1960). Second, the discontinuous savanna canopy allows juveniles a substantial probability of escaping severe competition. Most recruitment in savanna *Pinus* spp. is in patches opened by death of large trees (Cooper 1960; Platt and Rathbun 1993), and competition among juveniles in a patch is limited for several years (Platt and Rathbun 1993). When data from Buchman (1983) and Platt and Rathbun (1993) on four *Pinus* spp. are plotted as survival rate versus diameter, the curves are increasingly convex in the sequence: *P. palustris* (savanna) < *Pinus strobus* (moist forest) < *Pinus resinosa* (moist forest) < *Pinus banksiana*

(fire resilient). If the degree of canopy closure can serve as an indication of the advantage of body-size growth early in ontogeny, then we expect progressively more convex body-size/deterrence functions along the gradient: park-like forest/savanna species, dry forest species, moist forest species, and fire-resilient species maintained by catastrophic fire and fire-induced seeding.

The conditions that favor positive bark allometry are a strongly convex function for body size/deterrence and a concave or weakly sloped linear function for bark thickness/deterrence. These two conditions are expected to co-occur in mesic forest habitat and with the fire-resilient syndrome in *Pinus*. Because intense competition in regenerating stands of fire-resilient *Pinus* may cause an extremely convex body-size/deterrence relationship, mono-specific fire-resilient pine forests are predicted to have the most positive bark allometry among *Pinus* (table 2). A moderately convex body-size/deterrence function and a strongly convex bark-thickness/deterrence function favor negative bark allometry and are expected in park-like forest/savanna and dry forest habitats. Because we expect the most convex bark-thickness/deterrence relationship in park-like forest/savanna habitat, where fire is most frequent, we predicted this habitat to have the most negative bark allometry in both genera (tables 2, 3, 4). For *Pinus*, we divided park-like forest/savanna and dry mixed-species forest into eastern and western units because of the greater frequency of lightning-caused fire in the west (Schroeder and Buck 1970), and we predicted that the western units would have more negative allometry. Woodland *Pinus* habitat with slowly accumulating surface fuel loads combines high light availability with relatively infrequent surface fire and, hence, should favor bark allometry nearer to isometry than any of the other habitat types (table 2).

In the simulation model, the relation of maximal growth increment to body size, whether at 30% of greatest body size in von Bertalanffy growth or at 50% in logistic growth, strongly influenced optimal allometry. There is not sufficient information to evaluate habitat differences in growth pattern as a causal influence on bark allometry evolution. Such data must necessarily come from undisturbed forests, and, to be relevant to the evolution of bark allometry, a habitat-specific growth pattern must be the weighted average of individual growth patterns across the range from vigorous to suppressed individuals in the habitat. It is possible that greater insolation below the canopy, unless offset by infertile soil or other factors, may allow a higher average energy gain by juveniles in park-like forest/savanna than in closed-canopy forest. If so, dissimilar bark allometries in these habitats would be further favored (fig. 3).

