

Branch growth and biomass allocation in *Abies amabilis* saplings in contrasting light environments

DAVID A. KING

Ecosystem Dynamics, Research School of Biological Sciences, Australian National University, Canberra ACT 0200, Australia

Received May 14, 1996

Summary Aboveground biomass allocation, and height and branch growth were studied in saplings of the shade-tolerant conifer, *Abies amabilis* Dougl. ex Forbes growing in large openings and in the understory of an old-growth forest in western Oregon. The presence of annual overwintering budscale scars was used to infer extension growth histories; annual growth rings in branches and stems were used in combination with extension histories to compute partitioning of new biomass among leaves, branches and stems. Saplings growing in large gaps had conical crowns, whereas understory saplings had umbrella shaped crowns as a result of much greater rates of branch extension than stem extension. Understory saplings grew slowly in height because of low rates of biomass production and low allocation of biomass to stem extension. About 40% of new biomass was allocated to foliage in both groups, but understory saplings allocated more of the remaining growth increment to branches and less to stem than did saplings growing in large gaps.

These results differ from the patterns observed in shade-tolerant saplings of tropical forests, where allocation to foliage increases with shading and branch allocation is much lower than observed here. This difference in allocation may reflect mechanical constraints imposed by snow loads on the evergreen *A. amabilis* crowns, particularly on flat-crowned understory saplings.

Keywords: allometry, branch growth, conifer, height growth.

Introduction

The capacity of shade-tolerant trees to survive in shade and respond to canopy gaps with rapid height growth has been linked to plasticity in a variety of physiological and morphological characteristics. Compared with sun-grown plants, shade-grown saplings have thinner, more horizontal leaves (Carter and Smith 1985), flatter crowns (Tucker et al. 1987) and in tropical species, proportionally higher allocation of new biomass to leaves and lower allocation to branch and stem growth (King 1991a, 1994). These adaptations maintain efficient light interception in plants that fix just enough carbon to replace senesced leaves and meet respiratory demands, resulting in little height growth in deep shade.

Differences in shape between the umbrella crowns of shade-grown saplings and the conical crowns of sun-grown saplings are particularly noticeable in *Abies* Mill. (Kohyama 1980). These differences in crown shape are partly related to variation in branch spacing along the main stem, with shaded saplings having closely spaced branches. Although corresponding shifts in the dynamic allocation of new biomass among plant parts may be expected, such allocation patterns have not been reported in *Abies* saplings.

In tropical forests, shade-tolerant saplings respond to shade by allocating most of their new aboveground biomass increment to leaves, with little to stem thickening or extension. Whole-plant compensation points are lowered when carbon is directed preferentially to leaf growth, to replace senescing leaves at low irradiances and carbon fixation rates (Givnish 1988). However, tropical species, unlike *Abies* saplings, are not subject to winter snow loads that increase the requirement for wood to support new leaves.

To evaluate mechanical constraints on allocation and test the general applicability of allocation patterns observed in tropical species, I studied allocation and form in *Abies amabilis* Dougl. ex Forbes saplings growing in old-growth forests in the Cascade mountains of western Oregon. This species is more shade tolerant than *Pseudotsuga menziesii* (Mirb.) Franco, the usual dominant of remaining unlogged old-growth forests of the western Cascade mountains (Franklin and Dyrness 1973). *Abies amabilis* saplings are more common in canopy gaps than in understories (Stewart 1986), nonetheless suppressed individuals in deep shade are encountered, and these undergo pronounced shifts in morphology when exposed to full light after clearcutting (Tucker et al. 1987). An annual snowfall of 7 to 8 m and winter snowpacks of 1 m or more typify the *Abies amabilis* zone, where this species would dominate in the absence of fire (Franklin and Dyrness 1973).

Materials and methods

The study was conducted near Lookout Creek at the H.J. Andrews Experimental Forest in western Oregon (44°13' N, 122°8' W) in the lower *Abies amabilis* zone at 1000 to 1200 m elevation. This forest is dominated by 60–80-m tall *Pseudotsuga menziesii* of more than 400 years in age, but contains smaller *Abies amabilis* and *Tsuga heterophylla* (Raf.) Sarg.

trees, saplings and seedlings. Saplings harvested for allocation measurements were taken from lower west-facing slopes above Lookout Creek, within 40 m of a U.S. Forest Service access road. Additional saplings were measured nondestructively on both sides of Lookout Creek.

Extension growth histories of *Abies amabilis* branches are easily traced, until flushing ceases in older branches near the crown base. The branches produce one growth flush per year, delineated by overwintering terminal bud scale scars at the base of each successive flush. Branch and stem growth histories were traced for upper crowns of 13 saplings growing over a wide range of light conditions. To assess the light environment, hemispherical photographs were taken above the apex of each sapling with a red-filtered 7.5 mm Minolta fisheye lens. Rich's (1989) image analysis program, CANOPY, computed indirect site factors, defined as the fraction of above-canopy diffuse light penetrating canopy holes to the sapling apex.

