

Tree life history strategies: the role of defenses

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Analysis of energy partitioning between defensive investments and growth in woody plants indicates that increasing a tree's life-span should require increased energy investment in protective measures such as thick bark and defensive chemicals. Increased investment in such defenses, however, logically must slow down the growth rate, thereby raising the mortality rate for juveniles in competition for height growth. Early reproduction should also reduce the growth rate. It is hypothesized that rapid growth can substitute for these defenses, but the consequence is rapid decline upon reaching maturity. These predictions are tested with data compiled from the literature for 159 species of North American trees. Data analysis supports predictions. Longevity of angiosperms, but not of gymnosperms was correlated with increased investment in defenses as measured by volumetric heat content of the wood. Wood density was not as good a measure. Longevity of gymnosperms was predicted by resistance to wood decay. For both taxa there was a negative correlation between growth rate and longevity, supporting the hypothesis of growth trade-offs. Age of sexual maturity was closely predicted by longevity in angiosperms. There was no such relationship for conifers as a whole, though there was for pines. The lack of relationship for all conifers might be explained by (i) variation in reproductive opportunities for young trees of different species, or (ii) variation in growth rates of young trees in certain adverse habitats occupied by conifers.

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L'analyse de la répartition de l'énergie entre les investissements défensifs et la croissance chez les plantes ligneuses montre que la prolongation du cycle vital d'un arbre nécessiterait une énergie accrue sous forme de mesures protectrices, telles qu'une écorce épaisse et des produits chimiques défensifs. Cependant, un accroissement de ces défenses doit logiquement réduire le taux de croissance, haussant ainsi le taux de mortalité des jeunes sujets en compétition quant à la croissance en hauteur. La régénération initiale devrait aussi réduire le taux de croissance. On peut supposer qu'une croissance rapide pourrait remplacer de telles mesures de défense, mais il s'ensuivrait certes un déclin rapide à l'approche de la maturité. Ces prévisions ont été vérifiées sur la base de données provenant de la littérature pertinente à 159 essences nord-américaines. L'analyse de ces données confirme les prévisions. La longévité des angiospermes, mais non celle des gymnospermes, a été corrélée avec des investissements accrus dans les mesures de défenses, tels que mesurés par le contenu calorifique du bois estimé en volume. La densité du bois n'était pas une mesure aussi bonne. La longévité des gymnospermes a été déduite à partir de la résistance du bois à la carie. Pour les deux taxons, on a trouvé une corrélation négative entre le taux de croissance et la longévité, ce qui sous-tend l'hypothèse d'échanges quant à la croissance. L'âge de la maturité sexuelle a pu être prédit de près par la longévité chez les angiospermes. On n'a pas trouvé de relation de cette nature pour les conifères pris globalement, bien qu'il y en ait une pour les pins. L'absence de relation pour les conifères en général peut s'expliquer par (i) la variation dans les occasions de reproduction pour les jeunes sujets de différentes essences, ou (ii) la variation des taux de croissance des jeunes sujets dans certains habitats occupés par des conifères.

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Introduction

Most forest trees live at least 100 years, many of them over 300 years, and a few over 1000 years. Clonal tree species may occupy a site for thousands of years (Harper and White 1974; Harper 1977). There should be selection for great longevity in woody plants because of the time required to become a dominant member of the forest canopy and because of the long intervals between opportunities for successful regeneration. Why are some species long lived while others are not? Most work on longevity has focused on senescence of tissues (e.g., leaf drop) or of whole monocarpic plants resulting from flowering (Molisch 1938; Wareing and Seth 1967; Woolhouse 1974; Behnke *et al.* 1978; Thimann 1980), with little said about determinants of longevity in nonmonocarpic plants. The objective of this paper is to explore the determinants of differential longevity among tree species and to examine the consequences of longevity-enhancing adaptations for overall tree life history patterns.

In animals, natural mortality is brought about by accumulation of damage to tissue and DNA (Gensler and Bernstein 1981; but see Comfort 1964 for historical treatment and alternate views). This damage leads to "old age" and decreasing ability to function. Such accumulations of damage depend on per gram metabolic rate, which is inversely correlated with body size (Lindstedt and Calder 1981; Hofman 1983). Molisch (1938) suggested that high metabolic rate similarly leads to short life-span in plants. However, as discussed below, high metabolic rate in plants may be an effect of rapid growth, not a cause of short life-span.

Since new tissue is continually added in plants, tissue senescence is generally not the cause of plant senescence (Westing 1964; Thimann 1980), though earlier researchers believed it was (Molisch 1938). While cytoplasmic inheritance of viruses and other agents can cause deterioration of successive vegetative generations, this is not universally true. In fact, some clones of nonwoody plants thousands of years old show no sign of senescence (Harper 1977, p. 702; Thimann 1980). Clonal longevity is achieved by continually generating new ramets. In the case of nonclonal

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plants, however, structural integrity of the plant must be maintained. Even with continued generation of new cells at the cambium and growing tips, a bounded (as opposed to a fragmenting clonal type) organism should have some upper limit to longevity. The following sections explore the determinants of this upper limit in woody plants. I use a cost-benefit analysis in an evolutionary framework (see Bell 1984) and test predictions with data from the literature for longevity of woody plants.

The role of defenses

I propose that increased longevity in nonclonal woody plants requires specific investment in chemical and structural defenses to resist decay, herbivory, wind, and fire (noted previously by Wells 1976 and others). These defenses have costs in terms of both direct synthesis and photosynthate not available for growth (Horn 1971; Janzen 1981; Bloom *et al.* 1985; Gulmon and Mooney 1985; Bazzaz *et al.* 1987). Benefits of defensive chemicals in leaves have been established (Southwood 1981; Zucker 1983; Brown 1984; Coley *et al.* 1985; Rhoades 1985), but they also reduce the photosynthetic rate (Zucker 1983; Rhoades 1985) and have direct metabolic costs (Bloom *et al.* 1985; Gulmon and Mooney 1985). While leaf defenses are obviously important, I assert that a more significant determinant of tree longevity is structural defenses against breakage and pathogens and chemical defenses against wood pathogens. Various wood chemicals have been specifically implicated in defense against pathogens (Scheffer and Cowling 1966; Smith 1966; Horsfall and Cowling 1980; Bailey and Deverall 1983; Zucker 1983).

Wind-caused mortality is significant in many forest types. Reiners and Reiners (1965) studied natural mortality in an old-growth oak-hickory forest in New Jersey. Over a 15-year period, 323 trees were killed by windthrow or wind snap versus only 161 by disease, insects, stress, lightning, or old age. Some of these 161 trees probably died from pathogens of wood. Many of the wind-thrown or snapped trees were probably susceptible because of decay. In forests not dominated by catastrophic fire, it appears that failure of the structural support is a major cause of mortality in adult trees. Therefore, there should be strong selective pressure on such trees for strong structural support tissue and defense of these tissues from pathogens if continued reproduction of the adult tree is advantageous. Such is the case when reproductive opportunities near the tree only occur at long intervals.

Fire is a significant mortality factor, particularly in dry forests such as the coniferous forests of the southern and western United States. In some regions, fire is so frequent that all major tree species exhibit fire-resistant traits and selective pressures for investment in thick bark are apparently strong. The importance of fire in limiting tree life-span can be assessed by noting Schulman's (1954) observation that extremely old individuals of a species are almost always found on very cold or very dry sites where fire cannot spread due to lack of ground fuel. His generalization may also extend to very wet sites, though these tend to have very bad fires during droughts if peat has accumulated.

To summarize, extreme longevity in trees can be achieved only on fire-free sites or those with low-intensity fires, or by investing in structural integrity (wood strength and pathogen resistance), but these defenses have costs.

Defense of wood

Wood that is resistant to decay and insect attack should occur in longer lived trees in proportion to the significance of these sources of mortality for the species. Trees protect their vascular systems and support tissues by developing decay-resistant wood and by increasing defenses at sites of wounding and decay (Shigo and Marx 1977; Tippet and Shigo 1981). This resistance to decay is under moderate to strong genetic control (Shigo *et al.* 1983). Trees resist pathogens through increased wood density, incorporation of defensive chemicals, and compartmentalization of wound sites (Shigo and Marx 1977). Increased density also increases wood strength and, therefore, wind firmness, though other wood properties are also important (Wangaard 1981).

