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THE ADAPTIVE SIGNIFICANCE OF TREE HEIGHT

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Trees play a key role in structuring communities by providing a wide range of food and habitat for other organisms. Yet little attention has been paid to the evolutionary forces giving rise to the great stature of trees. Height confers obvious competitive advantages, but these benefits may be offset by support and maintenance costs and increased exposure to storm winds. The fact that height growth nearly ceases in older trees, whereas stem-diameter growth continues (Kira 1978), suggests that adult tree height reflects an evolutionary balance between the costs and benefits of stature.

In this paper, I consider the costs and benefits of tree height and use a game-theoretical model to predict patterns of height growth in even-aged, monospecific forests. The model computes the performance of the individual versus its competitors throughout the life cycle; that is, height growth is considered as a dynamic game in which the performance at each stage affects subsequent growth (Mäkelä 1985). Similar game models have been used extensively by behavioral ecologists and sociobiologists to analyze animal behavior (Wilson 1975; Maynard Smith 1982; Krebs and Davies 1984) and sex ratios (Charnov 1982). Predictions of the model are tested against the growth patterns reported in yield tables developed by foresters to estimate wood production. Predictions of tree allometry and maximum tree height generally agree with those reported in foresters' tables. An important conclusion is that the growth pattern maximizing individual survival may differ greatly from that maximizing collective wood production.

My approach follows that of other optimization models that have been used to evaluate the adaptive function of various traits, including leaf size and life span (Parkhurst and Loucks 1972; Givnish and Vermeij 1976; Orians and Solbrig 1977), herb leaf height (Givnish 1982), stomatal behavior (Cowan and Farquhar 1977), phenology (Cohen 1971; Vincent and Pulliam 1980; King and Roughgarden 1983), foliage arrangement (Horn 1971; Honda and Fisher 1978), and tree height (Iwasa et al. 1985; Mäkelä 1985). These models predict how variation in one particular trait affects processes related to fitness such as carbon gain or reproductive output. The models assume simple relationships between the variables involved

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and are designed to explain trends in the scaling of organisms rather than to predict the performance of a population in a particular environment. An advantage of such models is that their assumptions and predictions can be readily understood. Furthermore, the divergence between model predictions and observations indicates where the ignored complexity is and is not important. For example, models of annual plants that ignore competition may adequately predict reproductive effort for assemblages with a leaf-area index of less than one but fail to predict the proportionately greater vegetative growth observed in annuals of more-productive habitats (Gadgil and Gadgil 1975; King and Roughgarden 1983). This divergence suggests that competition for light affects the evolution of allocation patterns.

The model presented here is appropriate for trees of dense single-species stands in productive environments where competition for light is a key factor influencing the growth of individuals. Such stands occur naturally over a variety of mesic, temperate environments, including the Pacific Northwest and Great Lakes regions of North America, where destructive fires can initiate even-aged stands (Franklin and Dyrness 1973; Heinzelman 1973). The model also applies to those patches of mixed-species forests where a particular tree is surrounded by individuals of similar size and growth pattern. As in the case of other optimization models, I focus on one variable (height growth) and assume other traits, such as leaf life span and branching pattern, to be fixed. This procedure is followed to make the problem tractable and is not meant to imply that height growth is necessarily more important than other traits affecting the growth and survival of trees.

Because trees allocate carbon preferentially to new leaves and roots, and then to storage and stem-diameter growth, the latter is an indicator of a positive carbon balance (Waring and Pitman 1985). Diameter growth is also a reliable predictor of tree resistance to pests and pathogens (Waring and Schlesinger 1985) and is necessary to support the height growth and crown expansion required for an individual to maintain its competitive status. Hence, I have chosen stem-wood production (a close correlate of diameter growth) as an indicator of fitness, with the important constraint that enough energy is partitioned to leaves and roots to maintain and replace them. An advantage of choosing wood production over total production is that extensive tables describing the former have been constructed by foresters over the past century, whereas relatively few studies have attempted the more difficult task of estimating gross primary production as affected by forest age (Sprugel 1985). Note that I define stem-wood production as the rate of stem biomass increase, not to be confused with definitions of production that include respiration.

1. I develop a model of tree growth based on relative height, light interception, and respiration costs. The model predicts that trees of even-aged stands increase in height until reaching a critical height. This critical height is defined as a certain fraction of the theoretical break-even height, at which stem maintenance and leaf and root renewal costs require all available photosynthate, leaving none for wood production.

2. The break-even height is extrapolated from forest-yield tables, which give wood production and forest height as a function of forest age for lands of specified productivity.

3. Height-growth trends and allometric relationships given by yield tables are then used to test model predictions.

A GAME-THEORETICAL MODEL OF TREE GROWTH

To evaluate tree growth as an evolutionary game, I consider the case of an even-aged population of trees that has formed an unbroken canopy such that the lateral growth of each individual is constrained by its neighbors. Given this stand geometry, how should the wood production of individuals vary with their height? To answer this question we need to consider both the height of a tree relative to its neighbors and its absolute height. All else being equal, wood production is expected to increase with light absorption by the tree crown; thus, tall trees outproduce their shorter neighbors (Kozlowski 1971; Mohler et al. 1978). However, tall trees require a greater volume of sapwood to conduct water to the leaves and hence must allocate more energy to maintain this living tissue (Waring and Schlesinger 1985). Other factors, such as maintenance of the inner bark (phloem and cambium) or restriction of photosynthesis because of increases in leaf-moisture stress with crown height also reduce the carbon available for stem-wood production. Forest yield tables indicate a decline in wood production as even-aged stands grow taller, a pattern consistent with increased respiration costs (Möller et al. 1954; Kira and Shidei 1967), although it may also reflect other changes in allocation (Grier et al. 1981; Sprugel 1984).