Species Assignment to Habitat Types

Our assignment of *Pinus* species to habitat types (table 2) followed the ecomorphological categorization of McCune (1988) unless the primary literature indicated otherwise. It differs most from McCune (1988) in that our fire-resilient type contains fewer species. We included only those species that predominately regenerate in dense mono-specific stands after catastrophic crown fires (Harper 1913; Whittaker 1956; Zobel 1969; Vogl 1973). *Pinus glabra* was part of McCune's large fire-resilient group, but it does not meet the above criterion because it is very shade tolerant (Mohr 1897; Peters and Platt 1996) and grows as scattered individuals among hardwoods in mesic locales (Kurz and Godfrey 1962); we placed it in the moist mixed-species forest type. *Pinus contorta* in the Rocky Mountain region usually does meet the criterion, but we sampled the Sierra Nevada subspecies (*P. contorta* subsp. *murrayana*), which has a more variable relationship between fire and stand regeneration (Agee 1993, p. 342). *Pinus c.* subsp. *murrayana* is typically nonserotinous (Stuart et al. 1989), reproduces without crown fire (Parker 1986), can survive low-to moderate-intensity surface fire (Agee 1981), and has longevity much greater than typical fire-resilient species like *P. banksiana*, *Pinus clausa*, and *Pinus virginiana* (Fowells 1965). Because *P. c.* subsp. *murrayana* frequently co-occurs with other species (Barbour 1988; Rundel et al. 1977), we have placed it in the western dry mixed-species forest type. Similarly, we assigned *Pinus rigida* to the eastern dry mixed-species forest type because we sampled it in the Appalachians where, unlike in the coastal plain, it is typically not serotinous (Givnish 1981) and where primevally it dominated more xeric and fire-prone sites within multispecies forest (Bromley 1935). We assigned *Pinus serotina* to eastern park-like forest/savanna because it occurs primarily in flatwoods maintained by frequent surface fire (Abrahamson and Harnett 1990), although it also grows in shrub bogs that burn less often.

Quercus species were assigned to habitat types (tables 3, 4) based on information in Elias (1987), Fowells (1965), Harrar and Harrar (1962), Kurz and Godfrey (1962), and Miller and Lamb (1985). Assignment of bottomland *Quercus* follows Patrick et al. (1980), except for *Quercus laurifolia*, which we ranked as more mesic because we sampled it from a population not subject to alluvial flooding.

Data Collection and Analysis

Data and samples for estimating bark allometry were collected in the field by the second author for 32 *Pinus* spp. and by the first author for 23 *Quercus* spp. Each species sample was obtained from a single locality and included the full range of body sizes from small saplings to large

Table 2: Predicted allometric rank, rhytidome allometric coefficient, and rhytidome thickness for North American *Pinus* species by habitat type

Habitat type and species	Predicted allometric rank	Rhytidome allometric coefficient	R^{2a}	Rhytidome thickness			
				Sapling (cm) ^b	Adult (cm) ^c	Adult (%) ^d	Standard adult diameter (cm) ^e
Western park-like forest/savanna:							
<i>P. coulteri</i>	1	.862	.94	.58	4.42	5.4	82.1
<i>P. ponderosa</i>	1	.888	.97	.37	4.82	3.5	138.3
<i>P. jeffreyi</i>	1	.913	.96	.46	6.51	5.2	124.1
<i>P. torreyana</i>	1	.915	.93	.22	2.66	2.7	99.0
<i>P. sabiniana</i>	1	.981	.95	.35	5.55	6.2	89.7
Mean	1	.912		.40	4.79	4.6	106.6
Eastern park-like forest/savanna:							
<i>P. serotina</i>	2	.752	.94	.76	2.48	4.8	52.1
<i>P. palustris</i>	2	.834	.98	.49	2.31	4.6	50.5
<i>P. elliotii</i>	2	.906	.99	.38	2.57	4.9	52.6
Mean	2	.831		.54	2.45	4.7	51.7
Western dry mixed-species forest:							
<i>P. muricata</i>	3	.868	.95	.63	4.40	6.3	69.5
<i>P. lambertiana</i>	3	.877	.97	.35	5.13	2.9	178.7
<i>P. radiata</i>	3	.900	.99	.48	5.56	5.2	106.7
<i>P. contorta</i>	3	.937	.93	.15	1.97	2.0	97.8
Mean	3	.896		.40	4.26	4.1	113.2
Eastern dry mixed-species forest:							
<i>P. rigida</i>	4	.816	.92	.52	2.66	4.1	65.1
<i>P. taeda</i>	4	.887	.97	.38	3.09	4.1	76.0
<i>P. echinata</i>	4	.904	.96	.37	2.53	4.7	53.8
Mean	4	.869		.42	2.76	4.3	64.9
Woodland:							
<i>P. monophylla</i>	5	1.017	.97	.19	2.68	4.1	66.3
<i>P. balfouriana</i>	5	1.019	.95	.16	4.70	3.7	127.7
<i>P. leiophylla</i>	5	1.051	.98	.29	3.29	7.3	44.9
<i>P. edulis</i>	5	1.060	.93	.18	4.44	5.2	86.1
<i>P. albicaulis</i>	5	1.063	.98	.12	4.83	3.6	133.8
<i>P. quadrifolia</i>	5	1.114	.91	.14	1.47	4.2	34.8
<i>P. flexilis</i>	5	1.115	.98	.11	7.03	5.0	141.9
<i>P. aristata</i>	5	1.125	.93	.08	7.44	3.9	191.2
Mean	5	1.071		.16	4.49	4.6	103.3
Moist mixed-species forest:							
<i>P. monticola</i>	6	1.048	.94	.16	7.12	4.5	159.3
<i>P. strobus</i>	6	1.051	.96	.14	3.50	3.9	90.6
<i>P. resinosa</i>	6	1.139	.98	.13	2.43	4.8	50.1
<i>P. glabra</i>	6	1.198	.98	.09	3.09	4.8	63.9
Mean	6	1.109		.13	4.03	4.5	91.0
Fire-resilient monospecific forest:							
<i>P. attenuata</i>	7	1.051	.95	.19	2.70	5.0	54.6
<i>P. clausa</i>	7	1.055	.96	.16	1.42	4.1	34.8
<i>P. pungens</i>	7	1.091	.94	.18	2.09	5.3	39.2
<i>P. banksiana</i>	7	1.116	.91	.15	2.33	5.0	46.9
<i>P. virginiana</i>	7	1.179	.96	.13	2.28	5.5	41.6
Mean	7	1.098		.16	2.16	5.0	43.4