In chemical defense, phenolics, resins, and other defensive compounds are deposited in the wood, particularly at the transition from sapwood to heartwood and at wound sites (Horsfall and Cowling 1980; Bailey and Deverall 1983). Such compounds have a high energetic cost per unit weight (about twice that of wood; see Coley *et al.* 1985; Gulmon and Mooney 1985), but they significantly decrease decay and insect attack (Wangaard 1950; Horsfall and Cowling 1980; Bailey and Deverall 1983). Pines concentrate resin at wound sites, preventing entry of decay (Taras and Saucier 1967; Horsfall and Cowling 1980; Bailey and Deverall 1983) or killing pathogens (Smith 1966). Heartwood of many species is high in defensive compounds and is thus favored for structural lumber. These chemicals are not simply metabolic waste products with no energetic cost; rather, they are specifically synthesized for defense (Janzen 1981; Bloom *et al.* 1985; Coley *et al.* 1985; Gulmon and Mooney 1985; Bazzaz *et al.* 1987). Furthermore, they do not add much to wood strength (Wangaard 1981). It is difficult to quantify chemical protection because different defenses are used by various plants. Estimates of resin content for pines range from 86% of the dry wood weight of resin-soaked heartwood in ponderosa pine, to 3.5 to 14% in the sapwood of other pines (Taras and Saucier 1967). Thus, these compounds can represent a substantial energetic investment.

The cost of the defense can be quantified by energy invested, especially in wood, because it has a low mineral nutrient content. Volumetric energy (heat) content of wood ($\text{J}\cdot\text{cm}^{-3}$) is used here as a measure of cost of defenses (including mechanical strength). This measure merges wood density ($\text{g}\cdot\text{cm}^{-3}$) and caloric content ($\text{J}\cdot\text{g}^{-1}$), thereby combining the energy costs of structural and chemical defenses on a wood volume basis. It is a conservative measure of cost of defenses because it does not consider cost of synthesis, which can be substantial for defensive compounds (e.g., rubber, Simmonds 1985; lignin, Bloom *et al.* 1985).

Defensive adaptations

The high energetic cost of defenses implies a strategic trade-off (Bloom *et al.* 1985; Gulmon and Mooney 1985; Bazzaz *et al.* 1987). A tree can grow fast with few defenses or slower with more defenses. But while a well defended tree will be more resistant to mortality factors, it will be less competitive with respect to neighbors and might be overtopped more easily. Because this effect is particularly pronounced at the seedling and sapling stages, we can anticipate that pioneer-type trees will be lower in defensive investments. There are a significant number of pioneer species that are very long lived, particularly among the conifers. This seem-

ing anomaly will be shown in the discussion to occur largely in either very favorable or very unfavorable habitats.

Rapid growth, however, may compensate for lack of defenses at certain stages of the life cycle. A vigorous pioneer tree may tolerate a substantial load of pathogens by simply outgrowing them (Coley *et al.* 1985); for example, by shedding infected leaves for new ones or healing over bark wounds in a few seasons. Thus, on moist sites, where selection for rapid height growth is most pronounced, the efficacy of rapid growth rate as a defense is greatest. As the plant approaches maturity, however, relative growth rate slows due to site limitations of water and nutrients, and a decreasing ratio of photosynthesis to respiration due to increased respiration demands from support tissue. Absolute radial increment decreases even faster because wood must be spread over a greater surface area, giving narrower rings. At this point, rapid growth (particularly rapid trunk growth to heal over wounds) can no longer be used as a defense against pathogens, making the plant increasingly susceptible to pathogen attack. This susceptibility, combined with structural weakness, should cause a rapid decline phase in pioneer (low defense) species once the peak of vigor has passed. This is in contrast to long-lived species that, when old, may grow very slowly for decades or centuries with minimal trunk decay or branch breakage.

There are two primary strategies trees use to minimize the adverse consequences of constraints due to defensive allocation costs: pipe-style construction, and grow now, defend later chemical defenses. For vertical support, a hollow pipe is nearly as strong as a solid pole but uses much less raw material. Young trees of many weedy species are able to achieve increased growth rates by hollow stem construction, at the cost of a slight reduction in strength. A variant on this is production of lower density juvenile wood in the top of the crown, with successive layers after the first 5–7 rings being higher density (e.g., loblolly pine). Trees typically impregnate heartwood with a wide variety of defensive chemicals. It is true that trees are prevented from completely saturating sapwood with defensive chemicals because the wood is still alive, but the sapwood of some species is more heavily saturated than the heartwood of other species. Heartwood is rarely saturated immediately after the transition from sapwood; it usually takes many years. I propose that part of the reason that trees delay complete saturation of the sapwood is to ensure sufficiently rapid juvenile height growth and crown spread. Since a mechanism exists to go back and increase the defensive chemical load of heartwood many years after it is formed, it is advantageous to do so. After the juvenile period, a surviving tree has more surplus energy that can be allocated to wood defense at lower risk.

The traditional explanation of mortality (Westing 1964; Wareing and Seth 1967; Thimann 1980), that decline and mortality occur when photosynthesis can no longer match respiration demands, is therefore only partially correct. In the extreme, a very favorable habitat increases longevity by allowing continued growth, as is the case in the Pacific Northwest (Wareing and Franklin 1979). Thus habitat favorableness can contribute to longevity. However, species that differ dramatically in longevity are often found growing side by side (e.g., *Salix* sp. adjacent to *Taxodium* sp.). Furthermore, very long-lived species are often found in unfavorable habitats such as deserts (e.g., *Juniperus occidentalis*, maximum longevity 900 years). I maintain that the allocation of

defenses in relation to growth rate and longevity is a substantial part of the explanation for these differences. The contribution of a favorable environment is most important for low-defense species that depend on rapid growth as a defense. Such species do not decline upon maturity solely because of an unfavorable photosynthesis to respiration (P/R) ratio. Instead, because of a reduced energy budget, active defensive measures (e.g., compartmentalization, wound healing) become ineffective, or deterioration such as rot and breakage overtakes the tree because the tree did not invest in defenses when younger. Keeping photosynthesis in balance with respiration becomes a serious problem only for very long-lived trees because of the increased cambial mass of a continually growing trunk.

It is important to maintain the distinction between slow growth resulting from energy allocated to defenses and that due to site differences. Desert species will grow slowly, of course, but it is noteworthy that desert trees and shrubs are far higher in chemical and structural (e.g., thorns) defenses than are mesic forest species. Rapid growth to overcome pathogens or herbivores is not available in the desert, so defenses are more important. Successful seed germination is also likely more infrequent in the desert, so parent plant survival has increased value. There are only a few desert species (pinyon pine and juniper) in the data examined below, so extreme habitat-induced slow growth is not a confounding factor in testing hypotheses about growth trade-offs. Similarly, extremely favorable sites are few and are analyzed separately.

It is possible to summarize the arguments thus far as a set of predictions, stated as a set of if (assumption) – then (prediction or consequence) pairs.

Prediction 1: If investment in defenses is crucial to attaining greater longevity, then resistance to wood decay in particular should be significant, especially in habitats (warm and wet environments) where decay rates are rapid. Within a particular habitat, increased energy invested in defenses should correlate with increased longevity.

Prediction 2: If investment in defenses or reproduction slows down the growth rate because of limited energy and (or) nutrient supplies, then there should be an inverse relation, within any one habitat, between growth rate and longevity. Note that the photosynthesis to respiration ratio explanation of longevity makes the opposite prediction: that rapid growth (due to a favorable site) should contribute to longevity (Wareing and Franklin 1979). These two aspects of rapid growth are considered separately.

Prediction 3: If decreased growth rate increases mortality rates of juvenile trees, particularly under height growth competition, then pioneer-type trees should sacrifice defensive investments in order to maximize juvenile growth rates.

Prediction 4: If pioneer-type trees depend on rapid radial growth rate to resist pathogens, then they should decline rapidly when they approach their maximum size because their growth rate is slower then. This decline should be typified by limb breakage, dead patches on

the trunk, increased insect attack, rapid pathogen invasion, and hollowing of the trunk. These species should live longer on more favorable sites.

Prediction 5: In contrast, long-lived species should be able to maintain themselves at a low growth rate at maturity without excessive pathogen attack (see Prediction 1) and should have specific adaptations for keeping photosynthesis and respiration in balance. Greater investment in roots, slow growth at maturity, drought tolerance, cambial retreat (e.g., bristlecone pine; LaMarche 1969) and branch-tip dieback are some of the adaptations used.