Given these costs and benefits of tree height, I have assumed that stem-wood production is proportional to the light absorbed by the crown, but that it declines linearly with tree height; that is,

$$dw/dt = cL(1 - h/a), \quad (1)$$

where dw/dt indicates the derivative of stem-wood mass, w , with respect to time, t ; L is the light flux absorbed by the crown (averaged over the growing season); c is a constant indicating wood production per unit of light intercepted without stem maintenance costs; h is tree height; and a is a constant indicating the height at which no wood production occurs because of sapwood maintenance and other costs.

Several points of explanation are in order regarding equation (1). (1) Wood production may not be a linear function of light interception over the entire range of crown exposures encountered in forest trees. However, the model is designed to address small differences in relative tree height where linear approximations are valid. (2) The constants a and c are species- and site-specific, depending on total productivity, maintenance costs per unit of height, and fractional allocation to leaves and roots. (3) The assumed linear decline in wood production with tree height occurs only after the maximum leaf-area index is attained (i.e., canopy closure).

In order to use equation (1) to relate wood production to tree height, one must first specify the relationship between light interception and relative tree height. To calculate this relationship, I assumed that (1) trees have conical crowns, as is commonly observed in conifers (Peterson 1985) and young hardwoods (Kozlowski 1971); (2) the tree of interest is surrounded by six similar neighbors (the densest

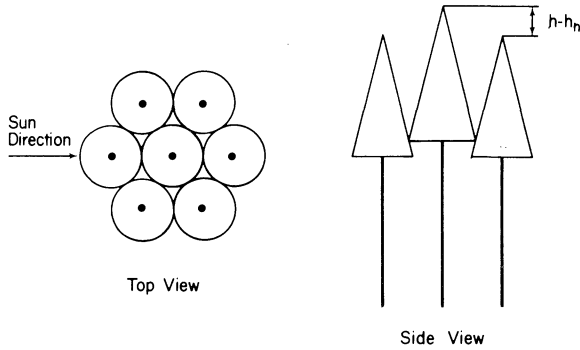


FIG. 1.—Diagram of crown geometry used to calculate light interception.

arrangement possible); (3) crown width increases to occupy available space as a tree overtops its neighbors but the shape of the crown remains constant, as shown in figure 1; (4) each crown absorbs all of the light incident upon it; and (5) the stand of interest is located at 45° latitude and experiences clear weather over a 6-mo growing season centered about the summer solstice.

Computing light interception as a function of sun angle with formulas given by Jahnke and Lawrence (1965), accounting for nearest-neighbor shading and atmospheric attenuation of the direct beam (Campbell 1977), and integrating (by computer) over the appropriate sun angles yields

$$L = L_0[1 + (h - h_n)/0.76w_n], \quad (2)$$

where h_n and w_n are, respectively, the height and crown width of the tree's nearest neighbors and L_0 is the seasonal light flux absorbed by a tree equal to its neighbors in height. The derivation assumes small differences between h and h_n and a ratio of crown length to width of 2. However, the result is rather insensitive to crown shape; assumption of a 1:1 ratio of crown length to width shifts the denominator of equation (2) from $0.76w_n$ to $0.68w_n$.

Substituting equation (2) into equation (1) expresses the rate of wood production in terms of absolute and relative tree height as

$$dw/dt = cL_0[1 + (h - h_n)/0.76w_n](1 - h/a) \quad (3)$$

for a tree of an even-aged stand at mid-latitude. A comparison of the relationship given by equation (3) with that calculated from Mohler et al.'s (1978) measurements of a 14-yr-old stand of the cherry *Prunus pennsylvanica*, shown in figure 2, indicates that the predicted and observed wood increments both increase dramatically with relative tree height in this young stand. There is a difference in the shape of the predicted versus observed relationships, but one cannot determine to what extent this difference reflects model error, small sample size (18 trees in 11 size classes), or other factors associated with the measured stand, such as variation in microsite.

The existence of a height above which height growth no longer benefits an individual can be determined by checking the derivative of wood production with

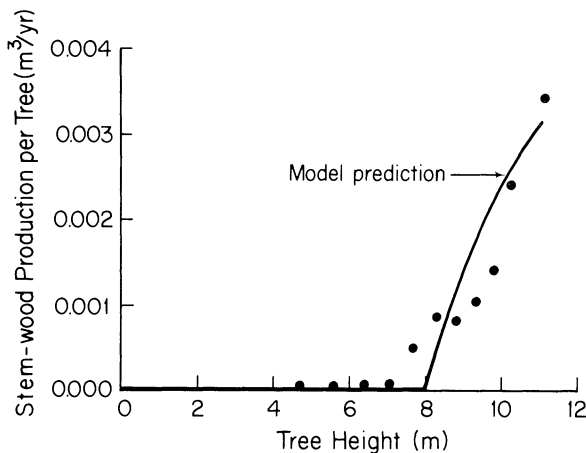


FIG. 2.—Model prediction of individual-tree wood production versus tree height for the 14-yr-old *Prunus pennsylvanica* stand sampled by Mohler et al. (1978). The points indicate wood-production estimates determined from the diameter growth rates and height-diameter relationships given by Mohler et al. The parameter c was adjusted so that the mean modeled increment for unsuppressed trees equaled that observed. The parameter a was set equal to twice the mean height of unsuppressed trees, on the basis of trends in the break-even height inferred for other species. Average crown width, w_n , was inferred from the density of unsuppressed trees.

respect to tree height,

$$\partial(dw/dt)/\partial h = cL_0[(1 + h_n/a - 2h/a)/0.76w_n - 1/a]. \quad (4)$$

Equation (4) is written as a partial derivative to indicate that we are examining how wood production varies with height for a tree with neighbors of specified height. For the case of $h = h_n$, the derivative changes from positive to negative when h exceeds the critical height,

$$h_c = a - 0.76w_n, \quad (5)$$

suggesting that height growth is favored until a tree and its neighbors reach this height.

