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Tree allometry, leaf size and adult tree size in old-growth forests of western Oregon

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Summary

Relationships between tree height and crown dimensions and trunk diameter were determined for shade-tolerant species of old-growth forests of western Oregon. The study included both understory and overstory species, deciduous and evergreen angiosperms and evergreen conifers. A comparison of adult understory species with sapling overstory species of similar height showed greater crown width and trunk diameter in the former, whether the comparison is made among conifers or deciduous trees. Conifer saplings had wider crowns than deciduous saplings, but the crown widths of the two groups converged with increase in tree height. Conifer saplings had thicker trunks than deciduous saplings of similar crown width, possibly because of selection for resistance to stem bending under snow loads.

The results suggest that understory species have morphologies that increase light interception and persistence in the understory, whereas overstory species allocate their biomass for efficient height growth, thereby attaining the high-light environment of the canopy. The greater crown widths and the additional strength requirements imposed by snow loads on conifer saplings result in less height growth per biomass increment in conifer saplings than in deciduous saplings. However, the convergence in crown width of the two groups at heights greater than 20 m, and the proportionately smaller effect of snow loads on large trees, may result in older conifers equalling or surpassing deciduous trees in biomass allocation to height growth.

Introduction

The dimensional relationships (allometry) of trees affect growth and survival through their influence on light interception, resistance to mechanical damage and in other ways. Light interception by saplings in the understory increases with increase in either height or crown width. However, both forms of growth depend on increased structural biomass for support. Past studies have established that trunk diameter frequently scales as the 3/2 power of total tree height (McMahon 1973), with departures from this relation associated with variation in wind exposure (Lawton 1982, King 1986). Other factors influencing tree allometry include snow loads (Petty and Worrell 1981, Cannell and Morgan 1989), adult tree size (King 1990), leaf size (Givnish 1984, Kohyama 1987) and the presence or absence of a vascular cambium (Rich et al. 1986). All of these factors may alter the energetic costs and benefits associated with a particular tree allometry.

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Patterns in trunk allometry are summarized in forest stand and yield tables (e.g., Assmann 1970, Bell et al. 1984). However, this information pertains primarily to commercial species in even-aged stands. Few allometric studies have dealt with saplings of the forest understory or compared canopy tree saplings with adult understory trees. The study described here of shade-tolerant species regenerating in old-growth forests of the Pacific Northwest, USA, included both understory and overstory species, deciduous trees, and evergreen conifers and angiosperms. An allometric analysis of this diverse group should increase our understanding of the principles of tree form.

Materials and methods

Most observations were made at the H.J. Andrews Experimental Forest in western Oregon (Table 1) in low elevation forest dominated by 60–80 m tall, > 400-year-old *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) (Grier and Logan 1977). Additional measurements were made in two other old-growth forests in the same region (Table 1). The climate is mild and wet in winter with warm, dry summers. Mean annual rainfall at the Andrews Forest meteorological station (at 426 m elevation) is 2300 mm, with 6% of the total falling during June–August (Bierlmaier and McKee 1989). Most precipitation at the study sites falls as rain with occasional snow which usually melts within two weeks (Harr 1981). The snowfall estimates shown in Table 1 are derived from values reported for other sites at similar elevations and distances inland (Franklin and Dyrness 1973).

The chosen species, *Acer macrophyllum* Pursh (bigleaf maple), *Acer circinatum* Pursh (vine maple), *Cornus nuttallii* Aud. (western dogwood), *Castanopsis chrysophylla* (Dougl.) DC. (chinquapin), *Rhododendron macrophyllum* G. Don, *Abies grandis* (Doug.) Forbes (grand fir), *Tsuga heterophylla* (Raf.) Sarg. (western

Table 1. Description of study sites.