While the above predictions are expected trends, exceptions will occur. A species may be generally well defended but nevertheless have a short life-span. For example, American chestnut has durable wood and was long lived until the introduction of a fungal pathogen that has reduced it to a short-lived shrub. The intent is not to predict longevity in each particular case, but to demonstrate some of the selective pressures and energetic trade-offs involved in tree growth and defense.

Because longevity of trees crucially depends on structural integrity of the support system, investment in wood defenses was chosen to test these predictions. Wood properties are also relatively easily quantified. Wood defenses and growth rate are tested as predictors of longevity. Because of the proposed suppression of growth rate by reproductive investments (see Bell 1980), age of sexual maturity is also examined.

The choice of wood properties related to longevity requires some explanation. It was hypothesized that increased density should contribute to longevity, so specific gravity is a logical test variable. Decay resistance of wood is also logically related to defenses and longevity and was thus tested. It was hoped that volumetric heat content ($J \cdot cm^{-3}$) would be a good measure of total energy invested in wood, both chemical and structural, but since it is measured as heat of combustion, it actually measures chemical bond energy, a crude measure of cost. A better measure of cost of defenses would be obtained by calculating costs of synthesis for chemical defenses. Wood extractive content was considered for quantifying this, but some problems exist. A wide range of defensive chemicals exists and trees use various mixtures of them. The cost of synthesis of these compounds varies widely, from $2.58 g CO_2 \cdot g^{-1}$ for a particular phenolic resin (diplacol) to $5.00 g CO_2 \cdot g^{-1}$ for an alkaloid (nicotine), according to Gulmon and Mooney (1985). Not all defensive compounds are extractable either (e.g., lignin). Ideally, a complete analysis of wood (cellulose, lignin, tannin, terpenes, etc.) in terms of synthesis cost would be useful, but this is a task beyond the scope of this paper. Perhaps the logic of the defensive cost argument and preliminary data in this paper will inspire others to perform such analyses. But for the above reasons I have chosen not to analyze wood extractives as a separate variable.

Reproductive trade-offs

Life history theory predicts that equilibrial or declining populations should mature later than those that frequently undergo population increases (Caswell 1982). Molisch made this same prediction for plants as early as 1928 (Molisch 1938 (German edition, 1928) but without using a theoretical

framework. A study of tree longevity provides a good test of this prediction, because trees are long lived compared with animals. Finding a longer prereproductive period in longer lived species does not, however, necessarily support the theory. It is possible for reproductive maturity to increase with longevity but to decrease as a percentage of longevity. Thus, a useful measure of reproductive maturity is an allometric measure of the percentage of the life-span occupied by the prereproductive period.

A study of reproductive maturity versus longevity by Harper and White (1974) was based on a smaller data set, and no statistical analyses were performed. Consequently, the following conclusions differ substantially from theirs. Herbaceous species and woody monocarps were not included in this study, in contrast to theirs.

Methods

Data on properties of woody plants were gathered from the literature (Appendix 1). All species in North America were included because no one region or habitat contains enough species for any valid statistical evaluations, particularly when missing values are considered. Possible concomitant confounding factors (e.g., north-south differences) were taken into account in the analyses and actually provided evidence to help test some of the hypotheses. Primary data, taken from Altman and Ditmer (1962), included minimum and typical ages of sexual maturity as well as typical and maximum longevity. Minimum age of sexual maturity is the youngest age at which viable seeds are observed in the field, usually for open-grown trees. Typical age of maturity is the age at which forest-grown trees typically produce a good crop of seeds. Obviously, a "good crop of seeds" is a subjective criterion. Typical longevity is the age of the older trees in an old-growth stand, whereas maximum longevity is the upper known maximum above which very few trees are found. Ages of maturation and longevity were checked against Fowells (1965) to fill in missing data. In the event of conflict, Fowells' data were used based on the assumption that more man-hours were spent in compiling that reference. Some ages for first seed production were obtained from Schopmeyer (1974) when not available in the above two sources. Data on 11 shrubs were taken from Harper and White (1974) using the original records of White (personal communication). The same values were used for minimum and typical maturity, as well as for average and maximum longevity in these short-lived shrubs because the values are so close that it is difficult to differentiate between them.

Growth rates (1, very slow; 5, very fast) were obtained from Altman and Ditmer (1962). Specific gravity was obtained from Wangaard (1950) in which weight was determined from overdry samples, volume from green condition (i.e., oven-dry weight of a volume of green wood). Tolerance rank was obtained from Fowells (1965) using a five-point scale where 1 is very intolerant and 5, very tolerant. Caloric values in gigajoules ($GJ \cdot m^{-3}$) for wood were obtained from Mullins and McKnight (1981). Only values for mature trees (i.e., sawtimber size) were used so that comparisons with specific gravity and other variables would be valid. Data that included immature trees, such as that from Gower *et al.* (1984) and Neenan and Steinbeck (1979), therefore could not be used. Various papers (e.g., Golley 1961) that provide energy density ($J \cdot g^{-1}$) could not be used; conversion to volume units ($J \cdot cm^{-3}$) amplifies the variance in the heat data because of multiplication by the specific gravity term, which has its own variance. Decay resistance was obtained from Wenger (1984), who classified species into increasing resistance classes from 1 to 3. Data not available in Wenger (1984) was obtained from Hunt and Garratt (1967). The two references agreed in almost all cases. Note that few species in Appendix 1 have all types of information. Different analyses are not, therefore, necessarily based on the same set of species.

TABLE 1. Predictive structure of variables related to growth rate versus longevity trade-off (all tests run on SAS 1982)

Test variable	Predictor variable
Shade tolerance	Growth rate (by χ^2 contingency test) All species: ns ($n = 109$)
Specific gravity	Shade tolerance (by Kruskal-Wallis test) Gymnosperms: $P < 0.001$ ($n = 41$) Angiosperms: $P < 0.1$ ($n = 58$) Growth rate (by Kruskal-Wallis test) Gymnosperms: ns ($n = 44$) Angiosperms: $P < 0.0001$ ($n = 76$)
Heat	Specific gravity (by regression) Gymnosperms: $R^2 = 0.57$, $\beta = 16.3$, $P > T = 0.0001$ ($n = 20$) Angiosperms: $R^2 = 0.93$, $\beta = 19.9$, $P > T = 0.0001$ ($n = 24$)
Typical longevity	Heat content (by regression) Gymnosperms: ns ($n = 20$) Angiosperms: $R^2 = 0.57$, $\beta = 28.6$, $P > T = 0.0001$ ($n = 22$) Specific gravity (by regression) Gymnosperms: ns ($n = 43$) Angiosperms: ns ($n = 65$) Decay resistance (class 1 vs. 3 by Kruskal-Wallis test) Gymnosperms: $P < 0.1$ Class 1 longevity = 274 ($n = 17$) Class 3 longevity = 465 ($n = 13$) Angiosperms: ns

NOTE: ns, not significant (> 0.1 level).

Results and discussion

Longevity

Hypotheses to be tested were that longevity might be predicted by wood decay resistance, specific gravity, and volumetric heat content (heat). Growth rate and longevity were predicted to be inversely correlated. Shade tolerance was thought to be related to longevity, but as a selective force, not as a causal one (i.e., shade tolerance per se does not enhance longevity). Possible interactions between these variables were explored to see which might be correlated. The correlation of growth rate with shade tolerance was explored using a contingency table χ^2 test (SAS 1982) because both variables are class rather than ordinal variables. Growth-rate classes 1 (with one species) and 5 (with two species) were dropped, leaving 109 observations for a 3×5 table analysis, which is an adequate sample size. Separate analysis by gymnosperms and angiosperms was not possible. For all species together, the χ^2 test was not significant (Table 1, $P = 0.15$), indicating that there is no relationship between shade tolerance and growth rate. Although this result seems surprising, it results from the fact that site quality is a greater contributor to the growth rate rankings than is shade tolerance at the geographic scale of this study. Shade tolerance and growth rate can therefore be used as uncorrelated variables.

Nonparametric tests showed that specific gravity was higher for more shade-tolerant trees for both life forms (angiosperms and gymnosperms) (Table 1). Specific gravity was higher for slower growing angiosperms, but not for gymnosperms (Table 1).

Two proposed measures of wood defense, heat and specific gravity, were tested for relationship. For angiosperms, heat was highly predicted by specific gravity (Table 1, $R^2 = 0.93$). For gymnosperms, however, the

unexplained variation was quite high, with an R^2 of only 0.57 (Table 1). This is probably because of the greater contribution of resins to the heat content of gymnosperms compared to angiosperms.