Mortality affects the critical height by allowing the average crown width (w_n) of surviving trees to increase as the stand grows. To assess this effect, I have assumed that the ratio of average crown width to tree height remains constant, as noted by King (1981) for stands of the self-thinning poplar *Populus tremuloides*. The crown width of a tree of height h_n can then be expressed as $w_n = bh_n$, where b is a constant, and equation (3) becomes

$$dw/dt = ch_n^2 L_1 [1 + (h - h_n)/0.76bh_n](1 - h/a), \quad (6)$$

where L_1 is the seasonal light interception of an average-sized tree of unit height. The associated critical height is

$$h_c = a - 0.76bh_c, \quad (7)$$

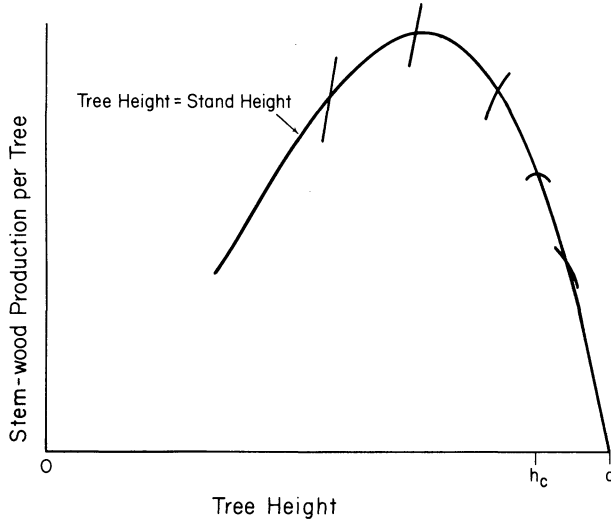


FIG. 3.—Rate of wood production versus tree height for a tree growing in an even-aged stand as given by equation (6). *Heavy line*, Wood production for a tree equal to its neighbors in height ($h = h_n$). Each curved segment indicates production versus height for a tree in a stand where stand height is given by the point of intersection of the segment and the heavy line; that is, the curves indicate production versus relative height. Wood production = 0 for trees of height a ; h_c is the critical height given by equation (7).

an expression identical to equation (5), except for the substitution of bh_c for crown width, w_n .

The effects of height on wood production specified by equation (6) are illustrated in figure 3. The heavy line indicates wood production for a tree growing at the same rate as its neighbors, that is, for $h = h_n$. In this case, the increase in crown area with tree height causes dw/dt to increase initially, but increasing respiratory costs eventually cause wood production to decline. (The line is not drawn back to the origin because the model is valid only after canopy closure.) The influence of relative tree height on wood production is illustrated by the curves crossing the above heavy line. Each curve indicates how production shifts with the height of the individual for a given stand height, specified by the intersection of the curve and the heavy line. As indicated by equation (7), a tree that is slightly taller than its neighbors ($h > h_n$) outproduces them when $h_n < h_c$, but this pattern is reversed when $h_n > h_c$. Thus, height growth is favored among competitors until this critical height is reached, despite the fact that wood production per tree begins to decline at a lower level (fig. 3).

This conclusion regarding height growth can be stated more formally by determining the evolutionarily stable strategy (ESS) for wood allocation, which maximizes the individual wood mass of competing trees. Note that the analysis applies strictly to the partitioning of new wood between height and diameter growth, given the constraint that adequate energy is allocated to other organs to maintain the production system. As defined by Maynard Smith (1974) and summarized by Mäkelä (1985), a strategy I is an ESS if and only if (1) no other strategy produces

as large a payoff when played against I as I played against itself or (2) when an alternative strategy J played against I equals the payoff of I played against I, then I against J is better than J against itself.

To determine whether a given strategy is an ESS requires an examination of variant strategies. As suggested by figure 3, a tree that allocated all new wood into extension growth when young would outproduce more slowly extending neighbors. However, extension growth is limited by requirements for mechanical support; that is, some wood must be allocated to stem-diameter growth to prevent the extending tree from toppling over because of elastic instability (McMahon 1973). Hence, a potential ESS might involve height growth at the maximum rate permitted by mechanical constraints until the stand reaches height h_c , at which time extension ceases abruptly. Possible variants from the above strategy are of three types: (1) trees that grow in height at less than the maximum rate for one or more intervals before reaching h_c ; (2) trees that follow the potential ESS until reaching h_c but then resume height growth and exceed h_c ; and (3) trees pursuing some combination of the preceding strategies.

Consider a variant of the first type surrounded by neighbors pursuing the potential ESS. Total wood mass increases with time in an identical fashion for all trees until the variant slows in height growth and falls behind its neighbors in height. After that time, the wood production rate of the variant lags behind its neighbors, as does its total wood mass. Because the maximum mechanically permissible height is a monotonically increasing function of wood mass, the variant cannot regain its competitive position until its neighbors reach the critical height and cease extension. Although the variant can eventually reach this critical height and again equal its neighbors in wood production, it cannot make up the wood-mass deficit incurred during the earlier period of slower growth unless it outlives its neighbors, an unlikely occurrence given the greater mortality of trees that lag behind their neighbors in size (Ford 1975). However, a variant of the second type remains identical to its neighbors until it exceeds the critical height, after which time its wood production rate falls below that of the rest of the stand (fig. 3). Similarly, a tree pursuing the first strategy suffers added growth deficits if it later pursues the second strategy. Because all variant strategies give rise to lower final wood masses, the proposed strategy is indeed the ESS for cumulative wood production. This strategy also maximizes an individual's wood production rate at any time, given the model constraints on allocation and crown geometry.