^a R^2 of log-log regression of bark thickness on diameter.^b Estimated from regression at diameter of 5.0 cm.^c Estimated from regression at standard adult diameter.^d Adult bark thickness divided by standard adult diameter.^e Standard adult diameter is greatest known diameter for the species divided by two.

Table 3: Predicted allometric rank, rhytidome allometric coefficient, rhytidome thickness, and phloem allometric coefficient for eastern North American red oak (*Quercus*) species by habitat type

Habitat type and species	Predicted allometric rank	Rhytidome allometric coefficient	R^{2a}	Rhytidome thickness			Standard adult diameter (cm) ^e	Phloem allometric coefficient
				Sapling (cm) ^b	Adult (cm) ^c	Adult (%) ^d		
Park-like forest/savanna:								
<i>Q. marilandica</i>	1	.730	.73	.27	1.37	2.0	68.3	.551
<i>Q. laevis</i>	1	.743	.75	.25	1.09	2.1	51.3	.597
<i>Q. incana</i>	1	.874	.78	.19	1.11	2.3	48.1	.684
Mean	1	.782		.24	1.19	2.1	55.9	.611
Dry upland forest:								
<i>Q. f. falcata</i>	2	.998	.73	.13	2.16	1.6	133.8	.671
<i>Q. velutina</i>	2	1.029	.87	.15	3.34	2.7	124.5	.675
<i>Q. georgiana</i>	2	1.053	.77	.11	.34	2.0	17.4	.812
Mean	2	1.027		.13	1.95	2.1	91.9	.719
Intermediate dry upland forest:								
<i>Q. imbricaria</i>	3	1.120	.86	.07	1.35	1.5	92.6	.689
<i>Q. coccinea</i>	3	1.252	.89	.05	1.60	1.6	100.3	.618
Mean	3	1.186		.06	1.48	1.5	96.4	.654
Moist upland forest:								
<i>Q. shumardii</i>	4	1.086	.89	.03	.71	.7	105.5	.784
<i>Q. rubra</i>	4	1.121	.76	.06	1.56	1.6	149.6	.626
Mean	4	1.104		.04	1.13	.9	127.5	.705
Infrequently flooded bottomland forest:								
<i>Q. laurifolia</i>	5	1.060	.86	.04	.84	.8	107.9	.852
<i>Q. f. pagodifolia</i>	5	1.263	.81	.02	.91	.6	140.7	.564
<i>Q. nigra</i>	5	1.319	.82	.01	.46	.4	110.4	.714
Mean	5	1.214		.02	.74	.6	119.7	.710
Frequently flooded bottomland forest:								
<i>Q. nuttallii</i>	6	.971	.74	.02	.28	.3	113.2	.601
<i>Q. palustris</i>	6	1.249	.83	.03	.89	.9	97.0	.574
<i>Q. phellos</i>	6	1.304	.85	.03	1.56	1.2	128.6	.769
Mean	6	1.175		.03	.91	.8	112.9	.648