The next step, then, was to test typical longevity against heat, specific gravity, decay resistance, growth rate, and shade tolerance. A simple test of longevity as predicted by heat did not reveal any trend for gymnosperms but gave a modest R^2 value of 0.57 for angiosperms. A more detailed treatment of the effect of the heat variable (below), however, yields some stronger results.

Specific gravity had no significant predictive power. While this result is contrary to expectations, the heat results below and the fact that extremely short-lived weedy species typically have very low density wood (Wells 1976) suggest that a more clever analysis would expose a role for density in wood defense. The alternative models (proposed by a reviewer), that dry sites produce high-density wood, which then allows greater longevity, and that great size (with concomitant greater longevity) requires high density wood, do not seem to be supported by this negative result. In fact, the size-density relationship does not seem particularly useful: the four tallest angiosperms in North America (yellow poplar, eastern cottonwood, sweet gum, and sycamore) all have average to low wood specific gravities (0.38, 0.37, 0.44, and 0.46, respectively).

Decay resistance of wood was tested as a predictor. This measures the effectiveness of passive defenses, but not active defenses involved in compartmentalization. For gymnosperms class 1 (least resistant), longevity was 274 years compared with a class 3 longevity of 465 years (significantly different at the 0.1 level; Table 1). There was no difference for angiosperms. When all species were combined, the most ($n = 27$) and least ($n = 60$) decay-resistant classes had a

TABLE 2. Breakdown of typical longevity by growth rate where a growth rate class of 1 is the slowest (tests by one-way ANOVA using SAS GLM procedure (1982))

Growth rate class	Typical longevity (years)	Sample size
Gymnosperms ($P < 0.1$ using 4a, ns using 4b)		
1	363	4
2	314	20
3	279	14
4a	213	16
4b	421	20
Angiosperms ($P < 0.001$)		
2	190	24
3	166	14
4	132	37
5	68	3

NOTE: 4b includes 4a plus *Pseudotsuga menziesii*, *Sequoia gigantea*, *S. sempervirens*, and *Thuja plicata*.

longevity of 251 and 178 years, respectively (significantly different at the 0.02 level).

Growth rate was a significant predictor of longevity (Table 2). The slowest growing angiosperms were nearly three times as long lived as the fastest growing (190 vs. 68 years). For gymnosperms, the difference was nearly double (363 years for the slowest vs. 213 for the fastest). The gymnosperm result is not significant if the four largest conifers (the Douglas-fir, the two redwoods, and the western red cedar) are included. These four species occur on very favorable sites where rapid growth can be maintained for centuries. This suggests that the growth rate classification as an indicator of energy invested in defenses instead of growth cannot be used on extremely good sites. On such sites, the prediction that good growing conditions should favor increased longevity (Waring and Franklin 1979; Waring, personal communication, 1987) is upheld. Trees on such favorable sites can allocate significant energy to defense and still maintain a rapid growth rate. On less than ideal sites, however, it appears that the longevity - growth rate trade-off is dominant. (An anonymous reviewer noted that both coast redwood and Douglas-fir are genetically unusual for conifers, supporting their separate treatment in these analyses.)

Shade tolerance was also a good predictor of longevity. When classes 1 and 2 (intolerant) were compared with 3, 4, and 5 (more tolerant), both gymnosperms and angiosperms showed more tolerant species to be longer lived (Table 3). All conifers were included in this analysis. I do not see tolerance as causing longevity, but to be a selective force favoring longevity. Shade-tolerant species must often spend decades to centuries in a suppressed state before reaching the canopy and achieving reproductive maturity. For such species extended life-span is almost essential.

Heat as a predictor variable, treated briefly above, is examined in more detail here as a measure of total energy invested in structural and chemical defenses. The relationship between typical longevity and volumetric heat content for angiosperms is illustrated in Fig. 1. Note that all heat data (Mullins and McKnight 1981) were collected from Canadian trees. Two statistically distinct groups are evident

TABLE 3. Breakdown of typical longevity by shade tolerance class where 1 is the least tolerant (Kruskal-Wallis test (SAS 1982))

Shade tolerance classes	Typical longevity (years)	Sample size
Gymnosperms ($P < 0.05$)		
1 + 2	259	17
3 + 4 + 5	461	29
Angiosperms ($P < 0.05$)		
1 + 2	147	33
3 + 4 + 5	191	23

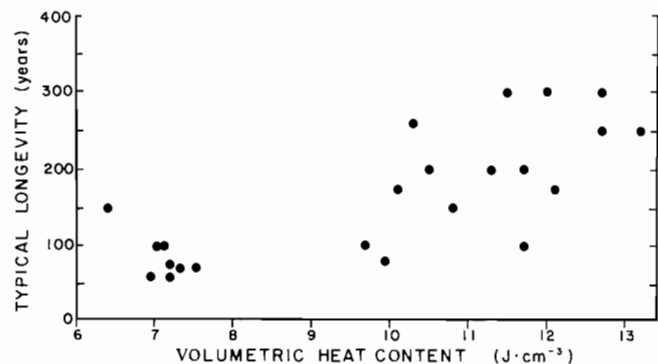


FIG. 1. Typical longevity versus volumetric heat content of sawtimber-size stem wood of angiosperms. Two groups are evident: a low heat content group that is shade intolerant and short lived, and a high heat content group that is longer lived and more shade tolerant. See Table 5 for statistical tests.

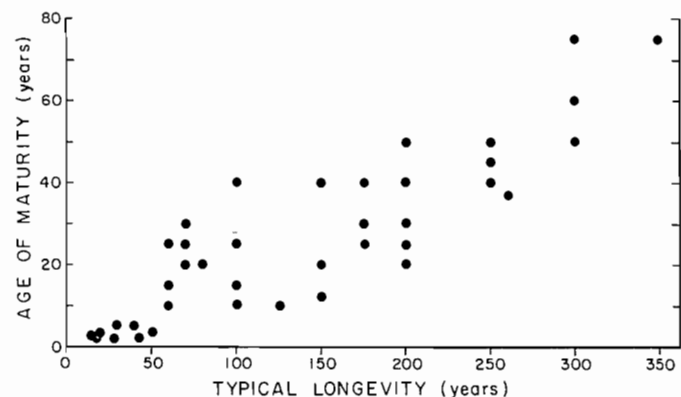


FIG. 2. Typical age of sexual maturity versus typical longevity for North American angiosperm trees and shrubs. See Table 6 for statistical tests.

(Table 4). The same relationship exists for gymnosperms, with the same, although narrower, gap separating the groups. The group of hardwoods with lower volumetric heat content is distinctly less shade tolerant than the high heat group (1.5 vs. 3.0) and is therefore referred to as pioneers. This tolerance relationship is reversed for conifers (3.8 vs. 1.6). This may be because habitats wet enough to support shade tolerant conifers are cool enough that decay rates are lower, and thus defensive investments are lower. For hardwoods, the pioneer group has a significantly shorter life-span (86 vs. 203 years). In distinct contrast, the difference in life-span between the two groups of conifers is not signifi-

TABLE 4. Comparison of groups of species (from Fig. 1) separated by distinct volumetric heat contents

	Angiosperms		Gymnosperms	
	Low heat	High heat	Low heat	High heat
Longevity (TYPMORT) (years)	86 (n = 8)	203*** (n = 15)	328 (n = 16)	456 ns (n = 5)
Shade tolerance (1, very intolerant; 5, very tolerant)	1.5 (n = 8)	3.0** (n = 16)	3.8 (n = 16)	1.6** (n = 5)
Growth rate (1, very slow; 5, very fast)	4.3 (n = 8)	3.1*** (n = 17)	2.9 (n = 16)	3.2 ns (n = 5)
Volumetric heat (J·cm ⁻³)	7.10 (n = 8)	11.09*** (n = 17)	7.30 (n = 16)	9.82*** (n = 5)
Minimum age first reproduction (AVEREP) (years)	11.5 (n = 8)	22.2** (n = 13)	15.5 (n = 16)	13.0 ns (n = 5)
Typical age first reproduction (AVEREP) (years)	20.0 (n = 3)	42.6* (n = 14)	30.9 (n = 16)	30.2 ns (n = 5)
Prereproductive % of life-span (MINREP/TYPMORT)	0.14 (n = 8)	0.11 ns (n = 12)	0.06 (n = 16)	0.05 ns (n = 5)
Maturity % of life-span (AVEREP/TYPMORT)	0.29 (n = 3)	0.22 ns (n = 13)	0.12 (n = 16)	0.15 ns (n = 5)

NOTE: Means within taxa are compared for low and high heat groups by *t*-test with correction for unequal variance when necessary. Shade tolerance and growth rate are treated as ordinal rather than class values on the assumption that the classes represent approximately equal intervals of tolerance or growth rate, respectively. Nonparametric tests (χ^2 contingency table) for growth rate and shade tolerance gave the same results as below except that angiosperm heat classes differed in growth rate at the 0.01 level rather than the 0.001 level. Tests were run on SAS (1982).