The single-switch ESS predicted here is similar to that derived by Mäkelä (1985) for a somewhat different formulation of the height-growth game. Mäkelä's thorough analysis of evolutionarily stable strategies for dynamic games provided the stimulus for this paper. However, I have assumed that wood production, rather than foliage production, is optimized, and I have associated maintenance costs with height.

To summarize, the model predicts that trees of even-aged stands at mid-latitudes should grow in height until reaching a height of three-fourths of the crown width below the break-even height. Height growth should cease abruptly once this critical height is attained. The assumption that trees produce only enough wood to maintain mechanical stability implies that height should be

related to basal trunk diameter, d , by $h \propto d^{2/3}$ for all trees of subcritical height, unless wood properties change significantly with tree size (McMahon 1973). Once trees attain the critical height, continued diameter growth is expected without further height growth. Because growth is closely coupled to light interception, the model suggests that trees that fall behind their neighbors because of differences in microsite or physiology are rapidly overtopped; that is, rapid self-thinning occurs after stand closure. These predictions can be tested by examining (1) the height growth of individuals, (2) the height growth of stands, (3) the allometric (height-diameter) relationships of trees within stands, (4) the allometric relationships of average-sized trees, as affected by stand age, and (5) the maximum height achieved by stands on lands of specified productivity. (The rationale for including stand attributes in a test of an individual-tree model is that the same allometry is predicted for all trees of subcritical height.)

TREE GROWTH PATTERNS: TESTING THE MODEL

The predicted evolutionarily stable growth strategy can be tested against the patterns shown in growth and yield tables for forests. These tables list tree height and wood volume as functions of stand age and site productivity. The tables have been constructed by fitting mathematical functions to dimensional measurements of trees from numerous plots and hence indicate averaged growth patterns (Bell et al. 1984). Because they generally apply to adequately stocked, even-aged stands, yield tables are well suited for testing the model predictions. The tables chosen to evaluate the model were generally based on the remeasurement of trees on established plots and/or on stem analysis in which past growth is inferred from the annual growth-ring patterns of stem cross sections.

Height Growth

Foresters use the term *site index* to define site quality or growth as indicated by total tree height at a specified age. Site-index curves project the expected height of dominant or codominant trees as a function of stand age for given site indexes and thus may be used to check the prediction of an evolutionarily stable strategy (ESS) that height growth ceases abruptly. To test the predicted growth pattern, I chose stand tables with the longest growth projections. The height-growth curves for Douglas-fir (*Pseudotsuga menziesii*), oak (*Quercus*, grown in Germany), and an extremely tall Noble fir (*Abies procera*) shown in figure 4 indicate continuous height growth with some decrease in the rate over time. Since wood production is also expected to decrease with stand height, these results suggest that the above species do not attain the critical height in the first two to four centuries of growth or that the model prediction of a critical height is incorrect.

Tree Allometry

If trees were to allocate just enough wood to diameter growth to prevent buckling due to instability in the absence of wind, then total height, h , and trunk diameter, d , would be related by $h = 94d^{2/3}$ (both variates in meters), according to McMahon (1973), who approximated trees as uniform wooden cylinders with

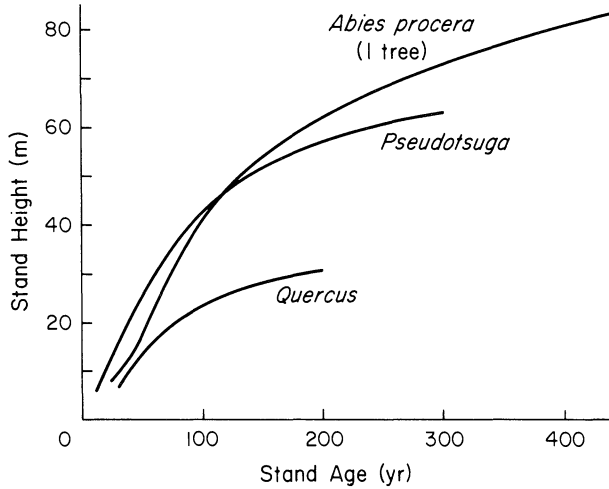


FIG. 4.—Height-growth curves for even-aged *Pseudotsuga menziesii* and *Quercus robur* and *Q. petraea* of intermediate site quality specified by Curtis et al. (1974) and Erteld (1962), respectively. The height-growth curve for *Abies procera* is for an extremely tall, forest-grown tree sectioned by Herman et al. (1975). Stand height refers to mean height of codominant and dominant trees for *Pseudotsuga* and to mean height weighted by trunk basal area for *Quercus*.

typical wood properties for temperate trees. Data collected by Beck and Della-Bianca (1970) indicate that in 40–70-yr-old stands of the tulip tree (*Liriodendron tulipifera*), smaller-than-average trees have low margins of safety against elastic instability, but larger trees have progressively larger margins of safety (fig. 5). This departure from the predictions of McMahon's model is undoubtedly because within-stand wind speeds increase rapidly with height within the canopy (Raynor 1971; Businger 1975), causing disproportionately high stresses in large trees and greater catastrophic damage to them despite their greater mechanical stability (King 1986). Larger trees, nonetheless, tend to outgrow their neighbors in young, even-aged stands (Mohler et al. 1978) because of their much greater light interception and associated wood production. Note that the imposition of greater mechanical requirements on dominant trees does not change the prediction of increasing wood production with increasing relative height in trees below the critical height. Height growth is still favored until the critical height is attained, but relatively greater diameter growth is expected in dominant trees.