A subset of the above saplings, including three understory individuals and three large-gap or forest-edge saplings, were harvested from June 22 to July 7, 1994. Saplings from sun-exposed environments were somewhat taller, but had narrower crowns than shaded saplings, as shown in Table 1. Saplings were harvested in mid-season. To circumvent possible bias caused by temporal shifts in allocation over the growing season, biomass allocation was calculated for the 2.5-year growth period including the current growing season till harvest, plus the past two years. This long integration period for allocation is possible because of the long lifespan of *Abies amabilis* needles.

Biomass partitioning was estimated from total dry mass of branches, stem, and foliage produced over the past 2.5 years, coupled with branch and stem lengths and basal diameters, at harvest and 2.5 years ago. In this study, the stem refers to the entire vertical main axis from base to tip, as distinct from laterally borne branches. Past branch basal diameters located inside the bark were measured in two perpendicular directions with an increment measuring machine equipped with a video camera and monitor. A regression relationship relating outside and inside bark diameters was used to estimate the latter. These measurements were then applied with regression relationships between branch biomass and branch length \times (basal diameter)²

to estimate dry mass of each branch 2.5 years ago. Similar methods were applied to cross sections taken at six heights along each stem, to infer past stem dry mass.

The height growth of a sapling depends on its production of aboveground biomass and extension achieved per unit of biomass, as analyzed by King (1994). Aboveground biomass production rate per unit leaf area was estimated as:

$$G = \Delta M / (LA \times \Delta T), \quad (1)$$

where ΔM is aboveground biomass produced over time interval ΔT (2.5 years for harvested saplings) and LA is mean leaf area over the same time interval. (Note that ΔM is gross biomass increment, so a sapling that did not increase in net mass would still have a positive ΔM if it replaced senescing tissues.) Parameter G is similar to net assimilation rate or unit leaf rate (Hunt 1982), except that it is computed in terms of aboveground rather than total biomass production. Sapling leaf area at the time of harvest was estimated as the product of total leaf dry mass and leaf area per unit dry mass, the latter was determined from a subsample of leaves for each sapling. Initial leaf area was estimated from the ratio of initial to final crown area, which was inferred from lengths of the four longest branches 2.5 years ago and at harvest.

A new growth parameter, height growth efficiency, was defined by King (1994) as:

$$HE = \Delta h \times LA / \Delta M, \quad (2)$$

where height growth increment, Δh , was determined over a similar time interval as G . Thus, HE is inversely proportional to the amount of new biomass required to extend a crown of given leaf area by a given height increment. Because support requirements increase with leaf area, defining HE as $\Delta h \times LA / \Delta M$ makes the quantity less dependent on crown size than defining it more simply as $\Delta h / \Delta M$. A further advantage of Equation 2 is that rate of height growth can then be written as $dh/dt = G \times HE$. Thus, the influence of biomass production on height growth is separated from effects related to how biomass extends the sapling.

Table 1. Characteristics of harvested *Abies amabilis* saplings. The indirect site factor is an estimate of the fraction of above-canopy diffuse light reaching the sapling apex.

| Indirect site factor | Height (cm) | Crown width (cm) | Stem diameter ¹ (cm) | Aboveground biomass (g) | Age ² (year) |
|----------------------|-------------|------------------|---------------------------------|-------------------------|-------------------------|
| <i>Large opening</i> | | | | | |
| 0.583 | 131 | 84 | 2.19 | 430 | 6 |
| 0.328 | 103 | 88 | 2.46 | 380 | 11 |
| 0.306 | 182 | 148 | 3.50 | 1373 | 20 |
| <i>Understory</i> | | | | | |
| 0.103 | 86 | 128 | 2.30 | 269 | 51 |
| 0.053 | 132 | 205 | 3.72 | 1256 | 78 |
| 0.013 | 90 | 118 | 2.06 | 252 | 35 |

¹ Stem diameter at $0.1 \times$ total sapling height.

² Age of stem cross section at 20 cm height interpolated from ages of cross sections above and below this height, inferred from annual ring counts.

To assess factors influencing shade tolerance, aboveground biomass production rate required to just maintain current leaf mass was defined by King (1994) as:

$$\text{Compensation } G = (\text{LM/LA}) / (F \times \text{LLS}), \quad (3)$$

where leaf dry mass per unit one-sided leaf area (LM/LA), fraction of aboveground production allocated to foliage (F) and leaf lifespan (LLS) are all estimated for shaded saplings, showing little or no increase in net biomass from year to year. For shaded saplings, it was assumed:

$$\text{LLS} = 1 + \frac{2 (\text{Mass of leaves } \geq 1 \text{ year old})}{(\text{Mass of 1 and 2 year old leaves})} \quad (4)$$

Equation 4 is appropriate if leaf lifespan is greater than 2 years, and no large shifts in leaf production rate have occurred over a period of one leaf lifespan.