Site	Location	Elevation (m)	Aspect & slope	Approx. annual snowfall (m)	Species
Andrews Exp. For. Ref stand 17[1]	44°13′ N 122°14′ W	530	20° NNW	1.5	*T. heterophylla* *T. brevifolia* *C. nutallii* *R. macrophyllum*
Andrews Exp. For. Adj ref stand 15[1]	44°13′ N 122°14′ W	680	30° NNW	> 1.5	*A. macrophyllum* *A. circinatum*
Andrews Exp. For. Ref stand 16[1]	44°13′ N 122°14′ N	670	40° SW	> 1.5	*C. chrysophylla*
McDonald For.	44°38′ N 123°19′ W	320	25° NNW	0.4	*A. grandis* *T. brevifolia*
Coastal Forest	44°16′ N 124°6′ W	130	30° S	< 0.15	*T. heterophylla*

[1] Reference stands described by Hawk et al. (1978).

hemlock) and *Taxus brevifolia* Nutt. (western yew) are common trees and shrubs of the western Cascade Mountains, the coast ranges of the Pacific Northwest or both. All species are more or less shade tolerant (Sudworth 1967, Franklin and Dyrness 1973) and reproduce in old-growth forests. *Tsuga heterophylla* is the potential climax species over most of this region: *Abies grandis* replaces *Tsuga* in this role in the eastern coast range where *Abies* was sampled. The dominant species, *Pseudotsuga menziesii*, was not measured, as it consists primarily of a > 400-year-old cohort, with no understory juveniles on the study sites. Characteristics of the study species are listed in Table 2.

Where possible, comparisons between overstory and understory species pairs were made in similar understory environments. Plants were sampled in both gaps and understory, but large gaps were avoided. Most of the species were measured in or adjacent to three reference stands (50 × 50 m plots) in the Andrews Forest, described in Table 1 and by Hawk et al. (1978). The Andrews sites ranged from wet mesic to dry mesic, with *Tsuga heterophylla* the potential dominant in the absence of fire (Franklin and Dyrness 1973). The understory conifer *Taxus brevifolia* was compared with *Abies grandis* in McDonald State Forest of the eastern flank of the Oregon coast range, and with *Tsuga heterophylla* at the Andrews Forest. To evaluate possible effects of snow on allometry, *Tsuga heterophylla* saplings were also sampled at a site 1.5 km inland from the Pacific Ocean, an area seldom receiving snow (Table 1).

Crown width (projected vertically in two perpendicular directions), tree height, trunk diameter at 1/10 tree height, and lowest leaf height were measured on each individual > 1 m tall, excluding plants with obvious crown or stem breakage or with trunks (from base to crown center) leaning more than 30° from the vertical. Sample sizes (Table 2) ranged from 20 to 37 plants per species. In the case of vine maple

Table 2. Description of study species. Branch orientation is orthotropic (O) (steeply inclined branch tips) or plagiotropic (P) (foliage borne on horizontal branches). Leaf habit is deciduous (D) or evergreen (E). Area per leaf was determined for saplings. Specific gravities from Markwardt and Wilson (1935) are based on oven dry mass and green volume. The two sample numbers listed for *T. heterophylla* refer, respectively, to the Andrews Forest and Coastal populations. The two numbers for *T. brevifolia* refer, respectively, to the Andrews Forest and McDonald Forest populations.

Species	Adult height (m)	Branch orient.	Leaf habit	Area per leaf (cm^2)	Wood specific gravity	Sample size
Angiosperms						
Acer macrophyllum	25–35	O	D	280	0.44	37
Castanopsis chrysophylla	15–25	P	E	16	0.42	20
Cornus nuttallii	8–15	P	D	32	0.58	32
Acer circinatum	4–10	P	D	38	0.56	31
Rhododendron macrophyllum	2–5	O	E	63		24
Conifers						
Abies grandis	40–60	P	E	0.29	0.37	31
Tsuga heterophylla	40–60	P	E	0.16	0.38	35, 28
Taxus brevifolia	7–15	P	E	0.22	0.60	28, 9

(*Acer circinatum*), which usually produces multiple stems, dimensions of the tallest ramet and the overall clump width were measured. Mid-crown height was estimated visually, based on the height of the highest and lowest leaves and an assessment of the vertical distribution of the foliage. Effective crown length, defined as $l_{eff} = 2(h -$ mid-crown height), where h is total tree height, was used as a more reliable estimate of crown length than the distance between the highest and lowest leaves, which is strongly influenced by the presence or absence of epicormic sprouts on the trunk.

