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Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State, U.S.A.

Hiroaki Ishii, Joel H. Reynolds, E. David Ford, and David C. Shaw

Abstract: A detailed analysis of diameter–height relationships was applied to an old-growth *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* – *Tsuga heterophylla* (Raf.) Sarg. forest in southwestern Washington State, U.S.A., to predict future development of vertical stratification among tree species. Differences among species in relative abundance and size structure resulted in diameter–height regressions of varying certainty and stability. Damage and shading had negative impacts on predicted heights and estimates of maximum attainable height (H_{\max}) in all species. However, species varied as to the main causes and size dependency of damage in relation to tree height. Current height-growth rates of the upper canopy species declined with increasing tree height, reaching minimum values near the predicted H_{\max} . The future development of the forest canopy would involve a slow invasion of the upper canopy by *Tsuga heterophylla* and *Thuja plicata* Donn ex D. Don, as *P. menziesii* are near their maximum attainable height, and *Abies amabilis* Dougl. ex Forbes and *Taxus brevifolia* Nutt. are restricted to the middle to lower canopy. However, if current height-growth rates continue, *P. menziesii* should maintain its dominant status in the upper canopy for at least another century.

Résumé : Une analyse détaillée de la relation diamètre–hauteur a été appliquée à une vieille forêt de *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* – *Tsuga heterophylla* (Raf.) Sarg., dans le sud-ouest de l'État de Washington, aux États-Unis, afin de prédire le développement futur de la stratification verticale des espèces arborescentes. Les différences dans l'abondance relative et la structure des dimensions entre les espèces faisaient que les régressions entre le diamètre et la hauteur avaient un degré de certitude et de stabilité variable. Les dommages et l'ombrage avaient un impact négatif sur les hauteurs prédites et sur les estimés de la hauteur maximale potentielle (H_{\max}) de toutes les espèces. Cependant, les espèces différaient quant aux principales causes de dommages et leur impact selon la dimension en relation avec la hauteur des arbres. Le taux actuel de croissance en hauteur des espèces de la canopée supérieure diminue en fonction de la hauteur de l'arbre, atteignant des valeurs minimales près de H_{\max} estimé. Le développement futur de la canopée de la forêt entraînera une invasion lente de la canopée supérieure par le *Tsuga heterophylla* et le *Thuja plicata* Donn ex. D. Don, vu que le *P. menziesii* est près de sa hauteur maximale potentielle et que l'*Abies amabilis* Dougl. ex Forbes et le *Taxus brevifolia* Nutt. sont limités aux canopées moyenne et inférieure. Toutefois, si le taux d'accroissement en hauteur actuel se maintient, le *P. menziesii* pourrait garder son statut dominant dans la canopée supérieure pour au moins un autre siècle.

[Traduit par la Rédaction]

Introduction

Vertical stratification among tree species has been found in various forest types including tropical rain forests (Richards 1952; Grubb et al. 1963; Ashton and Hall 1992), temperate broad-leaved forests (Kira et al. 1969; Sumida 1995), and temperate coniferous forests (Ogino 1990; Easter and Spies 1994). Vertical partitioning of the forest canopy

among tree species has been suggested as a factor promoting species coexistence (Cody 1986; Kohyama 1993). Vertical stratification is defined by both the regeneration ecology of species and their height-growth patterns (Johnson et al. 1994; Dubrasich et al. 1997). Regeneration ecology reflects the relative shade tolerance of species and determines whether individuals are found in the understory. It has been investigated in detail in studies on forest succession, e.g., Stewart (1986a), Franklin and DeBell (1988), and Gray and Spies (1996) in the Pacific Northwest, U.S.A. Height-growth patterns determine the height distributions of species and are defined by their height-growth rate and maximum attainable height. With the exception of Johnson et al. (1994) who reconstructed the recruitment, survival, and height-growth patterns of a *Pinus contorta* Loud. var. *latifolia* Engelm. (lodgepole pine) – *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) forest in western Canada, height-growth patterns of species have not been comparatively studied in mixed-species natural stands.

Silvicultural studies have estimated height-growth patterns of tree species from empirically derived site-index

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curves differing by site quality (Hann 1995; Miyajima 1989). A similar approach to inferring height-growth patterns of species has been applied to mixed-species natural stands by substituting tree diameter for tree age and deriving static diameter–height relationships of existing trees (Fujimori et al. 1976; Thomas 1996; Aiba and Kohyama 1996). Height-growth patterns inferred from static diameter–height relationships have been used to interpret current patterns of vertical stratification among species and to infer future forest dynamics. Thomas (1996) compared static diameter–height relationships among species in a Malaysian rain forest in relation to their life histories and onset of reproduction. Aiba and Kohyama (1996) used static diameter–height relationships to derive “projected maximum size” of tree species in a warm-temperate rain forest in southern Japan, and compared these values in relation to tree demography.