^a R^2 of log-log regression of bark thickness on diameter.

^b Estimated from regression at diameter of 5.0 cm.

^c Estimated from regression at standard adult diameter.

^d Adult bark thickness divided by standard adult diameter.

^e Standard adult diameter is greatest known diameter for the species divided by two.

adults. The average sample size was 27.5 individuals per species for *Pinus* and 30.1 for *Quercus*. Individual trees and bark segments were selected for measurement by a random protocol, except that suppressed individuals were excluded. Bole diameter was measured at 60 cm above the ground for *Quercus* and at 50 cm for *Pinus*. Mean bark thickness in large saplings and adults was estimated at 60 cm by contour method 1 for *Quercus* and at 50 cm by contour method 2 for *Pinus* (methodological details in Adams and Jackson 1995) and in small saplings was measured from bole cross sections under a dissecting microscope. Phloem and rhytidome were measured separately in *Quercus*. In *Quercus*, the phloem is as thick or thicker

than rhytidome and consequently feasible to measure separately, but phloem is only 10%–15% of total bark thickness in *Pinus* (Martin 1969). Because of this lesser thickness and because the rhytidome-phloem boundary was much more distinct in bore cores than the phloem-cambium boundary, we chose to measure only rhytidome in *Pinus*. Within each species sample, log-transformed mean bark thickness (rhytidome or phloem) was regressed on log-transformed inside-bark bole diameter by reduced major axis regression to estimate the allometric coefficient and intercept.

A parametric test of the correlation between empirically estimated bark allometry and allometric rank predicted

Table 4: Predicted allometric rank, rhytidome allometric coefficient, rhytidome thickness, and phloem allometric coefficient for eastern North American white oak (*Quercus*) species by habitat type

Habitat type and species	Predicted allometric rank	Rhytidome allometric coefficient	R^{2a}	Rhytidome thickness			Standard adult diameter (cm) ^e	Phloem allometric coefficient
				Sapling (cm) ^b	Adult (cm) ^c	Adult (%) ^d		
Park-like forest/savanna:								
<i>Q. macrocarpa</i>	1	.664	.90	.24	1.84	1.4	130.2	.523
Dry upland forest:								
<i>Q. stellata</i>	2	.806	.67	.26	2.69	2.8	95.4	.550
<i>Q. prinus</i>	2	1.027	.91	.22	4.45	4.2	106.7	.522
Mean	2	.917		.24	3.57	3.5	101.1	.536
Moist upland forest:								
<i>Q. alba</i>	3	1.269	.89	.09	5.23	3.5	151.2	.520
Infrequently flooded bottomland forest:								
<i>Q. michauxii</i>	4	.950	.80	.08	1.00	1.0	101.5	.554
<i>Q. virginiana</i>	4	1.556	.93	.02	5.33	3.0	177.5	.629
Mean	4	1.253		.05	3.17	2.0	139.5	.592
Frequently flooded bottomland forest:								
<i>Q. lyrata</i>	5	.768	.67	.20	1.43	1.3	108.3	.859

^a R^2 of log-log regression of bark thickness on diameter.