Results

Height growth rate

Rate of height growth of *Abies amabilis* saplings was highly correlated with the estimated fraction of diffuse light reaching the sapling apex (indirect site factor) (Figure 1). Most branches initiated from buds adjacent to the terminal bud, which expanded with the terminal shoot, resulting in a one to one relation between internode length and height growth rate (Table 2, Figure 2). However, slow-growing, shaded saplings produced only one branch per node, whereas the fastest growing saplings produced three or more branches per node, causing a more gradual increase in mean branch spacing (defined as number of branches per unit stem length) with height growth rate. This assessment ignores small branches scattered between main nodes of the fastest growing saplings, which contributed less than 2% of total branch mass per sapling.

Analysis of harvested saplings showed that increased height growth with irradiance resulted from increases in both aboveground production per unit leaf area and height growth efficiency (Figure 3). The shift from an umbrella crown shape to a conical crown shape with increasing height growth was associated with a shift in the ratio of lateral to vertical growth rates (Figure 4). Although branch growth rate increased with height growth rate, the two rates were not proportional, and a growth rate of 7 cm year⁻¹ was projected for upper branches of saplings with zero height growth (Figure 4, Table 2).

Allocation of new biomass

No difference between shaded and high-light saplings was observed in the fraction of aboveground growth allocated to foliage (Figure 5), despite the large shifts in the lateral versus vertical growth and height growth efficiency. However, shaded saplings allocated a significantly higher fraction of aboveground growth to branches and a lower fraction to stems than did high-light saplings (Figure 5). Shaded saplings therefore had a greater branch to leaf production ratio than saplings

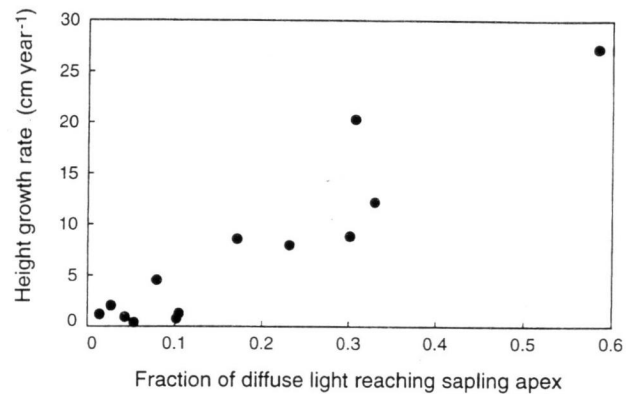


Figure 1. Height growth rate versus indirect site factor (estimated fraction of diffuse light received) for *Abies amabilis* saplings in or adjacent to old-growth forest in western Oregon. The height growth rate for each sapling is the average value determined from the spacing of branch nodes produced over the 3-year period up to the winter before harvest.

Table 2. Relationships between extension growth, morphology and light environment for *Abies amabilis* saplings. The relationships were all significant at $P < 0.001$, except the relationship between leaf dry mass/leaf area and indirect site factor (two-tailed $P = 0.0044$). dh/dt is the height growth rate of the apex inferred from internode length over 3 years; isf is the indirect site factor (estimate of the fraction of diffuse light received); internode length is distance between successive branch flushes; and branch spacing is internode length divided by number of branches per node. The terms gap and shade branch denote branches on saplings growing in large gaps or in shade, respectively. Branch diameter is basal diameter outside the bark.

| Relationship | Units | r | N |
|--|-----------------------|-------|-----|
| Leaf dry mass/leaf area = 130 + 185 isf | g m ⁻² | 0.842 | 9 |
| Height growth rate, dh/dt = -1.15 + 47.5 isf | cm year ⁻¹ | 0.936 | 13 |
| Internode length = 1.135 (dh/dt) ^{0.951} | cm | 0.995 | 13 |
| Branch spacing = 1.092 (dh/dt) ^{0.616} | cm | 0.963 | 13 |
| Branch extension rate = 7.12 + 0.239 dh/dt | cm year ⁻¹ | 0.600 | 47 |
| Gap branch diameter = 0.079 length ^{0.537} | cm | 0.916 | 56 |
| Shade branch diameter = 0.055 length ^{0.593} | cm | 0.923 | 56 |

growing in large gaps. Differences in leaf versus branch production between the two groups of saplings may be related to differences in crown shape and leaf dry mass/leaf area ratio (LM/LA). Conical, high-light saplings had a mean leaf area index (LAI) of 1.5, whereas flat-crowned, shaded saplings had