Heights above 4 m were determined by measuring eye to twig distances with a calibrated rangefinder and using clinometer-determined sighting angles to calculate vertical heights. Trunk diameter was measured at 1/10 tree height rather than breast height in order to describe how tree proportions (measured at the same relative position) change with tree size. Trunk diameter was inferred from circumference measured at 2.0–2.5 m on trees exceeding 25 m in height. The sample species exeeding this height (*A. macrophyllum*, *T. heterophylla* and *A. grandis*) exhibit little butt swell.

Linear regression was used to express crown dimensions as a function of total tree height (h) for each species. Trunk diameter, d, was expressed in terms of the allometric equation $d = ah^b$ (coefficients a and b were determined by linear regression of $\ln d$ versus $\ln h$ and corrected for logarithmic bias (Baskerville 1972)). This approach is useful for comparing observed allometries to the theoretical minimum diameter relation $d = 0.11h^{1.5}$ (d in cm, h in m) calculated by McMahon (1973) for trees that are just thick enough to prevent buckling due to elastic instability. Following conventions established for tropical trees (King unpublished data), separate regressions were computed for 1–6, 6–24, and > 24 m tall trees for crown width and trunk diameter, and 1–6 versus > 6 m trees for crown length. This subdivision allows assessment of size-dependent shifts in allometry.

Results

Among the three deciduous angiosperms, crown width in trees of the same height was inversely related to the height of the species at maturity (Figure 1b, Table 3). The same trend was not apparent in a comparison of the two evergreen angiosperms (Figure 1a, Table 3). Among the conifers, crown width in trees 2.5 m in height was similar in *Taxus*, an understory species, and *Abies* and *Tsuga*, which are overstory species (Figure 1c and 1d, Table 4). At a height of 10 m, however, *Taxus* had a significantly greater crown width than *Abies* at the same site (Figure 1c, Table 4).

Trunk diameter in trees of the same size height varied with the height of the species at maturity in the same way as crown width (Figure 2, Table 5).

At the low end of the height range, the conifers generally had wider crowns than the angiosperms, but there was convergence in crown width at a height of 15–25 m (Figure 1). Relative crown width (crown width/tree height) declined with increasing tree height in all species, most notably in the larger conifers (Table 4).

A comparison of plants 2.5 m tall indicated that the relative crown width of the conifers was twice that of *Acer macrophyllum* (Table 4), whereas the areas of