^b Estimated from regression at diameter of 5.0 cm.

^c Estimated from regression at standard adult diameter.

^d Adult bark thickness divided by standard adult diameter.

^e Standard adult diameter is greatest known diameter for the species divided by two.

from the model constitutes our test of the hypothesis of adaptive bark allometry. This correlation, like more traditional character-character correlations, should be tested by a method that avoids dependency among data points caused by phylogenetic relatedness (Felsenstein 1985; Harvey and Pagel 1991; Diaz-Uriarte and Garland 1996). We employed the method of phylogenetically independent contrasts (Felsenstein 1985). Lack of a complete published phylogeny for the 32 *Pinus* spp. required that we combine phylogenies of subsections of the genus. We used Baum's (1992) method to combine phylogenies available in Wheeler et al. (1983), Millar et al. (1988), Strauss and Doerksen (1990), Govindaraju et al. (1992), Malusa (1992), and Adams and Jackson (1997). Baum's method preserves the topology of the separate phylogenies, but branch-length information is lost. In its absence, an approach is to calculate independent contrasts under several arbitrary protocols for obtaining branch lengths in order to determine whether branch lengths affect the correlation (Garland et al. 1991). We used branch lengths equal to unity (FLIP of Martins and Garland [1991]), Grafen's (1989) arbitrary branch lengths, and Pagel's (1992) arbitrary branch lengths. Testing the correlation with tabulated probability values requires that each independent contrast be standardized through division by its standard deviation, which is the square root of the sum of its branch lengths, in order that contrasts associated with longer time spans not influence the correlation unduly. Standardization is

adequate only if there is no significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland et al. 1992). We standardized the independent contrasts and tested the adequacy of the standardization. Correlations of independent contrasts were based on regression through the origin. Comparative analyses for oak bark allometry were done separately for rhytidome and phloem and, within each of these, separately for white oaks (subgenus *Lepidobalanus*) and red oaks (subgenus *Erythrobalanus*) because of large differences in rhytidome hardness and histological structure between the subgenera (Howard 1977). Two published phylogenies exist for each oak subgenus: Solomon (1983b) and Guttman and Weigt (1989) for white oaks, and Solomon (1983a) and Jensen (1983) for red oaks. We performed separate comparative tests for the alternative phylogenies. In other respects, independent contrast standardization and statistical tests are as described for *Pinus*. Calculations for the comparative tests were done with PDTREE (Garland et al. 1993).

The allometric coefficient alone is not sufficient to test for adaptive defensive investment. In savanna species, negative allometry accords with the prediction in figure 3 only if there is thick bark in saplings. Negative allometry together with thin sapling bark in a savanna species would be inexplicable in terms of the hypothesized causal factors, as would positive allometry and thick sapling bark in moist forest species. Thus, we also tested correlations between

Table 5: Correlation coefficients between standardized independent contrasts of predicted allometric rank and measured allometric coefficient for *Pinus*, red oak, and white oak bark using multiple phylogenies and branch-length methods

Data set and branch-length method	<i>R</i>	<i>P</i>
<i>Pinus</i> rhytidome:		
BL = 1	.804	5×10^{-8}
Grafen's	.795	5×10^{-8}
Pagel's	.796	5×10^{-8}
Red oak rhytidome by Jensen (1983):		
BL = 1	.574	.02
Grafen's	.605	.02
Pagel's	.614	.02
Red oak rhytidome by Solomon (1983a):		
BL = 1	.745	.001
Grafen's	.764	.001
Pagel's	.753	.001
Red oak phloem by Jensen (1983):		
BL = 1	-.426	NS
Grafen's	-.398	NS
Pagel's	-.370	NS
Red oak phloem by Solomon (1983a):		
BL = 1	.096	NS
Grafen's	.161	NS
Pagel's	.175	NS
White oak rhytidome by Solomon (1983b):		
BL = 1	.302	NS
Grafen's	.302	NS
Pagel's	.327	NS
White oak rhytidome by Guttman and Weigt (1989):		
BL = 1	.394	NS
Grafen's	.395	NS
Pagel's	.389	NS
White oak phloem by Solomon (1983b):		
BL = 1	.891	.01
Grafen's	.945	.005
Pagel's	.917	.01
White oak phloem by Guttman and Weigt (1989):		
BL = 1	.702	NS
Grafen's	.720	.05
Pagel's	.715	.05