Reported trends in mean tree allometry through the course of stand development provide an additional test of the model. Stand-table projections indicate that the mean height, \bar{h} , is proportional to the $2/3$ power of the mean diameter at breast height over an intermediate interval of growth followed by a gradual shift to increased diameter growth (fig. 6). This increase in tree stability in older stands is accompanied by an increase in the ratio of inter-tree spacing to tree height. Because more widely spaced trees bear larger crowns that are subject to greater wind forces, one cannot infer whether the decline in height versus diameter

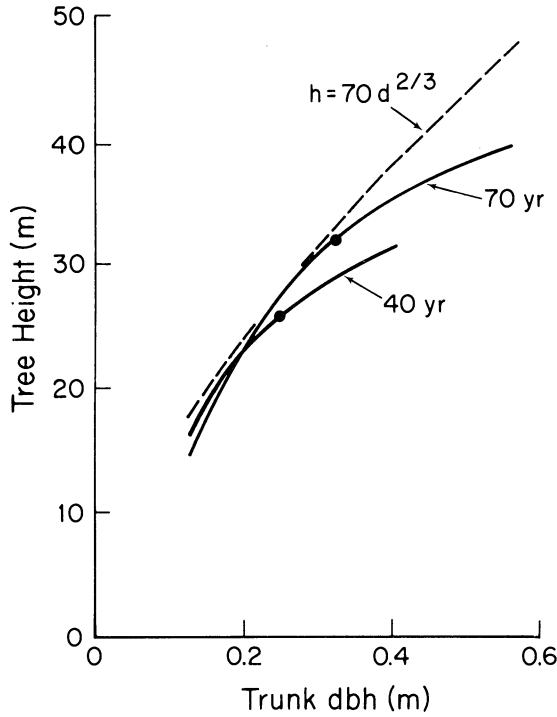


FIG. 5.—Relationship between tree height and trunk diameter at breast height (dbh) for *Liriodendron tulipifera* stands of two different ages, given by Beck and Della-Bianca (1970) for a tree density of 620/ha and a 50-yr site index of 33.5 m. Circles, Trees of mean basal area. Dashed curve, The theoretical height-diameter relationship for a tree that is three-fourths of the height that a vertical wooden cylinder could attain before buckling (as computed in McMahon 1973).

growth in older stands represents a gradual approach to the predicted critical height or whether it is only a response to greater tree spacing.

However, allometric measurements of coast redwood (*Sequoia sempervirens*) by Hallin (1934) and Fujimori (1977) suggest that height growth virtually ceases while diameter growth continues in old trees of dense stands. Figure 7 shows height-diameter relationships for an uneven-aged redwood stand of record biomass containing 700–1200-yr-old canopy trees and for exceptionally productive 47- and 260-yr-old stands. The fact that mean canopy-tree height and diameter were related by $h = 66d^{2/3}$ for the latter two stands indicates efficient use of wood for height growth for the first 260 yr. The much greater ratio of diameter to height for the old-growth stand suggests that redwood stands undergo a pronounced decrease in height growth soon after 260 yr. Curves of tree height versus trunk diameter derived by Fujimori (1977) are also given in figure 7 to illustrate within-stand patterns. The flat height-diameter curve for the old stand approaches the model prediction that all trees are of equal height in stands that have reached the critical height.

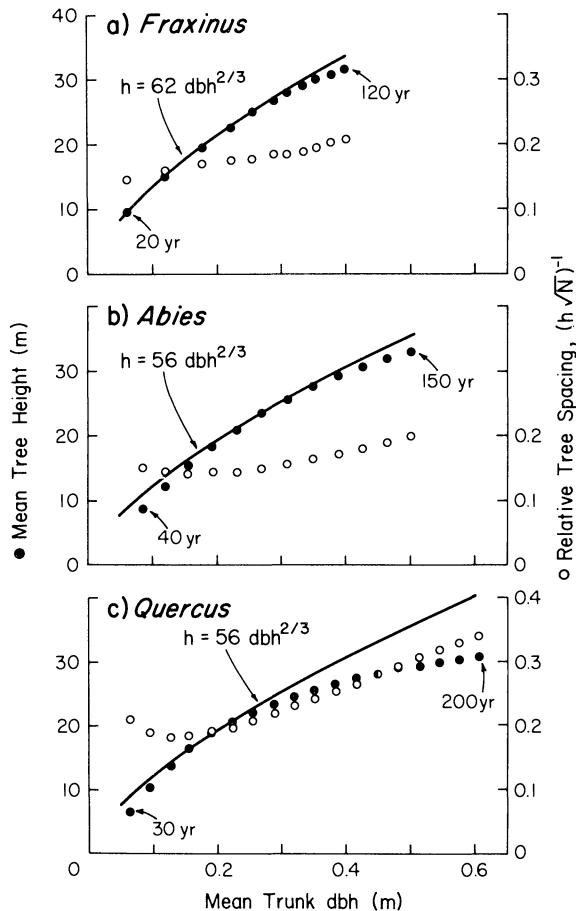


FIG. 6.—Projection through time of mean tree height versus mean trunk diameter at breast height (dbh) (both variates weighted by trunk basal area). Solid circles, Even-aged stands of three species at intermediate to good site quality: a, *Fraxinus excelsior* (Schober 1975); b, *Abies alba* (Schober 1975); c, *Quercus robur* and *Q. petraea* (Erteld 1962). Solid curves, Theoretical height-diameter relationship for trees that are 0.59 (*Quercus* and *Abies*) and 0.65 (*Fraxinus*) \times McMahon's (1973) buckling height of $h = 94d^{2/3}$. Open circles, The ratio of inter-tree spacing to tree height that would be achieved were trees spaced equidistantly on square grids. N , The number of trees per square meter; h , mean tree height (m).