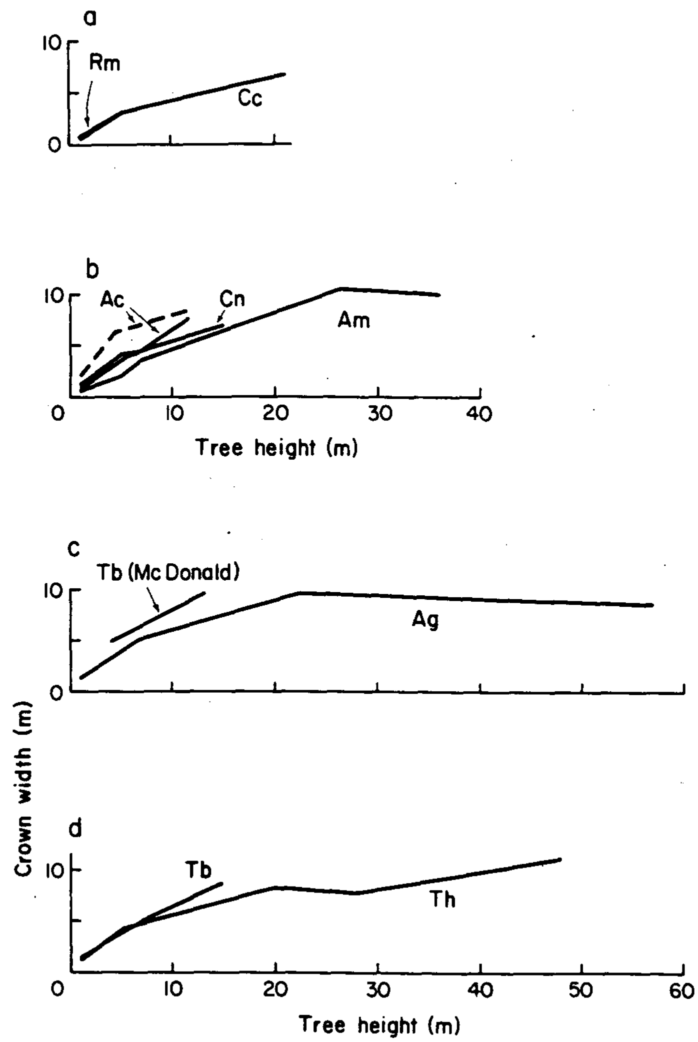

Figure 1. Regressions of crown width versus tree height. Linear interpolations were made for 5–7 and 20–28-m tall trees of those species with noticeable discontinuities between the regressions for adjacent height ranges. The dashed line indicates multiple-stem clump widths for *A. circinatum*. Species abbreviations are: (a) evergreen angiosperms—*Rhododendron macrophyllum*, Rm, and *Castanopsis chrysophylla*, Cc; (b) deciduous angiosperms—*Acer circinatum*, Ac, *Cornus nuttallii*, Cn, and *Acer macrophyllum*, Am; (c and d) conifers—*Taxus brevifolia*, Tb, *Abies grandis*, Ag, and *Tsuga heterophylla*, Th.

individual leaves of the two groups differed by a factor of 1000 (Table 2). A comparison of all species indicated a general decline in sapling crown width with increasing leaf size (Table 6). Multiple regression ANOVAS, by species, of crown width versus ln(area per leaf) + ln(adult height), indicated significant ($P < 0.05$) negative correlations between crown width and ln(area per leaf) for both 2.5- and 10-m tall trees. In 10-m tall trees, a weaker negative correlation ($P < 0.1$) was found

Table 3. Crown dimension regression slopes. Values within a column and subheading not sharing a common letter differ significantly (two-tailed $P < 0.05$). (Letters were deleted from sections lacking significant differences.) The asterisk (*) indicates that an entry is significantly less than the entry for the next lower height range (two-tailed $P < 0.05$).

Species	Crown width regression slope for height (m) range			Crown length regression slope for height (m) range	
	1–6	6–24	> 24	1–6	> 6
Angiosperms					
A. macrophyllum	0.36a	0.36a	–0.07*	0.66ac	0.39*
C. chrysophylla	0.63b	0.23a*		0.47ab	0.36
C. nuttallii	0.66b	0.32a*		0.45b	0.53
A. circinatum	0.74b	0.68b		0.76c	0.17
R. macrophyllum	0.56b			0.51ab	
Conifers					
A. grandis	0.65	0.29*	–0.03a*	0.54a	0.47a
T. heterophylla – Andrews	0.72	0.27*	0.17b	0.63a	0.72b
T. heterophylla – Coastal	0.76			0.82b	
T. brevifolia – Andrews	0.57	0.45		0.51a	0.62ab
T. brevifolia – McDonald[1]	0.50			0.79	

[1] Values for the McDonald Forest *T. brevifolia* are for a tree height range of 4–13 m.

Table 4. Relative crown width (crown width/tree height) and relative crown length (effective crown length/tree height) derived from the regression equations. Values within a column and subheading not sharing a common letter differ significantly (two-tailed $P < 0.05$). (Letters were deleted from sections lacking significant differences.) The asterisk (*) indicates that an entry is significantly less than the entry for the next lower height range (two-tailed $P < 0.05$).