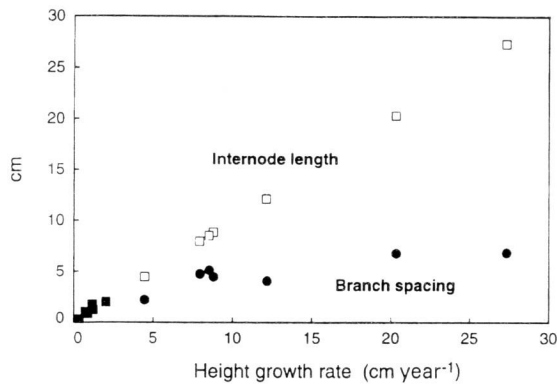


Figure 2. Relationship between branch and internode spacing and height growth rate for *Abies amabilis* saplings. Branch spacing is total number of branches produced over 3 years divided by the corresponding stem extension increment.

an LAI of only 0.5. (LAI was defined as estimated leaf area divided by the area of an ellipse that would just fit over the widest extremities of the crown; thus reported values are lower

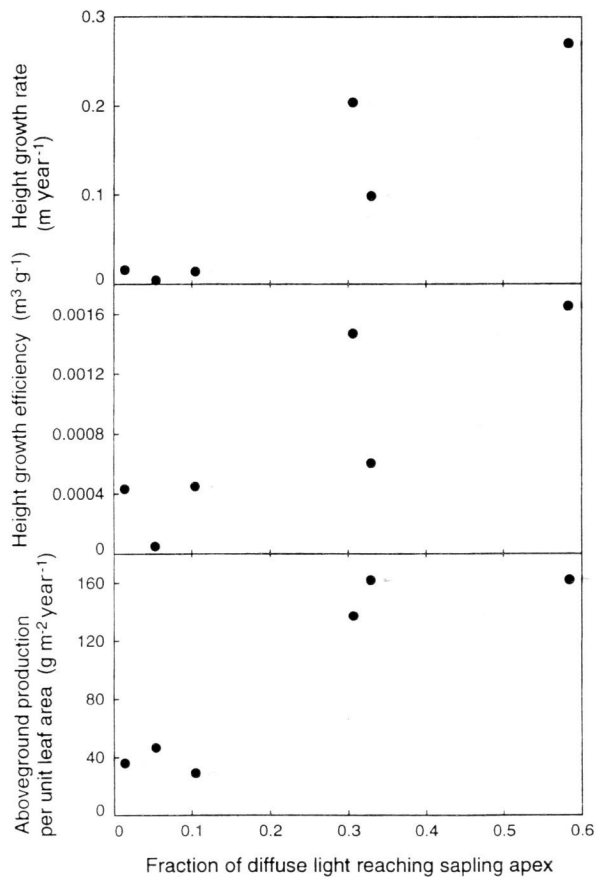


Figure 3. Height growth rate, height growth efficiency and aboveground biomass production rate per unit leaf area for harvested *Abies amabilis* saplings, plotted as a function of the indirect site factor (estimated fraction of diffuse light received). Height growth efficiency is defined as height growth rate divided by aboveground biomass production per unit leaf area.

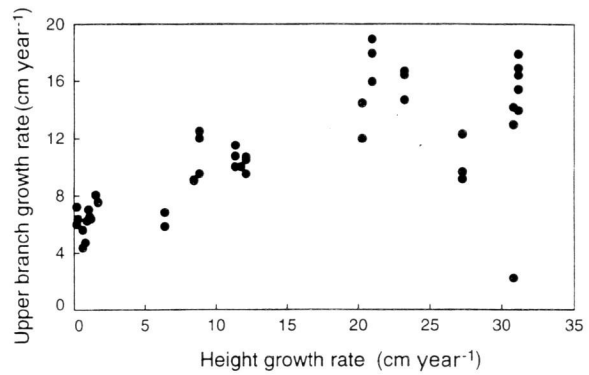


Figure 4. Growth rate of 1- to 3-year-old branches versus mean height growth rate over 3 years for *Abies amabilis* saplings growing over a wide range of light environments.

than if the whole crown edge had defined crown area.) The threefold difference in LAI indicates that shaded saplings must have wider crowns and longer branches to support the same leaf area than high-light saplings. The fact that LM/LA of high-light saplings was 1.6 times that of shaded saplings should also increase the ratio of leaf to branch production in high-light saplings.

A mean leaf lifespan of 9 years was estimated for shaded saplings (Table 3). Shaded saplings had aboveground biomass production rates that were similar to their compensation production rates, defined as the aboveground production rate per unit leaf area required to maintain current leaf area given the observed LM/LA, leaf allocation and leaf lifespan (Table 3 and Figure 3).