Using diameter as a surrogate for tree age and interpreting the static diameter–height relationship as the dynamic height-growth pattern of a species requires assuming that changing growth conditions through time at a given site does not alter the diameter–height relationship (Thomas 1996). However, as tree form and allometry are influenced by both environmental and competitive factors (Holbrook and Putz 1989; King 1991), temporal changes in these conditions are likely to affect the diameter–height relationship. In mixed-species natural stands, species differences in relative shade tolerance and successional status will result in differences, over time, in the abundance and range of tree sizes observed for each species. This may cause varied uncertainty among species in estimating diameter–height relationships at any given time. Variation and uncertainty resulting from temporal changes must be considered when interpreting static diameter–height relationships of mixed-species natural stands.

In addition, the effects of environmental and competitive factors on the diameter–height relationship must also be considered. The effects of environmental conditions and competitive interaction on height growth and diameter–height relationships are well documented (e.g., Ritchie and Hann 1986; Hann and Ritchie 1988; Krumland and Wensel 1988). Damaging agents such as wind, snow, herbivory, pathogens, and falling debris and litter have negative impacts on height growth (Shidei 1976; Putz et al. 1983; Clark and Clark 1991; Telewski 1995; Tainter and Baker 1996). Some forms of competitive interaction, such as shading from above, have also been found to result in reduction of resources and suppression of height growth (Kohyama 1980; O’Connell and Kelty 1994; King 1997). The effects of and response to environmental conditions and competitive interactions may vary depending on the species.

Information on current growth rates is also useful for inferring future dynamics of height growth. There is general agreement that height-growth rates decrease as trees near their maximum attainable height (Assman 1970; Halle et al. 1978; Ogino 1990). However, as Stevens and Perkins (1992) and Ryan and Yoder (1997) have noted, the underlying ecological and physiological mechanisms determining height-growth patterns are still to be investigated. A detailed analysis of diameter–height relationships coupled with current growth rates will help to elucidate patterns of tree height

growth and to predict future dynamics of mixed-species natural stands.

In this study, we explored the variability found in the diameter–height relationships of species in an old-growth *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Douglas-fir) – *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest in southwestern Washington State, U.S.A. We investigated the effects on the diameter–height relationships of damage and shading and how these effects differed among species. We also estimated current height-growth rates from measurements of terminal shoot elongation rates. Finally, we combine these observations to predict the future development of vertical stratification in this forest.

Study site and methods

The study was conducted in an old-growth *P. menziesii* – *Tsuga heterophylla* forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, U.S.A. (45°49’N, 121°57’W; altitude 300 m). The stand is dominated by *P. menziesii* and *T. heterophylla* in terms of basal area. *Thuja plicata* Donn ex D. Don (western redcedar), *Abies amabilis* Dougl. ex Forbes (Pacific silver fir), and *Taxus brevifolia* Nutt. (Pacific yew) are also abundant. Other tree species in the stand include *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Pinus monticola* Dougl. ex D. Don (western white pine), and *Cornus nuttallii* Audubon (Pacific dogwood). See Franklin (1972) and Franklin and DeBell (1988) for a detailed description of the area.

Four hectares of old-growth forest (400–500 years old) were mapped, and diameter at breast height (DBH) and height of all trees >5 cm DBH were measured. DBH was measured with a diameter tape 1.3 m above ground level, except for trees with multiple stems below 1.3 m, in which case it was measured below the point where the stems parted. Tree height was defined as the vertical distance from ground level to the highest foliage on the tree. Heights of trees shorter than ca. 10 m were measured with a 15-m telescoping height pole, while heights of taller trees were calculated by the Laser Impulse Rangefinder (Laser Technology Inc.) using angle–distance measurements.

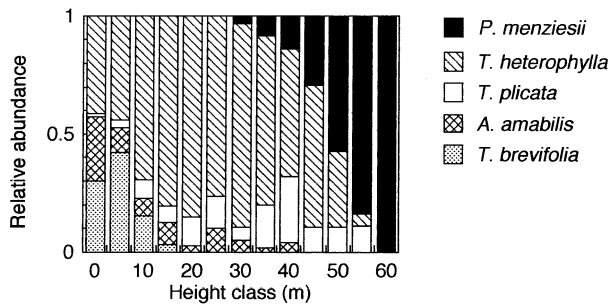
The main stem of each tree was examined for evidence of past damage, using binoculars and the Wind River Canopy Crane (Parker 1997) for tall trees. Damage was divided into five categories: (i) leaning of the main stem >15° from the vertical; (ii) forks and crooks in the main stem that reflect past breakage and resprouting; (iii) broken tops reflecting recent loss of the leader; (iv) top die-back or loss of foliage at the top of the tree; and (v) other damage which included infection of the leader by dwarf mistletoe (observed in *Tsuga heterophylla*), and significant branch loss due to abrasion from an adjacent tree fall. The categories are in order of dominant damage effects; a tree whose main stem leans and also forks was classified under the first category.