Species	Relative crown width for tree height (m) of			Relative crown length for tree height (m) of		
	2.5	10	30	2.5	10	30
Angiosperms						
A. macrophyllum	0.46a	0.46a	0.34*	0.34a	0.56a	0.45*
C. chrysophylla	0.57ab	0.42a*		0.55b	0.54a	
C. nuttallii	0.71c	0.54b*		0.31a	0.39b	
A. circinatum	0.93d	0.65c*		0.54b	0.52ab	
R. macrophyllum	0.66bc			0.40a		
Conifers						
A. grandis	0.92	0.61a*	0.32*	0.56	0.52	0.60
T. heterophylla – Andrews	0.94	0.57a*	0.27*	0.67	0.57	0.64
T. heterophylla – Coastal	0.82			0.70		
T. brevifolia – Andrews	0.94	0.64a*		0.55	0.55	
T. brevifolia – McDonald		0.79b			0.63	

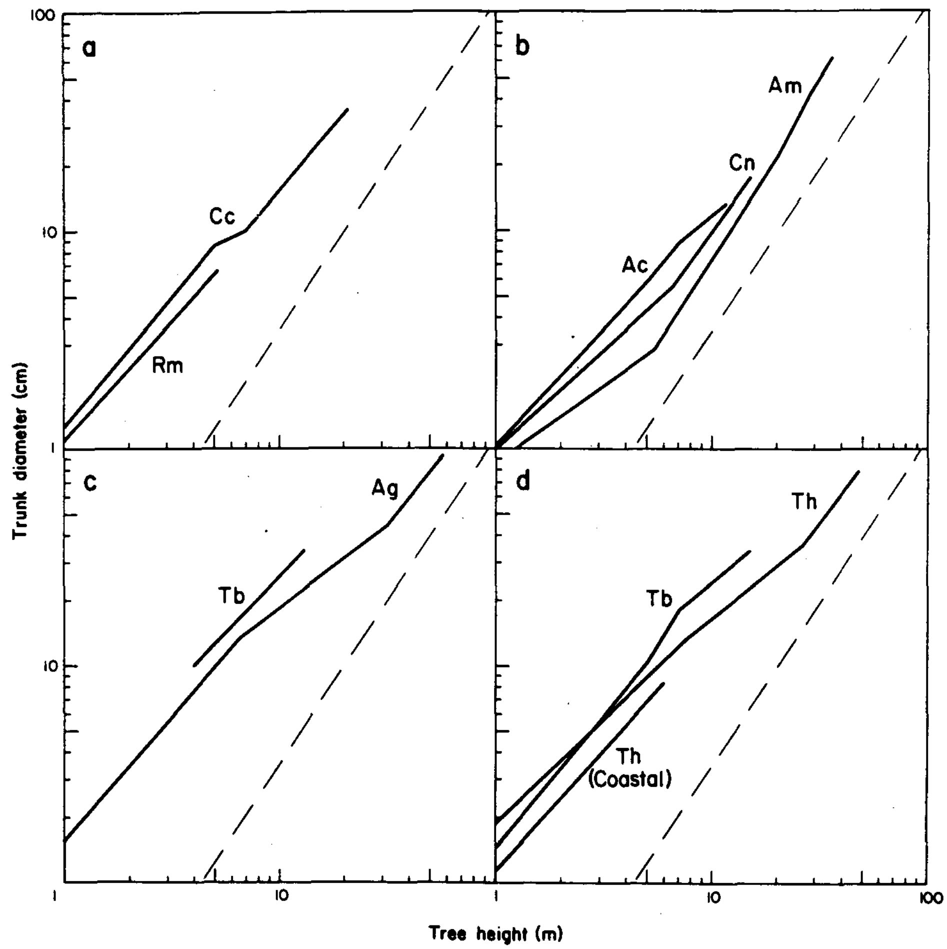

Figure 2. Trunk diameter versus tree height derived from logarithmic regressions, corrected for logarithmic bias. The dashed line indicates the minimum diameter required to prevent buckling, calculated by McMahon (1973). The panels include (a) evergreen angiosperms—*Rhododendron macrophyllum*, Rm, and *Castanopsis chrysophylla*, Cc; (b) deciduous angiosperms—*Acer circinatum*, Ac, *Cornus nuttallii*, Cn, and *Acer macrophyllum*, Am; (c) conifers of McDonald Forest, and (d) conifers of the Andrew Forest—*Taxus brevifolia*, Tb, *Abies grandis*, Ag, and *Tsuga heterophylla*, Th.

between crown width and ln(adult height) of the multiple regression model (Table 6). This correlation reflects the greater crown width of adult understory trees compared with overstory tree saplings among the conifers and deciduous species.

Trunk diameter power exponents, shown in Table 5, were significantly less than 1.5 for all species over the 1–6 m height range, for all evergreens over the 6–24 m height range, and for *Abies* > 24 m tall, i.e., small trees appeared to have thicker trunks with respect to McMahon's (1973) minimum design criterion than large trees (Figure 2).

Trunk diameters determined from multiple regressions of ln$d$ versus ln$h$ plus ln(crown width) allow comparisons of trees of similar width and height. Except for