*, difference significant at 0.05 level; **, difference significant at 0.01 level; ***, difference significant at 0.001 level; ns, not significant.

cant, though the trend is in the same direction as for hardwoods. A plot of the conifer data (not shown) indicates that this is not merely due to small sample size. A test of longevity versus specific gravity, using the same species as in Fig. 1, produced a plot very similar to Fig. 1, as might be expected from the 0.93 R^2 value for heat as predicted from specific gravity. In contrast, when specific gravities for all species were plotted by life-form, distinct subgroups were not found (not shown) and the regressions by life form were not significant (Table 1). This suggests that there is geographic variation in specific gravity that may not be related to longevity, so that when species from a limited region (Canada in this case) are used, the predictive power of specific gravity and heat goes up considerably.

It is interesting that five of the eight species in the angiosperm low heat (pioneer) group are in the genus *Populus*, noted by Shigo (personal communication) to be particularly poor wound compartmentalizers, which again suggests a relationship between heat content as a measure of defensive investments and Shigo's compartmentalization concept (this is the only analysis where there is an obvious possibility of a phylogenetic bias possibly affecting the significance level). The longest lived member of the pioneer group, *Populus trichocarpa*, is also by far the largest, due to its occupation of a more favorable habitat (see Waring and Franklin 1979). If *P. trichocarpa* uses growth rate as a defense against decay (as postulated), then it is not sur-

prising that it is an outlier. It is noteworthy that other short-lived species also live longer on better sites, for example, jack pine (*Pinus banksiana*) and aspen (*Populus tremuloides*) (Fowells 1965). A clear example is yellow poplar (*Liriodendron tulipifera*). It typically becomes a massive tree, 200 years old or more, in moist coves and valleys in the east, towering over the forest and having diameters exceeding 10 ft. Every giant I have seen had massive butt rot or was hollow in the lower trunk, in contrast to nearby oaks and hemlocks. Yellow poplar is able to keep ahead of the decay only so long as it can maintain a rapid growth rate. On poor sites, it is not nearly so long lived. In contrast, for species that are typically long lived, the longest lived individuals are often found on the driest or coldest sites (Schulman 1954) because fire may be very rare on such sites. This supports the hypothesis that growth rate acts as a crucial defense for fast growing, short-lived species but is not as important for species with high defensive investments.

The hypothesis that energy investment in defenses slows growth rate was also tested for the two heat groups (Table 4). For broadleaf pioneers ($n = 8$), the mean growth rate (on a scale of 1 to 5) was 4.25 (fast); for the other group ($n = 17$) the mean was 3.12 (moderate). The difference was significant at the 0.001 level, supporting the hypothesis. The difference was not significant for conifers. Nonparametric tests yielded the same results. This suggests that for angiosperms, Molisch's (1938) contention that plants with

TABLE 5. Prediction of age of reproduction of angiosperm trees and shrubs from longevity. Eight models are tested. The variables are R_M = minimum age of first reproduction, R_T = typical age of first reproduction, L_T = typical longevity, and L_M = maximum longevity

Model	<i>n</i>	<i>a</i>	<i>b</i>	R^2	<i>P</i> (for slope)
$R_M = a + bL_T$	68	2.65	0.092	0.64	0.0001
$R_M = a + bL_M$	53	3.87	0.050	0.52	0.0001
$R_T = a + bL_T$	53	1.39	0.187	0.73	0.0001
$R_T = a + bL_M$	46	6.71	0.091	0.58	0.0001
$\ln(R_M) = a + b\ln(L_T)$	68	-1.71	0.890	0.72	0.0001
$\ln(R_M) = a + b\ln(L_M)$	53	-1.35	0.744	0.72	0.0001
$\ln(R_T) = a + b\ln(L_T)$	53	-2.39	1.136	0.78	0.0001
$\ln(R_T) = a + b\ln(L_M)$	46	-1.92	0.959	0.81	0.0001

NOTE: Data are from Appendix 1. R^2 adjusted by DF analyses from SAS (SAS 1982). Results were rejected if $P > 0.1$ or $R^2 < 0.3$. R^2 and regression parameters not presented for results that are not significant. All tests for gymnosperms were not significant and are therefore not shown.

a high metabolic rate have a shorter life-span is most likely due to a lack of investment in defenses by fast-growth types. Such species have higher green to total biomass ratios (Strauss and Ledig 1980) and higher photosynthesis rates per unit leaf area, partially due to fewer chemical defenses. Thus, total energy capture and concomitant respiration rate are higher. High respiration rate is probably not a direct contributor to short life-span as high metabolic rate is in animals (Linstedt and Calder 1981; Hofman 1983).

A test was made of the multivariate relationship between heat, longevity, growth rate, and shade tolerance. The high and low heat groups (Fig. 1, Table 4) were used to define two a priori groups. Canonical discriminant analysis was used to assess the separation of the groups. For angiosperms, a highly significant ($P > F = 0.002$) canonical correlation (0.723) based on longevity, growth rate, and shade tolerance was found (the latter two treated as ordinal variables), with all three variables contributing. This reinforces the univariate results in Table 4. Results for conifers are also consistent with Table 5, with only shade tolerance contributing to discriminating the two groups.

The apparent failure of low and high heat groups of conifers to differ in longevity and growth rate supports another aspect of the theory. The low heat group in this sample is dominated by genera such as *Picea* and *Abies* from cold climates, where decay is slower than in warm climates (Hepting and Shigo 1972; Shigo, personal communication). The high heat group is dominated by species from environments in which decay rates are faster and (or) from habitats where fire (and thus fire wounding) is more common. The lack of selective pressure by decay-induced mortality allows trees in low-decay habitats to evolve reduced energetic investment in wood defenses. This habitat dichotomy confounds this small data set and eliminates the ability to ascertain the effects of tolerance and growth rate for the conifers. Separate analyses by moist-temperate/fire-prone versus cold and (or) fire-free habitats would be a logical step, but the sample size available precludes this test until more heat content data can be obtained.

These results support the hypothesis that trees protect themselves against mortality factors via energetic investments and that these investments decrease growth rate. This

makes investment in long-term wood defenses incompatible with a pioneer strategy.

What is particularly surprising about this study is that two distinct groups occurred along the heat axis (Fig. 1). At first glance, the theory in this paper predicts a trade-off between defensive investments and longevity, not a dichotomy. Let us examine, however, the regeneration process in a deciduous forest. Typical gaps created by wind, pathogens, and other agents leave many seedlings and saplings intact. These species, which may be shade intermediate or tolerant, then begin rapid growth. Where fire has occurred, there may be prolific stump and root sprouting of tolerant species. There will then be a race between established advance regeneration and new seedlings of intolerant pioneer types (Williamson 1975). The seedlings and saplings of the pioneers must grow significantly faster than either the stump sprouts or the advance regeneration in order to overcome their initial disadvantage. I contend that part of this necessary growth rate difference is achieved via a shade intolerant photosynthetic system and production of a limited root system, as noted by Strauss and Ledig (1985). The rest is made up by sacrificing a major portion of stem defensive investments. This creates the two distinct groups in Fig. 1.

Age of sexual maturity

Equations for predicting age of sexual maturity from longevity are presented in Table 5. Raw data and natural log transformed data were analyzed. The number of species per test varied due to missing values. Gymnosperms gave a nonsignificant fit for all regressions. A significant fit was found for angiosperms. With raw data, typical longevity was a better predictor of age of maturity than was maximum longevity, as expected, because of the greater difficulty in estimating maximum longevity. The benefit of logarithmic transformation of angiosperm data was not significant, even though R^2 increased somewhat, because three out of four regressions had b values very close to 1, indicating a linear relationship (Table 5).

The intercept of the fitted linear curves should be close to zero if the data reflect a biological relationship between maturity and longevity. The linear model for all four regressions had small intercepts. The regressions with the highest

R^2 values also had the smallest intercepts. This confirms the reliability of the fitted curves.