From the trends presented in figures 4 through 7, I conclude that (1) average-sized trees of even-aged stands follow the predicted ESS until reaching at least 70%–90% of their maximum height; (2) larger-than-average trees have thicker-than-expected trunks to withstand disproportionately greater wind forces; (3) height growth may cease in very old stands, as predicted; and (4) height growth appears to cease gradually rather than suddenly, although direct measurements of this transition were not found. Features that are not in the model but might favor a gradual cessation of height growth include the greater wind exposure of the upper canopy and unpredictable environmental variation. Other dynamic-optimization

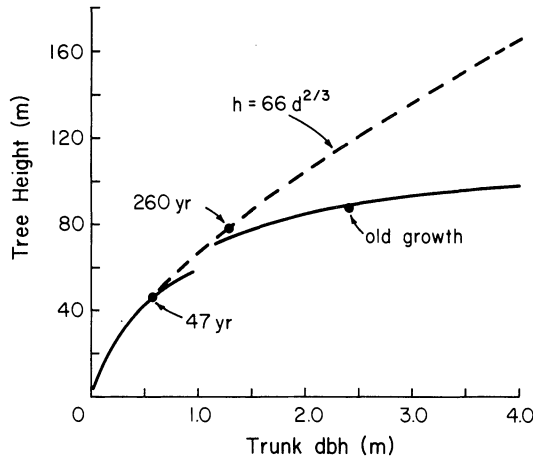


FIG. 7.—Height-diameter relationships for *Sequoia sempervirens* under optimal growing conditions. *Solid curves*, The relationship between tree height and trunk diameter obtained by Fujimori (1977) for a 47-yr-old stand and for canopy trees of an uneven-aged, old-growth stand. The points indicate average height and diameter for trees of the 47-yr stand taller than 40 m, for old-growth trees taller than 70 m, and for codominant and dominant trees of the 260-yr-old stand measured by Hallin (1934). *Dashed curve*, The theoretical height-diameter relationship for a tree that is $0.70 \times$ the buckling height computed by McMahon (1973). Trunk diameter was measured at 1.3 m, 1.4 m, and 1.7 m for the 47-yr, 260-yr, and old-growth stands, respectively.

models dealing with annual plants predict that reproductive yield is maximized by one or more abrupt switches from vegetative to reproductive growth (Vincent and Pulliam 1980; King and Roughgarden 1982a). (Abrupt switches are expected in solutions to dynamic-optimization problems for which the generalized objective function [Hamiltonian] is a linear function of the control variable [Mäkelä 1985].) However, a gradual shift to reproduction may maximize the long-term population growth of annuals in unpredictable environments (King and Roughgarden 1982b). A model that considered multiple generations of trees and climatic fluctuations might also predict a smoothed ESS, but this is more easily said than done!

Maximum Tree Height

The testing of the model to this point has dealt with the pattern of height growth but not with the magnitude of the predicted maximum height. The latter can be predicted with equation (7) once b , the ratio of crown width to tree height, and a , the break-even height, have been estimated. In old stands, crown widths are typically about one-fifth of the stand height, as illustrated by Franklin and Waring (1980) for old-growth Douglas-fir. Hence, I assume that $b = 0.2$, which implies that height growth should cease when trees reach the critical height of $h_c = a - 0.15h_c$; that is,

$$h_c = 0.87a. \quad (8)$$

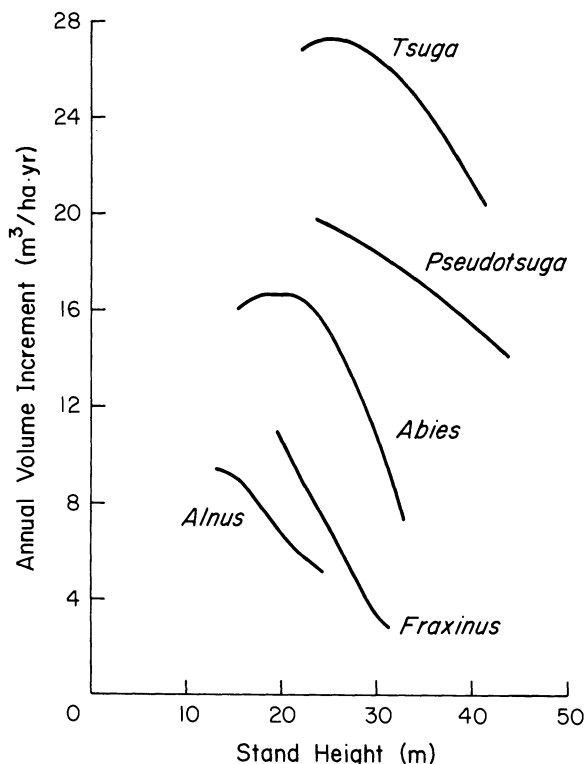


FIG. 8.—Example yield-table projections of annual stem-wood production (mortality not subtracted) versus stand height for *Tsuga heterophylla* (Wiley 1978), *Pseudotsuga menziesii* (Curtis et al. 1982), *Abies alba* (Schober 1975), *Fraxinus excelsior* (Schober 1975), and *Alnus glutinosa* (Schober 1975). The curves were hand-drawn to fit projections made at 5–10-yr intervals for sites of intermediate to good quality.