Note: Significance levels are one-tailed.

predicted allometry rank and estimated bark thickness of 5-cm diameter saplings. In addition, we estimated bark thickness at a standard adult size (half the diameter of the largest individual of the species recorded in American Foresters' National Register of Big Trees; Cannon 1998).

Results of Comparative Tests

Habitat type assignments, predicted allometry ranks, and measured allometric coefficients are presented in tables 2, 3, and 4 for *Pinus*, red oaks, and white oaks, respectively. The allometric coefficients range from strongly negative

($\ll 1.0$ in *P. serotina*, *Quercus macrocarpa*, and *Quercus marilandica*) to strongly positive ($\gg 1.0$ in *P. glabra*, *Q. virginiana*, and *Quercus nigra*). For *Pinus*, none of the branch-length protocols showed statistically significant trends between absolute values of standardized independent contrasts and the standard deviations of the contrasts. There are significant correlations between phylogenetically independent contrasts of predicted allometry ranks and independent contrasts of measured allometric coefficients for all three branch-length protocols (table 5). The independent contrasts for Grafen's branch-length protocol are shown in figure 5. In summary, measured allometric

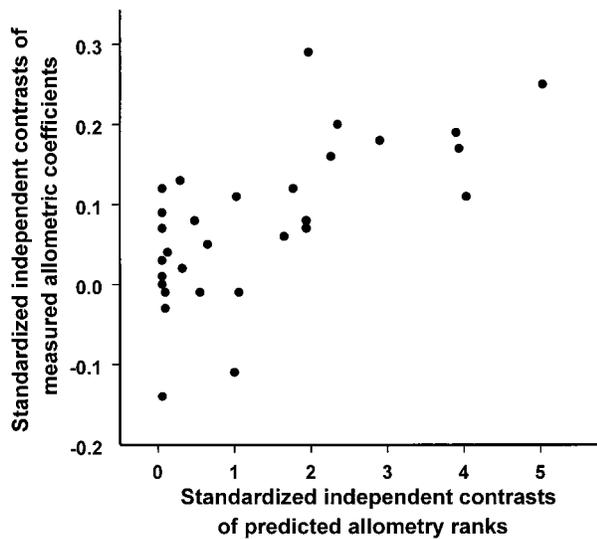


Figure 5: *Pinus* rhytidome allometric coefficient contrasts plotted against predicted allometry rank contrasts, based on the composite phylogeny with branch lengths determined by Grafen's (1989) protocol.

coefficients of *Pinus* correspond reasonably well with relative allometric ranks predicted from habitat type: positive bark allometry tends to occur in species characterized by massive episodic recruitment and species whose habitats are characterized by closed canopies and long fire-return intervals; negative bark allometry tends to occur in species whose habitats are characterized by partially open canopies and short fire-return intervals.

Red oak rhytidome displayed significant correlations between independent contrasts of predicted allometric ranks and measured allometric coefficients for all three branch-length protocols using both Jensen's (1983) and Solomon's (1983a) phylogenies (table 5). However, using Solomon's phylogeny there were significant correlations between standardized contrasts and their standard deviations for all three protocols. Because no such correlations existed when using Jensen's phylogeny, we base our conclusion of statistical significance ($P < .02$) on Jensen's (1983) phylogeny (Diaz-Urriarte and Garland 1996). Phloem showed no significant correlation between independent contrasts for either red oak phylogeny. In white oaks, the results were just the opposite. Both white oak phylogenies produced nonsignificant correlations of independent contrasts for rhytidome. For phloem, while contrasts from Guttman and Weigt's (1989) phylogeny could not be adequately standardized, contrasts from Solomon's phylogeny (1983b) were adequately standardized without transformation and were significantly correlated ($P < .01$ by all three branch-length protocols). For all data sets, Pearson correlation coefficients between predicted rank and allo-

metric coefficient (TIPS of Martins and Garland [1991]) were very close in magnitude to those for the independent contrasts and yield similar statistical conclusions.