The ratio of average age of reproduction to typical longevity (AVEREP/TYPMORT from Appendix 1) for angiosperms (0.20, $n = 53$) was not significantly different from that for gymnosperms (0.16, $n = 46$) even at the 0.1 level. The 10 gymnosperms with TYPMORT ≥ 400 years in Table 1 have a much shorter typical prereproductive period (as a percentage of life-span) than do the other gymnosperms. For very long-lived trees, age at maturity may depend more on achieving some minimum size. When they are excluded, the two groups have almost identical values of 20% of the life-span ($P > t = 0.999$).

The result for minimum age of reproduction is quite different than that for typical age. Conifers have a much lower MINREP/TYPMORT ratio (0.07, $n = 51$) than do angiosperms (0.12, $n = 68$); this difference is significant at the 0.0001 level. When the 10 longest lived conifers are excluded, this ratio for conifers becomes 0.08, which is still different at the 0.0001 level.

An explanation of these maturity trends is possible. In general, the evolutionarily optimum age at which reproduction should begin is based on investment of resources in current growth to promote future increased reproduction, versus current reproduction at the expense of growth (Hamilton 1966; Bell 1980). Growth is exponential during early stages for open-grown plants; any investment in reproduction could result in failure to keep up with the stand and, therefore, an early death. In an even-aged stand of herbaceous plants, for example, the difference between survival and death can be due to just a few days difference in germination time (Harper 1977). For trees, a more subtle advantage to delayed reproductive maturity is that seed dispersal distance is enhanced by plant height. A 10-ft Douglas-fir may disperse seeds 10 ft radially, scarcely out of the zone of influence of the tree itself, whereas a 170-ft tree might disperse seeds 1000 ft (Fowells 1965). The ratio of areas covered here is 10000:1. Even for a 100-ft dispersal radius the ratio is 100:1.

Early reproduction may be favored in species that commonly colonize large forest openings. If invading trees reach a modest size while the site is still open, seeds from such colonist trees are more likely to become established with sufficient space for full growth. Disturbance patches in many coniferous forests tend to be larger than those in deciduous forests (Pickett and Thompson 1978). Invading trees in the large inner zone of these patches may be isolated, with great reproductive opportunities and consequent selection for early reproduction in spite of the depression in growth rate caused by early reproduction. In deciduous forests, fire is usually followed by prolific stump sprouting so that trees seeding in after a burn are not isolated and do not have exceptional opportunities for second generation seeds to germinate. Windthrow or insect kill in deciduous forest does not destroy abundant advance regeneration. Early reproduction should therefore be more disadvantageous in angiosperms.

Conifers in North America typically grow on a wider range of sites than do broadleaf trees. Those in boreal, mountaintop, and bog habitats grow slowly, whereas southern species (e.g., *Pinus taeda*) and coniferous rain forest trees have very rapid growth. Thus, the time required to achieve a given size varies. If maturity depends on size,

then the correlation of maturity with age weakens, as observed in this study, particularly for very long-lived species. Strauss and Ledig (1985) described a significant relationship between maturity and longevity in pines, a genus generally restricted to drier and warmer sites. Including genera from more extreme sites may have obscured the significant relationship they observed and led to a high variance in conifers.

The fact that prereproductive period as a percentage of life-span differs for earliest age of reproduction (but not typical age of maturity) between conifers and hardwoods suggests that early reproduction is selected for differently between pioneers and long-lived types, but only at the level of major taxa.

A demographic model compared

The results of this study relate to Caswell's (1982) theory concerning selection of life history parameters in relation to the equilibrium status of populations. Using a demographic approach, he argued against the traditional view that K -type traits are selected for in populations at equilibrium. He proposed that species whose populations are expanding experience r -selection, whereas those whose populations are declining will experience K -selection. He stated that most of the same traits selected for under equilibrium conditions will also be selected for under declining population conditions. The existence of species with K -selected traits is not necessarily evidence for the importance of equilibrium in the evolution of life history traits. His model predicts that divergence will occur over evolutionary time, producing suites of species with distinctly "declining" (i.e. K -selected) characteristics (long life-span, slow development, delayed reproduction, iteroparity, and perhaps high investment per offspring) and distinctly "increasing" characteristics (short life, fast development, early reproduction, semelparity, senescence, and perhaps less investment in individual offspring). I will refer to these types as persistent and ephemeral types, respectively, to avoid the r - versus K -concept emphasis on resource availability. Pioneer and climax are also misleading terms because some invaders of disturbed sites are very long-lived and some small shade-tolerant species are short-lived.

Trees, because of their wide range of longevities, are ideal candidates for testing this theory. Caswell contrasted iteroparity with semelparity, but when applied to trees the distinction is not useful because very few trees are semelparous, and the dichotomy is inconsistent with the prediction of early maturity in ephemeral types. Energetic investment per young (seed) produced also presents some problems because much of the interspecific variation in seed size is related to habitat. Turner (1985), for example, failed to find a significant relationship between successional status and seed weight, seed longevity, or crop frequency, though Strauss and Ledig (1985) did find some relationships within pines. While an analysis of seed weight might be useful, the variable usually considered in life history theory is total reproductive effort, for which little data exists for trees.

The four traits remaining in Caswell's treatment are life-span, senescence, growth rate, and age of maturity. I have proposed that growth rate and life-span are necessarily inversely related in trees because long life requires energetic investments in defenses that slow down the growth rate; this is a physiological rather than a demographic explanation.

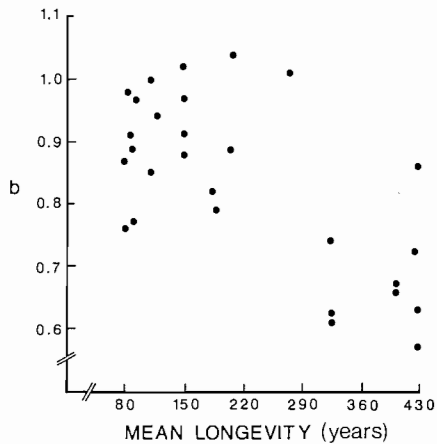


FIG. 3. Allometric coefficient b (eq. 1) versus longevity. Data from Strauss and Ledig (1985).

This prediction was upheld by data analysis. Further, my model predicts the existence of abrupt decline in ephemeral types because they depend on rapid growth as a major defensive measure, particularly for the stem. The question that Caswell (1982) raised is whether the ephemeral and persistent strategies are distinct suites of traits rather than a continuous gradation. Figure 1 and Table 4 support the existence of two distinct groups in angiosperms. An ephemeral type can be identified as one that is shade intolerant, fast growing, early maturing, short lived and has an abrupt decline (senescence) phase. A persistent type can be identified as one that is more shade tolerant (but not always), slower growing, later maturing, longer lived and has a persistent adult stage. It is not the case, however, that shade-intolerant species are early maturing when maturity is measured as a percentage of the life-span (data presented in text, above). Furthermore, extremely long-lived species have the smallest relative prereproductive period (as percentage of life-span).

There is a distinct separation of the groups, as Caswell (1982) predicted. The separation, however, is on the defensive energy investment axis (volumetric wood heat content or specific gravity), with some overlap in life history traits between the two groups. It seems that a successful pioneer tree must sacrifice the maximum possible defensive investments in exchange for rapid growth. This leads to a distinct dichotomy of behaviors. The existence of two distinct groups in conifers was inconclusive because of confounding habitat factors (on very cool sites decay rates are lower so trees can have reduced defenses without reduced longevity). A further distinction made here, but not by Caswell (1982), is that between minimum and typical age of sexual maturity. These two parameters behave differently in conifers and hardwoods, most likely due to bet-hedging selection for early maturity in species (such as most conifers) of open or heavily disturbed habitats.

An alternative approach to the problem, taken by Strauss and Ledig (1985), also partially confirms Caswell's prediction of distinct suites of traits. Strauss and Ledig calculated the allometric coefficient b in 20 species of pines:

$$Y = aX^b$$

where Y is leaf mass and X is total plant mass for seedlings. They showed that these allometric coefficients change little over the tree's life-span. Species with lower b values invested

more energy in stem and (or) root mass. They proposed that this represents investment in competitive components such as root mass that are advantageous in a crowded habitat where longevity is favored. The long-lived group had a low b value and the short-lived group a high b value. The clustering is very distinct (Fig. 3). Their result is consistent with the idea that longevity depends on increased investment in defenses, since their Y and X variables are total mass units. In addition, increased root mass provides a structural defense against windthrow. How much of the investment is due to competitive (root) versus defensive investments is impossible to say without more data, but Caswell's and my predictions of distinct suites of traits, particularly with respect to longevity, are upheld for conifers when the analysis is carried out within a genus. Other life history traits in Strauss and Ledig (1985) for pines trend in the expected direction (i.e., similar to hardwoods in this study). These results suggest that at least part of the inverse relation observed in this study between growth rate and longevity is due to greater investment in roots among long-lived species.