Branch growth

Branch size generally increased with branch age, but smaller-than-average old branches were usually thinner than younger branches of the same length (Figure 6). For understory saplings, this pattern was associated with cessation of basal diameter growth before cessation of extension growth in aging branches, which had fewer basal growth rings than extension

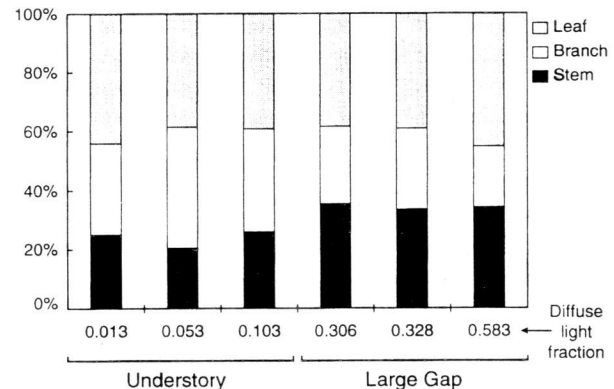


Figure 5. Allocation of new biomass produced over the past 2.5 years among aboveground parts of six *Abies amabilis* saplings.

Table 3. Characteristics of understory *Abies amabilis* saplings compared with shade-tolerant understory saplings of a lowland tropical forest in Panama. The ratio LM/LA is leaf dry mass per unit (one-sided) leaf area, leaf allocation fraction is the fraction of new aboveground production allocated to leaves, and compensation production rate is the calculated aboveground biomass production rate per unit leaf area required to maintain current leaf area, given the observed LM/LA, leaf allocation fraction and leaf lifespan. Parameter HE is height growth efficiency, defined by Equation 2. Values for *Abies* are an average for three understory saplings; tropical sapling values are for an indirect site factor of 0.03, close to observed whole plant light compensation points for these species. Note that HE values for tropical saplings are about 0.000001 of those of Table 3 of King (1994) because of a unit conversion error in the data presented by King (1994).

| Species | LM/LA (g m ⁻²) | Leaf allocation fraction | Leaf lifespan (year) | Compensation production rate (g m ⁻² year ⁻¹) | HE (m ³ g ⁻¹) |
|--|-------------------------------|-----------------------------|-------------------------|---|---|
| <i>Abies amabilis</i> | 127 | 0.41 | 8.8 | 36 | 0.00031 |
| Panamanian species: | | | | | |
| <i>Alseis blackiana</i> Hemsl. | 26 | 0.71 | 0.9 | 39 | 0.0012 |
| <i>Calophyllum longifolium</i> Willd. | 85 | 0.50 | 3.6 | 46 | 0.0024 |
| <i>Coccoloba manzanillensis</i> Beurl. | 71 | 0.67 | 2.4 | 45 | 0.0022 |
| <i>Herrania purpurea</i> (Pitt.) R.E. Schult. | 38 | 0.75 | 1.4 | 36 | 0.0011 |
| <i>Protium panamense</i> (Rose) I.M. Johnston | 68 | 0.59 | 3.2 | 36 | 0.0019 |
| <i>Tachygalia versicolor</i> Standl. & L.O. Wms. | 52 | 0.69 | 2.2 | 34 | 0.0011 |
| <i>Trichilia tuberculata</i> C. DC. | 72 | 0.47 | 3.8 | 40 | 0.0023 |

increments (Figure 7). Examination of midbranch cross sections of several old branches indicated that diameter growth may only extend about half way down the branch during the years preceding cessation of all growth in the branch. The ratio of branch to foliage biomass production for individual branches, shown in Figure 8, was lowest in youngest branches, rising to a constant value in branches more than 5 years old. This ratio did not continue to increase with branch age because diameter growth ceased in the lower half of older branches.

Discussion

The allocation of aboveground biomass production observed in *A. amabilis* differed from that observed in Central American forest saplings (King 1991a, 1994). As shown in Figure 9, allocation to branches was greater in *A. amabilis* than in *Virola sebifera* Aubl., a shade-tolerant neotropical species that also bears tiered branches. *Virola sebifera* also showed a more pronounced shift in allocation over a smaller range of irradiances than did *A. amabilis* saplings studied here. *Virola* saplings growing in intermediate light environments had similar foliar allocation, but greater stem allocation than *Abies* saplings in both high- and low-light environments. Heavily shaded *Virola* saplings had similar stem allocation, but much greater leaf allocation than understory *Abies* saplings. Branch allocation approximately equalled leaf allocation in understory *Abies*, but represented only one sixth of leaf allocation in shaded *Virola*.