Forest yield tables can be used to estimate the break-even height, so that the evolutionarily stable maximum tree height can be specified for a given species and site quality. The tables used for this purpose were chosen to meet the following criteria. (1) The species involved were native to the region in question, rather than exotics that might not pursue an ESS in a foreign environment (e.g., *Pinus radiata*). (2) The chosen tables emphasized species of productive forests, because the model predictions are most appropriate for healthy forests with closed canopies. (3) The tables listed total annual stem-wood volume increment (i.e., current annual increment), in addition to the more usually tabulated net rates, which subtract losses due to mortality. (4) Tables extending to old age were selected so that predictions of maximum height could be tested. (The chosen tables extended 80–200 yr.)

Figure 8 shows the annual stem-wood increment graphed as a function of stand height for two conifers of the northwestern United States and three European species. The curves for the U.S. species (*Pseudotsuga* and *Tsuga*) apply to self-

TABLE 1

COMPARISON OF MAXIMUM TREE HEIGHTS PREDICTED BY THE MODEL AND THOSE FROM TABLES FOR FOREST STANDS FROM SITES OF AVERAGE OR ABOVE-AVERAGE QUALITY

Species	Site Index (m)*	Model Prediction (m)†	Observed Mature Tree Height (m)†	Mature Tree Age (yr)	Observed/Predicted Height	Latitude (degrees)‡	Sources§
Conifers							
<i>Abies alba</i>	25.7	35.2	32.9	150	0.93	48-50	1
	26.8	29.9	30.4	140	1.02	52-60	1
<i>Larix decidua</i>	29.5	32.9	32.4	140	0.98	48-54	1
<i>Picea abies</i>	29.3	43.0	32.1	120	0.75	51-54	1
	29.3	33.0	31.6	120	0.96	47-54	2
<i>Pinus contorta</i>	27.4	50.5	30.0	130	0.59	43-44	3
<i>Pinus sylvestris</i>	24.1	31.8	27.3	140	0.86	51-54	1
	24.9	31.0	28.5	150	0.92	58-62	4
<i>Pseudotsuga menziesii</i>	44	56.7	70	400+	1.23	43-49	5
	44	74.6	70	400+	0.94	43-53	6
<i>Tsuga heterophylla</i>	44	60.9	57	300+	0.94	46-49	7
Angiosperms							
<i>Alnus glutinosa</i>	24.5*	31.8	24.5	90	0.76	51-54	1
<i>Betula</i>	26.0*	27.6	26.0	80	0.93	51-54	1
	28.5	27.6	28.5	100	1.02		8
<i>Fagus sylvatica</i>	27.4	55.9	33.7	150	0.60	51-54	1
<i>Fraxinus excelsior</i>	29.9	30.4	31.4	120	1.03	50-52	1
<i>Quercus robur</i> & <i>Q. petraea</i>	22.8	38.8	30.2	200	0.78	51-54	1
	23.4	37.1	30.2	200	0.81	52-54	9

* The site index used here is the mean tree height (weighted by basal area) expected for a 100-yr-old stand. For *Pinus contorta*, *Pseudotsuga*, and *Tsuga*, site index is defined in terms of the mean height of dominant plus codominant trees.

† Predicted and observed tree height is the mean tree height (weighted by basal area), except for *Pinus contorta*, *Pseudotsuga*, and *Tsuga*, for which these heights refer to the mean height of dominant plus codominant trees. Predicted height is 0.87a.

‡ Approximate latitudes of the forest stands used to construct the yield tables.

§ Sources.—1, Schober 1975; 2, Assmann 1970; 3, Dahms 1975; 4, Brantseg 1969; 5, Curtis et al. 1982; 7, Wiley 1978; 8, Anuchin 1970; 9, Erfteld 1962.

|| Maximum tree heights for *Pseudotsuga* and *Tsuga* were approximated from heights reported by Franklin and Dyrness (1973) for old-growth trees at sites with above-average quality.

* For *Alnus* and the upper *Betula* row, site index is the mean height of 90- and 80-yr-old stands, respectively.

thinning, unmanaged stands; those for the European species are for managed stands subjected to repeated thinnings of moderate intensity (Schober 1975). The tabulated wood increment initially increases and then decreases with increasing stand age and height, with the peak in production occurring at ages of 25–75 yr in the examples shown in figure 8. Lower wood production in younger stands may reflect incomplete development of leaf area (Waring and Schlesinger 1985) and conventions for measuring wood volume that exclude stems less than 4 cm in diameter in the American tables and stem sections smaller than 7 cm in diameter in the European tables. However, the decline in wood production with increasing stand height projected for the older stands is in general agreement with the linear decline assumed in the model.

The height at which wood production would go to zero was estimated for 12 species by comparing the tabulated annual wood increment and the stand height over the interval of declining productivity for each species at sites of specified productivity. The evolutionarily stable maximum height was then taken to be 87% of this break-even height (eq. 8) and compared with the stand height at the maximum age projected in the yield tables. These values for predicted versus “observed” maximum heights are listed in table 1. A standard deviation in the ratio of observed to predicted height of 0.16 was calculated for the six species with double estimates of a . None of the ratios of observed to predicted height shown in the table differed significantly from one. However, predicted heights exceeded observed heights in 14 of the 18 estimates shown for the 12 species, and the mean ratio of observed to predicted height was 0.89 (± 0.04 SE). Both shade-tolerant genera (*Abies*, *Fagus*, and *Tsuga*) and shade-intolerant genera (*Alnus*, *Betula*, *Larix*, *Pinus*, and *Pseudotsuga*) showed similar ratios of observed to predicted maximum height. This pattern indicates selection for height growth in canopy trees of both groups, even though tolerant trees can regenerate under canopies by enduring suppression. Because height growth had not ceased at the stand ages used to estimate critical height, it is not surprising that the predicted heights were not quite achieved. However, maximum life spans for the respective species may be several times those used here (Franklin and Dyrness 1973; Mitchell 1974), enabling some trees to reach the critical height before death.