Standardized independent contrasts of rhytidome thickness, estimated at a bole diameter of 5.0 cm, and of predicted allometry rank are significantly negatively correlated in *Pinus* ($r = -.662$; $P < .00001$) and in red oaks ($r = -.801$; $P < .001$). Thus, thick rhytidome in saplings and negative allometry constitute a tenable adaptive syndrome that is correlated with well-insolated, short fire-return interval habitats. Thin rhytidome in saplings and positive allometry are correlated with long fire-return interval habitats where sapling access to light is probably more limited.

The allometry results can be perceived less abstractly by comparing sapling and adult rhytidome thickness across habitats. In *Pinus* (table 2), habitat differences in adult rhytidome thickness when scaled by adult diameter yield adult rhytidome percentages that are similar among habitats. Sapling rhytidome thickness (and percentage of diameter) varies with habitat. Thus, adult investment in rhytidome is similar across habitats, but sapling investment is not, and this leads to habitat differences in rhytidome allometry. In red oaks (table 3), adult rhytidome percentage declines as habitat becomes wetter, while sapling rhytidome percentage changes in the same direction but to a more extreme degree. This incongruity between sapling and adult patterns yields between-habitat differences in allometry.

Discussion

Our findings reveal a relationship of tree bark to fire that is more subtle than the notion that species typical of fire-prone habitats have thick bark. In pine and oak species of fire-prone habitats, saplings have thick bark, but, because bark growth subsequently slows relative to body-size growth (negative bark allometry), adult bark thickness is not necessarily greater in fire-prone habitats. Among *Pinus* species, we found little between-habitat variation in adult bark thickness as a percentage of diameter. In *Pinus*, the principal between-habitat differences in bark thickness occur at the sapling stage. In red oaks, however, there are both associations of thick sapling rhytidome and negative bark allometry with fire-prone habitat, and a trend of thicker adult rhytidome in habitats with higher fire frequency. Among white oaks, phloem may play a greater role in fire resistance than is the case for red oaks, as evidenced by its tendency among white oaks toward more negative allometry in fire-prone habitats. These differences among taxa suggest that bark allometry will be a necessary element for fully understanding the species composition dynamics of tree communities. Not only does it help explain persistence in fire-prone habitat (e.g., Harmon 1984),

but it should also contribute to explaining shade tolerance from the perspective of individual energy budgets.

Certain features of tree bark facilitated the comparative tests. Bark is accreted, not integrated with other functional units, so its ontogeny is probably not developmentally constrained, unlike that of a turtle shell in which early investment in bone thickness may interfere with dimensional shell growth. Second, the tree habitat types differ concordantly in putative functional relationships: both the putative body-size/deterrence and defense-size/deterrence relationships of savanna habitat favor negative allometry, whereas, in moist forest habitat, both favor positive allometry. Such combinations do not yield conflicting selection pressures, so predictions are possible from natural history information rather than requiring quantitative information on the relative importance of conflicting pressures.