The increase in height growth rate with increased light availability observed in *Abies amabilis*, also occurs in other forest saplings whose growth is light limited (Kohyama 1980, Brokaw 1987, Canham 1988, King 1994, O'Connell and Kelty 1994). This increase in height growth rate is correlated with an increase in biomass production per unit leaf area (Loach 1970,

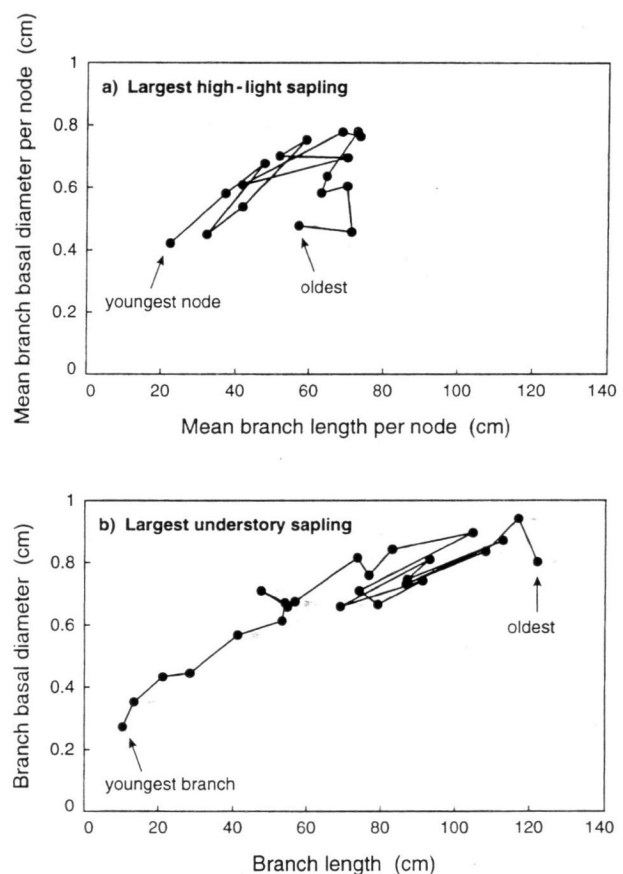


Figure 6. Relationships between basal diameter (measured 2–4 cm from branch base) and branch length for representative high-light and understory *Abies amabilis* saplings. Successively older branches are connected. Mean dimensions of branches of successive nodes are plotted for the high-light sapling that bore several branches per node.

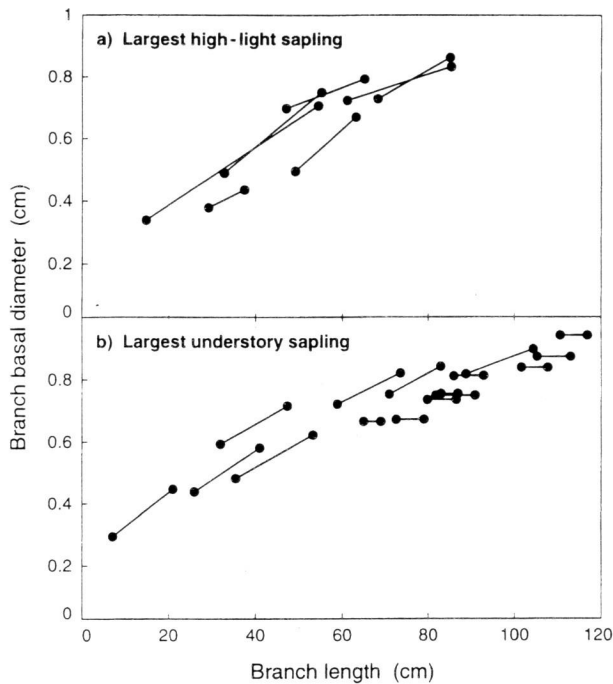


Figure 7. Height and diameter growth over the past 2.5 years, as indicated by line segments for branches selected for intensive analysis for representative high-light and understory *Abies amabilis* saplings.