Table 5. Logarithmically transformed trunk diameter–tree height regression slopes and corresponding trunk diameters for 2.5-, 10- and 30-m tall trees. Values within a column and subheading not sharing a common letter differ significantly (two-tailed $P < 0.05$). Regression slopes followed by an asterisk (*) are significantly less than 1.5 (two-tailed $P < 0.05$). Trunk diameters corrected for logarithmic bias with Baskerville's (1972) procedures.

Species	Ln*d* vs. ln*h* regression slopes for tree height (m) range			Trunk diameter (cm) for tree height (m)		
	1–6	6–24	> 24	2.5	10	30
Angiosperms						
A. macrophyllum	0.72a*	1.56a	1.58	1.64a	7.5a	47
C. chrysophylla	1.20b*	1.17b*		3.72b	15.2b	
C. nuttallii	0.92ac*	1.40ab		2.30c	10.0c	
A. circinatum	1.09bc*	0.82ab		2.76d	11.9c	
R. macrophyllum	1.10bc*			2.96d		
Conifers						
A. grandis	1.14*	0.76*	1.24*	4.41a	18.3a	41
T. heterophylla – Andrews	0.97*	0.79*	1.32	4.56a	16.8a	43
T. heterophylla – Coastal	1.12*			3.15b		
T. brevifolia – Andrews	1.23*	0.83*		4.40a	24.4b	
T. brevifolia – McDonald[1]	1.03*				25.5b	

[1] Values for the McDonald Forest *T. brevifolia* are for a tree height range of 4–13 m.

Table 6. Interspecific relationships between crown width (CW) for trees of the height specified in parentheses and area per leaf (AL) and adult height (HT). Probability P refers to two-tailed tests. Analysis includes all sampled populations except coastal *T. heterophylla*, which was not paired with other species.

Relation	Slope	*P*
Simple regression		
CW(2.5) versus ln(AL)	−0.051	0.02
CW(2.5) versus ln(HT)	0.019	0.83
CW(10) versus ln(AL)	−0.023	0.11
CW(10) versus ln(HT)	−0.061	0.33
Multiple regression		
CW(2.5) versus ln(AL)	−0.062	0.02
CW(2.5) versus ln(HT)	−0.074	0.24
CW(10) versus ln(AL)	−0.029	0.04
CW(10) versus ln(HT)	−0.089	0.08

the coastal *Tsuga* population, the conifers had trunk diameters twice that of *A. macrophyllum* for both 2.5- and 10-m tall trees of similar crown width (Table 7). However, trunk diameters were quite similar for 30-m tall trees.