Several factors not considered in our prediction of allometry rank could have led to inadequacies of prediction that limited the correlations in the comparative tests. First, interspecific differences in insulating capacity per unit of thickness would mean that bark thickness would not perfectly reflect the probability of cambial protection. Such differences exist, but they are considered small (Martin 1963; Reifsnnyder et al. 1967). Second, interspecific differences in postfire resprouting ability would influence the probability that cambial damage would lead to mortality. Good resprouting ability could shift the optimum closer to positive allometry under a regime of moderately frequent surface fire. Third, in the two habitats favoring negative allometry, the allometries were less negative in the west (table 2), suggesting that fire frequency on a per individual basis may not be higher in western North America. The data of Schroeder and Buck (1970) may not adequately sample episodes of prolonged drought in the southeast, and temporally more extensive data might show less regional difference in lightning-caused fire. Even if the frequency of lightning-caused fires is higher in the west, topographic complexity may limit the extent of surface fire more than in the less dissected southeast. If fire extent were less, then per individual fire frequency may have been no greater than in the southeast. Separately, steep topography may place crowns of downslope trees closer to a surface fire than is the case for similar-sized trees on level ground. If steeper topography in the west favored height growth to avoid crown scorch from surface fire, it would lead to less negative bark allometry. Fourth, no gradation of severity was considered within the low-severity surface fire regime, but it is probably relevant. The park-like forest/savanna *Pinus* species with the most negative allometries in the east (*Pinus serotina*) and in the west (*Pinus coulteri*) sometimes grow above shrub understories that provide more fuel and hotter fire than grass and pine needles

(Wright and Bailey 1982). Fifth, although there was a rationale and some data by which to infer between-habitat differences in convexity of body-size/deterrence curves, potential between-habitat differences in curve elevation that could impact bark allometry can only be assessed when mortality curves become available for many species. Sixth, whether growth pattern differs among habitats is not known. Tree growth curves are so much influenced by site quality (Wenger 1984, pp. 322–333) that estimating averages for species will be difficult. Nonetheless, data on growth pattern may be necessary for fine-scaled prediction of bark allometry. The positive allometry found in woodland *Pinus* could result from low rates of juvenile energy gain in their low-precipitation and/or low-temperature environments (Barton 1993). Seventh, for certain species, particular relevant factors were not included. For example, *Quercus nuttallii* deviated greatly from predicted rank, having slightly negative rhytidome allometry in a habitat that never burns. But because rhytidome in *Q. nuttallii* is extremely thin, investment in it may be so minimal as to have elicited no evolution of adaptive allometry. And eighth, if there is intraspecific geographic variation in allometry, then a single local sample may not correlate well with the species' habitat characterization from the literature. Geographic variation in bark thickness is known (Stott et al. 1990), and it is likely that bark allometry varies geographically in some species.

Aspects of our study suggest that a search for allometry in other constitutive defenses would be worthwhile. The model components are general. A convex body-size/deterrence relationship is probably common in species lacking parental care, but its degree of convexity may depend on each species' array of competitors and predators. Defense-size/deterrence relationships may vary interspecifically from convex to concave according to how predators react to the defense, and the shape of the relationship can sometimes be estimated experimentally (Reimchen 1991). The differences in bark allometry among closely related trees encourage the belief that allometry of defense will be found in other organisms; a wide range of defenses, from echinoid spines to plant secondary compounds, awaits study. Whereas life history theory has been able to draw on a large empirical database of standard natural history information regarding reproduction, information on allometry of defense is minimal. This database must be developed purposefully.

From his optimal control model, Perrin (1992) argues that positive allometry of defense is generally expected because when, as in early ontogeny, there is a low value of the function defining immediate return on investment ($P/[r^* + \mu]$), allocation to production-enhancing organs, rather than to defense-enhancing organs, is favored. This effect will be magnified when defensive organs are ener-

getically expensive, when defense must be full-blown before it substantially reduces mortality risk, and when mortality risk declines sharply with increasing size of the whole body. A common functional reason for the latter situation in animals is attainment of a size refugium from predation (Unger and Lewis 1983). Defenses that can evolve negative allometry despite the bias in $P/(r^* + \mu)$ are likely to be energetically cheap and/or immediately capable of substantially reducing mortality risk. Spines of crab zoea and of cacti may meet these requirements, as apparently does bark of savanna-inhabiting species of pines and oaks.

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