A purely demographic analysis such as Caswell's (1982) is insufficient for predicting life history traits. A physiological approach based on strategies of energy allocation allows us to compare certain life history traits via the mechanism of energetic trade-offs. This approach also can predict the relative rapidity of individual senescence. Key traits defining distinct ephemeral and persistent types are (i) the extent of defensive investments and (ii) the leaf versus wood and stem versus root investment ratios. A new demographic parameter is minimum age of reproduction (as a percent of the life-span), which differs between hardwoods and conifers and represents bet-hedging in disturbance-prone habitats. Typical reproductive maturity as a percentage of the life-span does not appear to differ between shade tolerance classes or between hardwoods and conifers; therefore it is generally an allometric variable rather than one that is subject to independent selection pressure.

The various measures of tree defenses used in this study did not yield entirely consistent results, but enough strong results emerged to point to this type of analysis as potentially highly profitable. Future work can deepen our understanding of life history traits by exploring certain issues in more depth. Geographic variation in traits within a species could be usefully studied. Assessment of the cost of various components of growth should include costs of synthesis rather than merely caloric content. Biomass alone as a measure is completely inadequate. The nature of conifer defenses, particularly the energetics of resin production and deployment, needs further study. The roles of quantitative (carbon-based) versus qualitative (nitrogen-based) defenses and of determinate versus indeterminate growth need evaluation. More consistent criteria are needed for defining species characteristics such as age of maturity and longevity because trees are more phenotypically plastic than animals. When these types of data have been collected, then a re-analysis of tree life histories should be even more informative and make a major contribution to evolutionary theory and to attempts to model succession (e.g., Huston and Smith 1987).

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Appendix 1

Typical species values for life history traits and wood properties compiled from the literature. Data sources are described in the text. Unusual values are described in note at bottom of table. MINREP, minimum age of first reproduction; AVEREP, average age of first reproduction; TYPMORT, typical age of mortality (few trees live longer than this age); MAXMORT, maximum longevity

Species	MINREP (years)	AVEREP (years)	TYPMORT (years)	MAXMORT (years)	Specific gravity	Growth rate	Shade tolerance	Volumetric heat (J·cm ⁻³)	Decay resistance
Gymnosperms									
<i>Abies amabilis</i>	20	30	400	590	0.35	3	4	6.83	1
<i>Abies balsamea</i>	15	30	125	150	0.34	4	5	6.42	1
<i>Abies concolor</i>	30	40	150	500	0.35	3	5		1
<i>Abies fraseri</i>	20	40	125	170		3			1
<i>Abies grandis</i>	20	30	200	400		3	4	7.20	1
<i>Abies lasiocarpa</i>	15	25	150	250	0.31	3	5		1
<i>Abies magnifica</i>	35	45	250	400	0.37	3	3		1
<i>Abies procera</i>	50	60	400	650		4	2		1
<i>Chamaecyparis lawsoniana</i>	8	20	500		0.40	3	5		3
<i>Chamaecyparis nootkatensis</i>			1000	3500	0.42	2	4		3
<i>Chamaecyparis thyoides</i>	7	20	200		0.31	2	3		3
<i>Cupressus arizonica</i>			100	300		2			3
<i>Juniperus deppeana</i>			300	500	0.48	1			3
<i>Juniperus occidentalis</i>			300	900		2	1		3
<i>Juniperus osteosperma</i>			650	800		1			3
<i>Juniperus scopulorum</i>	10	50	250	300		2	1		3
<i>Juniperus virginiana</i>	10	25	150	300	0.44	2	1		3
<i>Larix laricina</i>	20	45	150	180	0.49	3	1	9.93	2
<i>Larix occidentalis</i>	25	40	700	915	0.48	2	1	11.00	2
<i>Libocedrus decurrens</i>			500	550	0.35	2	4		3
<i>Picea engelmannii</i>	16	25	450	550	0.31	2	4	7.28	1
<i>Picea glauca</i>	10	20	150	350	0.37	2	4	6.70	1
<i>Picea mariana</i>	10	18	150	250	0.43	2	4	7.91	1
<i>Picea pungens</i>	20	50	150	350		2			1
<i>Picea rubens</i>	15	30	200	300	0.41	2	4	7.49	1
<i>Picea sitchensis</i>	20	40	500	800	0.42	4	4	6.58	1
<i>Pinus attenuata</i>	5		100	150		4			
<i>Pinus banksiana</i>	5	25	80	150	0.46	4	1	8.94	
<i>Pinus clausa</i>	5	35	60		0.45	2	2		
<i>Pinus contorta</i>	5	20	120	300	0.43	2	2	8.32	2
<i>Pinus echinata</i>	8	20	200	300	0.54	4	3		2
<i>Pinus edulis</i>	25	75	350	540	0.57	1	1		
<i>Pinus elliotii</i>	10	20	150	250	0.66	4	2		2
<i>Pinus flexilis</i>	10	30	200	400	0.42	2			
<i>Pinus glabra</i>	10		75	150		4			
<i>Pinus jeffreyii</i>	8		400	500	0.42	3	2		
<i>Pinus lambertiana</i>	7	100	400	600	0.38	4	3		
<i>Pinus monophylla</i>	20	25	150	225		1			
<i>Pinus monticola</i>	10	40	400	615	0.42	4	3	7.70	
<i>Pinus palustris</i>	16	28	300	400	0.62	4	1		2
<i>Pinus ponderosa</i>	5	16	600	726	0.42	3	2	9.15	2
<i>Pinus radiata</i>	4	20	85	150		4	3		