Discussion

The results indicate the following patterns in the sampled forests: (1) a tendency for

Table 7. Trunk diameters derived from multiple regressions of ln*d* versus ln(crown width/tree height) + ln(tree height). The chosen relative crown widths are approximate averages across the study species for the corresponding tree heights. Values within a column and subheading not sharing a common letter differ significantly (two-tailed $P < 0.05$). Diameters corrected for logarithmic bias with procedures of Baskerville (1972).

Species	Trunk diameter for height (m) and crown width (m), respectively:		
	2.5, 1.88	10, 6	30, 9
Angiosperms			
A. macrophyllum	1.91a	8.4a	38
C. chrysophylla	4.07b	17.4b	
C. nuttallii	2.32c	10.5c	
A. circinatum	2.40c	11.0c	
R. macrophyllum	3.32d		
Conifers			
A. grandis	4.20a	18.3a	41
T. hetrophylla – Andrews	4.21a	16.9a	44
T. hetrophylla – Coastal	2.89b		
T. brevifolia – Andrews	4.06a	21.9b	
T. brevifolia – McDonald		17.6ab	

adult understory trees to have wider crowns and thicker trunks than canopy tree saplings of the same height, (2) a decline in sapling crown width with increasing leaf size, and (3) thicker trunks in conifers than deciduous trees in the sapling stage.

Similar trends in understory versus overstory allometry were observed in a seasonal and a wet tropical forest (King 1990, King unpublished observations). Understory species had a higher wood density than overstory species (Table 2), which suggests that they have substantially greater biomasses than overstory saplings of similar height. This pattern can be interpreted in terms of the different life histories of understory and overstory species. Larger crowns, thicker stems and denser wood in understory trees may increase light interception and persistence in the understory environment. Lifespans of 90 and up to 350 years have been reported by Sudworth (1967) for *A. circinatum* and *T. brevifolia*, respectively. In contrast, smaller crowns, thinner stems and less dense wood should result in a greater height growth increment per unit of new biomass in saplings of canopy trees (King 1981), enabling them to reach the high-light canopy environment more quickly.

The negative correlation between sapling crown width and leaf size may reflect an underlying relationship between whole-plant allometry and leaf size, or merely a difference between conifers with small leaves and angiosperms with large leaves. To help resolve this issue additional measurements were made on *Thuja plicata* D. Don, a conifer similar in adult size to *Tsuga heterophylla*, but with an area per leaf 1/4 that of the latter. The 2.5-m tall *Thuja* saplings of the Andrews Experimental Forest had a relative crown width of 1.20, which was significantly greater ($P < 0.02$) than the value of 0.94 determined for *Tsuga*. Negative correlations between sapling crown width and leaf size were also observed for dicotyledonous species of similar adult stature in a wet tropical forest (King unpublished observations), suggesting a general relationship between whole-plant allometry and leaf size.

Interactions between leaf size and branch construction cost could promote the evolution of this trend. A crown composed of small leaves requires branches that bifurcate repeatedly (White 1983). Once such a branch is in place, it may be energetically more efficient to continue branch extension (resulting in greater crown width) than to shade the branch by extending a higher branch (Givnish 1984). The two species with the largest leaves have orthotropic (upwardly angled) branches (Table 2), which allows height growth by the upward extension of existing branches, thereby reducing the cost of height growth relative to that of lateral growth.

Although the conifers had twice the crown width of *A. macrophyllum* at a plant height of 2.5 m, little difference in crown width was found in 30-m tall trees. This pattern may be due in part to spatial constraints. As sapling height increases, the crown is more likely to be impeded laterally by the deep-crowned canopy and subcanopy trees common to old-growth Douglas-fir forests. Deep, narrow crowns may also increase whole-plant photosynthesis of adult conifers of temperate areas where the sun is never directly overhead and maximum solar irradiance exceeds the photosynthetic saturation point (Jahnke and Lawrence 1965, Horn 1971).