DISCUSSION

The success of the model in explaining patterns of tree growth suggests that competition for light is the primary factor responsible for the evolution and maintenance of the arboreal life form. This competition between individuals has produced a growth pattern that reduces per-hectare wood production in older stands because the distance between leaves and roots increases to the point at which little photosynthate is available for processes other than root and leaf turnover and stem maintenance. In contrast, the strategy maximizing collective wood production should include a cessation of height growth once stand closure and an optimal leaf area are attained; that is, trees should remain short. The evolutionarily stable strategy (ESS) for competitors generally results in a smaller payoff than that expected for group-selected populations employing a cooperative strategy (Mirmirani and Oster 1978; Mäkelä 1985).

In many ESS models, reproductive output is assumed to be the payoff most closely related to fitness (Mirmirani and Oster 1978). In the model developed here, wood production was chosen as a more tractable payoff function, and long-term reproduction was assumed to be correlated with wood production. Forest trees typically allocate a small fraction of photosynthate to reproduction. For example, reproductive structures made up only 6% of the aboveground production of an old-growth Douglas-fir forest (Grier and Logan 1977). However, greater allocation to reproduction would reduce allocation to other tree parts, thereby reducing future competitive status, vigor, and life span. The combination of lower biomass production because of maintenance costs and a low fractional allocation to reproduction in trees suggests even more-pronounced differences between competitive and cooperative strategies when reproduction is considered as the payoff of interest. A reproductive output of 450 kg/ha · yr was noted for the above Douglas-fir forest, as compared with the average U.S. corn yield of 6000 kg/ha · yr (USDA 1985). Strong group selection is expected in the latter case, since cultivars are selected for collective yield rather than for the performance of individual competitors. Fruit trees also have high reproductive output (Cannell 1985), again reflecting group selection by humans.

This analysis has implicitly regarded the physiology of growth as a “black box,” which is adjusted by natural selection to produce an ESS. What physiological mechanisms might produce an ESS? The meristematic activity causing shoot-tip extension and stem-diameter growth is known to be influenced by carbohydrate, mineral, and hormone balances and by tissue water potential (Kozlowski 1971). Waring and Schlesinger (1985) suggested that soil moisture deficits, water-transport resistances, and the gravitational component of water potential limit tree height by lowering turgor pressure in expanding buds below that required for further height growth. An alternative hypothesis, which integrates water relations with the ESS approach, is that tissue water potential serves as a signal controlling meristematic activity, rather than acting as an absolute limit to growth; that is, water potential is the proximal factor limiting height, but its effect is mediated through natural selection. According to this view, natural selection could give rise to the proposed ESS, so long as there is genetically based variation in the response of meristems to tissue water potential. Water requirements also play an evolutionary role in limiting tree height by affecting the ESS via sapwood maintenance costs.

The approach taken here has focused on light interception and mechanical costs, with no explicit mention of photosynthesis. Yet, selection for prolonged height growth may also involve photosynthetic capacity and stomatal behavior. According to the ESS model, maximum tree height is determined by the net photosynthate remaining after root and foliage requirements are met and by the maintenance cost per unit of height. Adaptations that reduce photosynthesis may still be favored if they reduce maintenance costs by a greater proportion. The tendency for stomata to close in response to increased vapor-pressure deficit (Waring and Franklin 1979; Sanford and Jarvis 1986) may represent such an adaptation. Because the roots of individuals overlap, one might expect selection to favor the rapid use of all available water, just as competition for light favors

height growth. However, sapwood requirements should increase with the rate of water use during high-demand periods (Tyree and Sperry 1988). Restriction of photosynthesis during periods of high vapor-pressure deficit could reduce maintenance costs substantially, allowing trees with conservative water-use strategies to outgrow "water spenders." This example illustrates the potential for using game-theoretical models to integrate physiological processes and morphological constraints, thereby providing a unified approach to adaptation.

SUMMARY

A game-theoretical model of tree growth is developed to evaluate the adaptive significance of height growth. The model balances the advantages of height for light interception against height-related costs, such as increased maintenance respiration, that reduce the energy available for stem growth. The model predicts an evolutionarily stable strategy (ESS) for trees of even-aged stands. This ESS consists of a prolonged interval of height growth that terminates when the trees reach 87% of the theoretical break-even height, at which stem maintenance and root and leaf renewal costs require all available photosynthate, leaving none for wood production.

Tests of the model with data from forest yield tables indicate that (1) average-sized trees of even-aged stands follow the predicted ESS until reaching at least 70%–90% of their maximum height; (2) trees that are larger than average have thicker-than-expected trunks to withstand disproportionately greater wind forces in the upper canopy; (3) height growth may cease in very old stands, as predicted; and (4) height growth appears to cease gradually rather than suddenly. Features that are not in the model but might favor a gradual cessation of height growth include the greater wind exposure of the upper canopy and unpredictable environmental variation.

The general success of the model in explaining patterns of tree growth suggests that competition for light is the primary factor responsible for the evolution and maintenance of the arboreal life form. The resulting evolutionarily stable growth pattern maximizes the competitive ability of the individual but reduces the collective wood production of older stands because of costs associated with height. This result is consistent with other analyses of individual versus group selection that have found productivity to be lower in individual-selected than in group-selected populations.

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