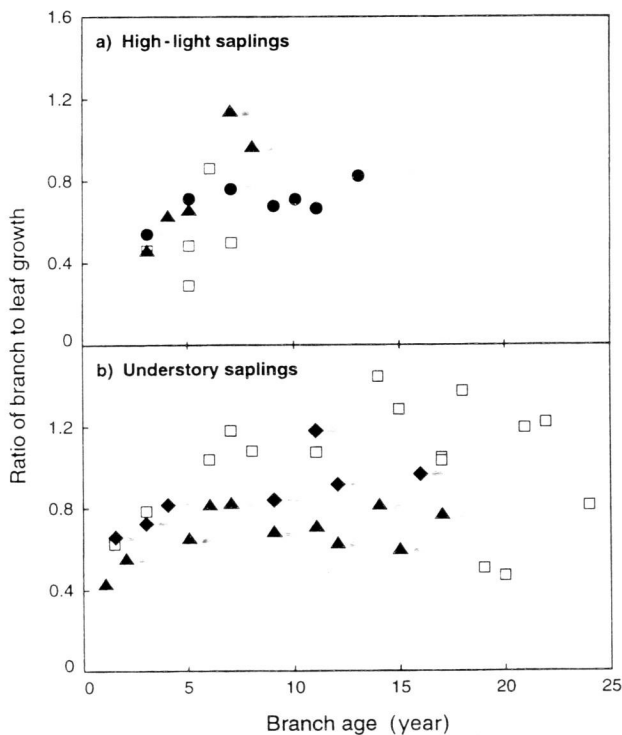


Figure 8. Ratio of branch biomass to leaf biomass production (over the past 2.5 years) for branches selected for intensive analysis from harvested *Abies amabilis* saplings. Each symbol within a panel refers to branches of a particular sapling.

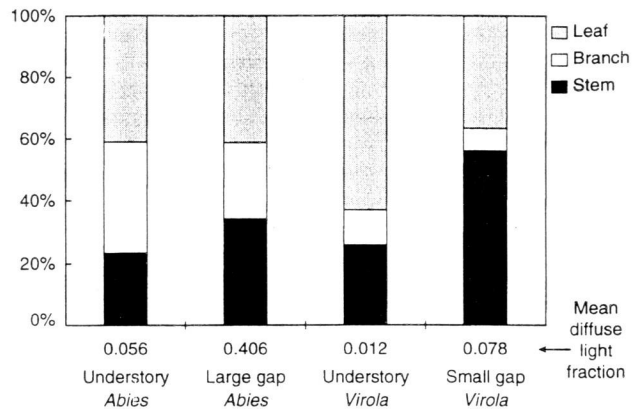


Figure 9. Aboveground allocation of biomass between plant parts for *Abies amabilis* compared with saplings of the neotropical species, *Virola sebifera*.

King 1994, Figure 3c). In studies of *A. amabilis* and tropical saplings (King 1994), increases in height growth rate, defined as being equal to $HE \times G$, also correspond to increases in height growth efficiency, HE.

The height growth efficiencies of tropical saplings near their whole-plant light compensation points (Table 3) were four to eight times greater than those reported here for *A. amabilis* saplings. The low height growth efficiency in *Abies* saplings was associated with stem cross-sectional areas that were five to 15 times larger than those of tropical saplings of similar height. For saplings with similar allocation, wood density and allometry, height growth efficiency is inversely proportional to stem cross-sectional area (King 1994).

Factors that may explain the differences in height growth efficiency and allocation, include differences in leaf size and crown dimensions, and the occurrence of heavy winter snowloads on *A. amabilis* saplings. Understory *Abies* saplings had wider crowns and much smaller leaves than *Virola* saplings, factors that could contribute to greater branch biomass requirements in *Abies*. Most branches on 1-to 2-m-tall *Virola* saplings have no laterals, whereas older *Abies* branches bear two or more additional orders of side branches. More branches are needed to foliate a given spatial area when leaves are small than when leaves are large (White 1983). Snow loads place additional mechanical demands on *Abies* saplings because snow coats the entire finely branched crown rather than slipping through the branches. Antos and Zobel (1982) noted that, in the *Abies amabilis* zone near Mount St. Helens, WA, shrubs and saplings become embedded in and flattened by wet winter snowpacks, because much of the snowpack melts from its base. Although snowpack depths may be greater near Mount St. Helens than at the study site, recovery from flattening had occurred on several occasions as indicated by the presence of compression wood arcs in different quadrants of stems of shaded *A. amabilis* saplings.

Stem diameter of understory saplings of western Oregon can be related to snowfall and propensity of saplings to catch snow.

King (1991b) found that the stem diameter of plagiotropic conifer saplings was twice that of deciduous angiosperms when comparing saplings of similar height and crown width. Similarly, stems of coastal saplings of *Tsuga heterophylla*, which seldom receive snow, were two-thirds as thick as stems of *T. heterophylla* saplings of the lower elevations of Andrews Experimental Forest, which do receive snow. Impact of snow on mechanical costs is most evident for 1–3 m tall saplings and diminishes with increasing tree size, because tree weight and wind forces increase more rapidly with total height than do crown area and snow loading (King 1991b). Nonetheless, additional allocation studies on conifers from snowless areas and larger leaved conifers of more tropical areas, such as *Agathis Salisb.* and *Podocarpus L'Hér. ex Pers.*, are required to rule out the alternative possibility that foliar allocation is less plastic in conifers than in angiosperms.