<i>Pinus resinosa</i>	22	55	200	300	0.51	4	1	8.15	
<i>Pinus rigida</i>	8	12	100	200	0.52	4	1		
<i>Pinus sabiniana</i>	6		80	150		3			
<i>Pinus serotina</i>	4	30			0.50	2	2		
<i>Pinus strobus</i>	10	22	200	450	0.37	4	3	7.08	2
<i>Pinus taeda</i>	6	15	100	300	0.54	4	2		2
<i>Pinus virginiana</i>	5	50	100	200		3			
<i>Pseudotsuga menziesii</i>	10	25	750	1200	0.51	4	3	10.10	2
<i>Sequoia gigantea</i>	20	100	2000	3000		4	3		
<i>Sequoia sempervirens</i>	20	60	1250	2200	0.42	4	5		3
<i>Taxodium distichum</i>	20		600	1200	0.42	2	3		3
<i>Taxus brevifolia</i>			250	350	0.67	2			3
<i>Thuja occidentalis</i>	20	30	300	400	0.32	2	4	6.75	
<i>Thuja plicata</i>	15	25	1000	1200	0.34	4	5	6.95	
<i>Tsuga canadensis</i>	20	50	450	800	0.43	2	5	7.41	1
<i>Tsuga heterophylla</i>	20	30	400	600	0.44	3	5	7.99	1
<i>Tsuga mertensiana</i>	20	30	400	800	0.51	3	5		1
Angiosperms									
<i>Acer macrophyllum</i>	10	20	150	300	0.44	4	4		1
<i>Acer negundo</i>			75	100		5			1
<i>Acer rubrum</i>	4		80	150	0.49	4	2	9.93	1
<i>Acer saccharinum</i>	20	40		125	0.44	4	2	8.98	1
<i>Acer saccharum</i>	40	60	300	400	0.56	2	5	12.00	1
<i>Aesculus glabra</i>	8					3	3		1
<i>Aesculus octandra</i>			60	80	0.33	4	4		1
<i>Alnus rubra</i>	8	10	60	100	0.37	4	2	7.20	1
<i>Arbutus menziesii</i>	5				0.58	2	3		
<i>Betula alleghaniensis</i>		40	150	300	0.55	4	3	10.80	1
<i>Betula lenta</i>		40	150	250	0.60	3	3		1
<i>Betula papyrifera</i>	15	40	100	140	0.48	4	2	9.68	1
<i>Betula populifolia</i>	8		50		0.45	4			1
<i>Carya cordiformis</i>		30	175	200	0.60	2	2	12.10	1
<i>Carya glabra</i>		30	200	300	0.66	2	2		1
<i>Carya illinoensis</i>	20	75	300		0.60	3	2		1
<i>Carya laciniata</i>	40	75	350			2	2		1
<i>Carya ovata</i>		40	250	300	0.64	2	2	12.7	1
<i>Carya tomentosa</i>		25	200	300	0.64	2	2		1
<i>Castanea dentata</i>			100	300	0.40	4			3
<i>Castanopsis chrysophylla</i>			200	400	0.42	4			
<i>Catalpa speciosa</i>	10	20	100		0.38	4			3
<i>Celtis laevigata</i>	15	30			0.47	3	4		
<i>Celtis occidentalis</i>			150	200	0.49	4	3		1
<i>Cornus florida</i>	5		125		0.64	2	5		
<i>Cornus nuttallii</i>		10	125		0.58	2			
<i>Diospyros virginiana</i>	10	25	60	80	0.60	2	1		
<i>Fagus grandifolia</i>	40	60	300	400	0.56	2	5	11.50	1
<i>Fraxinus americana</i>	20	37	260	300	0.55	4	2	10.30	1
<i>Fraxinus latifolia</i>			150	250	0.50	3			1
<i>Fraxinus nigra</i>					0.45	2		9.35	1
<i>Fraxinus pennsylvanicum</i>					0.53	4	2		1
<i>Fraxinus quadrangulata</i>		25	200	300	0.53	4			1
<i>Gleditsia triacanthos</i>	10		120		0.60	4	1		3
<i>Ilex opaca</i>	5		100	150	0.50	2			
<i>Juglans cinerea</i>	20		75		0.36	4	1	7.20	1
<i>Juglans nigra</i>	8	12	150	250	0.51	4	2		3
<i>Liquidambar styraciflua</i>	20	30	200	300	0.44	4	2		1
<i>Liriodendron tulipifera</i>	15	20	200	250	0.38	4	2		1
<i>Lithocarpus densiflora</i>	30	40	200	300		3	4		
<i>Maclura pomifera</i>	10		75	100	0.76	3			3
<i>Magnolia acuminata</i>	30		80	250	0.44	4			
<i>Magnolia grandiflora</i>	10	20	80	120	0.46	3	4		1
<i>Morus rubra</i>	10		125			3			3
<i>Nyssa aquatica</i>	5	30			0.46	4	2		1
<i>Nyssa sylvatica</i>					0.46	4	2		
<i>Ostrya virginiana</i>		25			0.60	2			
<i>Platanus occidentalis</i>	25	50	250	500	0.46	4	2		1
<i>Populus balsamifera</i>	9		100	150	0.30	4	2	7.12	1

<i>Populus deltoides</i>	10		60	100	0.37	5	1	6.95	1
<i>Populus grandidentata</i>	15	30	70		0.35	4	1	7.53	1
<i>Populus sargentii</i>	10		50	90		4	1		1
<i>Populus tremuloides</i>	5	20	70	200		5	1	7.33	1
<i>Populus trichocarpa</i>	10		150	250	0.32	4	1	6.42	1
<i>Prunus serotina</i>	10	15	100	250	0.47	4	2		3
<i>Quercus agrifolia</i>	15		150			2			
<i>Quercus alba</i>	20	50	300	600	0.60	2	3	12.70	3
<i>Quercus bicolor</i>	35	75	300		0.64	2	3		
<i>Quercus chrysolepis</i>			200	300	0.70	2			
<i>Quercus coccinea</i>	20		50		0.60	3	2		
<i>Quercus falcata</i>	25	50	200	275	0.52	3	3		1
<i>Quercus gambelii</i>			90	120	0.62	2			3
<i>Quercus garryana</i>				500	0.64	2			3
<i>Quercus kelloggii</i>	30		175	300	0.51	2			1
<i>Quercus laurifolia</i>	15	20			0.56	3	4		
<i>Quercus lobata</i>			200	300		4			
<i>Quercus lyrata</i>	25		300	400		2	4		
<i>Quercus macrocarpa</i>	35		200	400	0.58	2	3	11.70	3
<i>Quercus marilandica</i>			100			2			1
<i>Quercus michauxii</i>	20	40	100	200	0.60	2	2		2
<i>Quercus nigra</i>	20	25	175		0.56	4	2		
<i>Quercus palustris</i>	15	25	100	150	0.58	4	2		1
<i>Quercus phellos</i>	20				0.56	3	2		
<i>Quercus prinus</i>	20		300	400	0.57	3	3		3
<i>Quercus rubra</i>	25	50	200	400	0.56	4	3	11.30	1
<i>Quercus stellata</i>	25		250		0.60	2	2		3
<i>Quercus velutina</i>	20	40	100	200	0.56	3	3	11.70	1
<i>Quercus virginiana</i>			200	300	0.81	3			
<i>Rhamnus purshiana</i>	5		40	50		4			
<i>Robinia pseudoacacia</i>	6	15	60	100	0.66	4	2		3
<i>Salix nigra</i>	10	25	70	85	0.34	4	1		1
<i>Sassafras albidum</i>	10	25	100	500	0.42	4	1		3
<i>Tilia americana</i>	15		100	140	0.32	4	3	7.04	1
<i>Tilia heterophylla</i>	15		100			3	4		1
<i>Ulmus americana</i>	15	40	175	300	0.46	4	3	10.10	1
<i>Ulmus rubra</i>	15	25	200	300	0.48	4	4	10.50	1
<i>Ulmus thomassi</i>	20	45	250	300	0.57	4	4	13.20	
Angiosperm shrubs									
<i>Umbellularia californica</i>	30	40	200		0.51	3	2		
<i>Dryas octopetala</i>	3	3	50	50					
<i>Thymus drucei</i>	3	3	20	20					
<i>Erica cinerea</i>	2	2	18	18					
<i>Erica tetralix</i>	2	2	15	15					
<i>Dryas drummondii</i>	5	5	40	40					
<i>Purshia</i> spp.	10	10	100	100					
<i>Calluna vulgaris</i>	5	5	30	30					
<i>Coffea arabica</i>	3.5	3.5	50	50					
Shrub 9 * 2	2	2	43	43					
Shrub 10* 2	2	2	28	28					
Shrub 11* 2	2	2	15	15					

NOTE: In certain instances, extrapolations or calculations were necessary. Typical ages of maturity were inferred from verbal descriptions and other data in Fowells (1965) for *Acer macrophyllum*, *A. saccharinum*, and *Magnolia grandiflora*. For *Pinus strobus* and *Fraxinus americana*, typical ages of maturity were calculated from height or diameter breast height (dbh) at maturity and growth rate information (Fowells 1965). For *Populus trichocarpa*, maximum longevity of 250 years was extrapolated from reported good growth up to 200 years (Fowells 1965). Longevity for a number of western conifers were taken from Waring and Franklin (1979). Typical age of maturity for *Pinus clausa* was obtained from Walker (1967). Oosting and Billings (1951) conducted a detailed study of spruce-fir forests in the Appalachians, including north-south differences. Their maximum longevity value for *Picea rubens* of 300 years was taken in preference to the Fowells (1965) value of 400 years since the latter was based on an 1894 reference. *Abies fraseri* maximum longevity of 170 (vs. 200 in Fowells), and *A. balsamea* typical and maximum longevities of 125 and 150 (vs. 200 and 300 in Fowells) were similarly chosen because of the greater rigor of the Oosting and Billings (1951) data. Brotherson et al. (1983) provided detailed data, based on cores and sections of hundreds of trees in the Southwest. *Juniperus osteosperma* had typical and maximum longevities of 650 and 800 years, taken in preference to data in Fowells (1965) of 150 and 300, respectively. Similarly, data for *Pinus edulis* of 350 and 540 years was taken in preference to data in Fowells (1965) of 400 and 900 years. Their data for *Acer negundo* agreed with Fowells (1965). They supplied longevity data for *Quercus gambelii*. Any extreme longevity value was not used when it was attributed to a single tree because of the difficulties of statistical comparison of the extreme tails of a distribution. The following extreme values for age in years from Fowells (1965) were excluded in favor of values in Table 1: *Chamaecyparis thuyoides* (1000), *Larix laricina* (335), *Pinus banksiana* (230), *P. edulis* (over 800), *J. Jeffreyi* (600), *Juniperus scopulorum* (300), and *Tsuga canadensis* (988). Longevity for *Castanea dentata* reflects pre-blight conditions.

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