The relationships between trunk diameter and tree height, shown in Table 5, suggest that the mechanical stability of trees declines with height in old-growth forest understories. Saplings 2.5 m in height had trunk diameters 4–10 times the minimum diameter calculated by McMahon (1973) for a vertical wooden column just thick enough to resist bending under its own weight. Trees 30 m in height were twice this minimum diameter. The decrease in stability with height would be less pronounced if saplings had lower values of Young's modulus than mature trees, as reported by Cannell and Morgan (1987) for plantation-grown conifers. In this there may be a difference between shade-tolerant and gap-associated species, as the former show little change in wood density with tree size, whereas the latter often produce much denser wood as adults than as saplings (Wiemann and Williamson 1989).

The decline in mechanical stablility with tree height occurred across a greater height range for the evergreens than for the deciduous species. This trend coupled with the greater trunk diameter of evergreen compared with deciduous saplings may be due to the differential impact of snow loads on the two groups. When trunk diameter is calculated for saplings of identical height and crown width, the following order was found; plagiotropic evergreens > orthotropic evergreen > plagiotropic deciduous > orthotropic deciduous, with significant ($P < 0.05$) differences between each group (Table 7). The same order was noted in the amount of snow caught by crowns of these species. The one exception to the trend was the coastal population of *Tsuga*, which rarely receives snow (Table 7).

The convergence in trunk diameter between evergreen and deciduous species with increase in tree height is consistent with the postulated selective influence of snow loading. Because biomass increases more rapidly with tree height than does crown area, snow loads make up a greater fraction of the load on small saplings than on larger trees. Cannell and Morgan (1989) report that wet snow loads of 4–8 cm on sapling *Picea sitchensis* branches weighed 3–4 times the fresh weight of the branches. King (1987) found that such loads caused tropical understory saplings to arc over, again suggesting that snow loads may be an important agent of selection for thicker trunks in temperate evergreens. Although the study sites receive most winter precipitation as rain, only occasional snow loads would be necessary to remove thin-stemmed saplings. For example, extensive snow damage to young conifers was reported by Kangur (1973) in Oregon Coast Range stands at and above 300 m elevation, during 1965 and 1966. Thus, the greater stem thickness of saplings of species prone to the heaviest snow loading may be a result of genotype selection, although growth responses to snow loading may also contribute (Kozlowski 1971).

The lower hydraulic conductivities of conifers relative to those of angiosperms (Tyree and Sperry 1988) might also favor greater trunk diameters in conifers, but does not explain the convergence of conifer and angiosperm trunk diameters with increasing tree height. Hydraulic conductivity is important, because trees operate near the point where increasing xylem embolisms could disrupt water transport (Tyree 1988, Tyree and Sperry 1988). However, the presence of nonconducting heartwood in stems and branches exceeding about 5 years in age (Kyer-Snowman and Wilson 1988) suggests that water requirements do not constrain overall stem diameter. Mechanical and conductance requirements may be met simultaneously by diameter growth to provide stability and by adjustment in the thickness of the sapwood shell to provide sufficient conductivity (Long et al. 1981).

Greater trunk thickness in conifer than in deciduous tree saplings has also been reported for other forest stands in regions receiving snow (Hamilton and Christie 1971, Schober 1975). This allometric difference may contribute to the relatively slow early growth of conifers compared with hardwoods. The thicker the trunk of a tree at a particular height, the more biomass must be accumulated to reach that height (King 1986). On the other hand, among taller trees, the increase in trunk diameter with height is less in conifers than in angiosperms (Figure 2), which may allow conifers to surpass angiosperms in rate of height growth as maturity is approached. Another factor contributing to this pattern is the greater thickness (and hence greater biomass per unit area) and longer lifespan of conifer needles compared with leaves of deciduous trees. Thick needles result in a lower rate of increase in leaf area initially, but long needle retention times allow for the accumulation of a large leaf area over a period of years (Cannell 1987). This, among other factors, contributes to the dominance of conifers in many forest regions despite their slow initial height growth (Waring and Franklin 1979).

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