The arrangement of flattened needles in umbrella crowns rather than in conical crowns greatly improves light interception by understory *Abies* (Kohyama 1980, Tucker et al. 1987), but incurs substantial cost in stem and branch support requirements. In snowy regions this mechanical requirement precludes the possibility of increasing allocation to foliage to replace senescing leaves of shaded saplings. However, compensation biomass production rate (i.e., the rate required to just maintain foliar biomass), was as low for *A. amabilis* as reported for saplings of several tropical species (King 1994) (Table 3). Because the compensation production rate is inversely proportional to fractional foliage allocation \times leaf lifespan and directly proportional to LM/LA (Table 3), the long leaf lifespan of shaded *A. amabilis* saplings compensates for both the relatively low allocation to foliage and the high LM/LA ratio.

Branch diameter–length relations (Table 2) showed a more gradual increase in branch construction costs with length than in previous studies of larger trees where branch diameter was proportional to length to the 1.16–1.5 power (McMahon and Kronauer 1976, King and Loucks 1978). A 1.5 power relation may be expected in branches designed to flex through a given angle under their own weight (McMahon and Kronauer 1976). The much lower power function exponents shown in Table 2, indicate that young branches of *A. amabilis* saplings flex less under their own weight than older branches (ignoring snow loads). However, young branches are composed entirely of sapwood (Kyker-Snowman and Wilson 1988), so water conduction requirements may constrain their diameters (Tyree and Sperry 1988). Furthermore, the relationship between branch diameter and length at branch senescence may be more important to sapling energy balance than the temporal pattern of branch thickening, because the former represents total investment in the branch. Allocation to branchwood versus foliage increased over the first few years of branch growth (Figure 8), even though there was only a modest increase in branch diameter with extension. In old branches, diameter growth was restricted to the upper, younger sections.

Thus, the relationship between branch diameter and length for mature branches on trees of different size, differs from the allometric trajectory of a single growing branch. This distinc-

tion may be important in mechanistic models of branch growth that link branchwood requirements to branch dimensions (e.g., Ford et al. 1990).

Acknowledgments

I thank A. McKee and the Forest Research Laboratory of Oregon State University for permission to conduct the study at H.J. Andrews Experimental Forest, and A. Gray and B. Gardner, respectively, for aid in analyzing hemispherical photographs and tree rings with the canopy photograph and increment analysis systems of Oregon State University. J. Evans and O. Atkin provided helpful reviews of the manuscript.

References

- Antos, J.A. and D.B. Zobel. 1982. Snowpack modification of volcanic tephra effects on forest understory plants near Mount St. Helens. *Ecology* 63:1969–1972.
- Brokaw, N.V.L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *J. Ecol.* 75:9–19.
- Canham, C.D. 1988. Growth and architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69:786–795.
- Carter, G.A. and W.K. Smith. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiol.* 79:1038–1043.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep., PNW–8, 417 p.
- Ford, E.D., A. Avery and R. Ford. 1990. Simulation of branch growth in the *Pinaceae*: interactions of morphology, phenology, foliage productivity and the requirement for structural support on the export of carbon. *J. Theor. Biol.* 146:15–36.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. *Austr. J. Plant Physiol.* 15:63–92.
- Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. University Park Press, Baltimore, MD, 248 p.
- King, D.A. 1991a. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Funct. Ecol.* 5:485–492.
- King, D.A. 1991b. Tree allometry, leaf size and adult tree size in old-growth forests of western Oregon. *Tree Physiol.* 9:369–381.
- King, D.A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. *Am. J. Bot.* 81:948–957.
- King, D. and O.L. Loucks. 1978. The theory of tree bole and branch form. *Rad. Environ. Biophys.* 15:141–165.
- Kohyama, T. 1980. Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. *Bot. Mag. Tokyo* 93:13–24.
- Kyker-Snowman, T.D. and B.F. Wilson. 1988. Total wood, sapwood, and heartwood in branch bases of three conifers. *Can. J. For. Res.* 18:1332–1336.
- Loach, L. 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. *New Phytol.* 69:273–286.
- McMahon, T.A. and R.E. Kronauer. 1976. Tree structures: deducing the principle of mechanical design. *J. Theor. Biol.* 59:443–466.
- O'Connell, B.M. and M.J. Kelty. 1994. Crown architecture of understory and open-grown white pine (*Pinus strobus* L.) saplings. *Tree Physiol.* 14:89–102.
- Rich, P.M. 1989. A manual for analysis of hemispherical photography. LA-11733-M Manual, Los Alamos National Laboratory, Los Alamos, NM, 80 p.

- Stewart, G.H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. *Can. J. For. Res.* 16:558-568.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem disfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88:574-580.
- Tucker, G.F., T.M. Hinckley, J.W. Leverenz and S.-M. Jiang. 1987. Adjustments of foliar morphology in the acclimation of understory Pacific silver fir following clearcutting. *For. Ecol. Manage.* 21:249-268.
- White, P.S. 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bull. Torrey Bot. Club* 110:203-212.