Trees growing under the closed canopy were examined for evidence of vertical suppression due to shading. A tree was considered suppressed when the terminal shoot could not be clearly distinguished (observed in *Thuja plicata* and *Tsuga heterophylla*) or had stunted growth and was lower in height than the lateral shoots (observed in *A. amabilis* and *Taxus brevifolia*). If a tree was both damaged and suppressed it was classified as damaged. Trees without evidence of damage or suppression were classified as “intact.”

Variability of diameter–height relationships

We fit the exponential generalization of the allometric equation (Arabatzis and Burkhardt 1992; Thomas 1996):

Fig. 1. Relative abundance of the five most abundant tree species by height class showing vertical stratification of species.



$$[1] \quad H = H_{\max}(1 - \exp(-aD^b))$$

to all trees of the five most abundant species (in order of abundance: *Tsuga heterophylla*, *Taxus brevifolia*, *A. amabilis*, *P. menziesii*, and *Thuja plicata*). a , b , and H_{\max} are nonnegative parameters estimated using the bounded nonlinear least squares regression function, NLREG, in S-Plus 4.5 (MathSoft). H_{\max} is the model estimate of maximum attainable height for the species. While this fitting procedure does not account for measurement error in the diameter observations, it does allow direct fitting of the nonlinear equation.

Uncertainty in the parameter estimates must be considered when comparing estimates among species. We, therefore, calculated 90 and 95% confidence intervals for each estimate of H_{\max} . For each regression, the statistical assumptions required for use of parametric confidence interval estimation, namely constant variance and normality of residuals, were visually investigated. Nonconstant residual variance can result in biased standard error estimates and, hence, biased confidence intervals. If these assumptions were violated, we calculated bias-corrected and accelerated bootstrap confidence intervals using 1000 bootstrap replicates (Huet et al. 1990), following the procedure in Lunneborg (1999).

Effects of damage and shading

The above procedure was repeated using only the intact trees of each species to examine the effects of damage and shading on the diameter–height relationship and on estimates of H_{\max} and its uncertainty. In addition, the frequency of damaged and suppressed trees was calculated for each species by height class to determine if these effects were random or size dependent. The relative distributions of each species' damaged and suppressed trees were compared with that of the intact trees using the Kolmogorov–Smirnov two-sample test (K–S test; Conover 1980). If the effects are random, then the height distributions of damaged and suppressed trees should not differ from that of the intact trees.

Current height-growth rates

Terminal shoot elongation rates were measured for intact, nonsuppressed trees of the four canopy-level species (22 *P. menziesii*, 44 *Tsuga heterophylla*, 17 *Thuja plicata*, and 9 *A. amabilis*), assuming that healthy, nonsuppressed trees of various sizes would represent the current maximum height-growth rates of the species in the stand. Trees were chosen that had a clearly distinguishable terminal shoot, had no evidence of damage or suppression to the main stem, and were not growing under any other tree. The terminal shoot of each tree was visited using the Wind River Canopy Crane at the end of the 1997 growing season. For *P. menziesii*, *Tsuga heterophylla*, and *A. amabilis*, distances between bud scars on the terminal shoot were measured for the past 3 years of growth (1995–1997) and averaged to obtain mean terminal shoot elongation rate per year. *Thuja plicata* produces no dis-

tinguishable bud scars, and determining past terminal shoot elongation can be difficult and possibly inaccurate (Parker and Johnson 1987). Therefore, terminal shoot elongation for the following year (1998) was measured by marking the base of the terminal shoot at the end of the 1997 growing season, and returning at the end of the following season to measure the increase in the distance from the mark to the tip of the terminal shoot.

Results

The relative abundance of the five most abundant species by 5-m height classes showed evidence of vertical stratification among species (Fig. 1). *Pseudotsuga menziesii* dominated in height classes above 50 m but was completely absent in height classes below 30 m. No regeneration of *P. menziesii* was observed in the stand. *Tsuga heterophylla* dominated in height classes from 10 to 45 m, *Thuja plicata* was found throughout all height classes, *A. amabilis* was found mainly in height classes below 45 m, and *Taxus brevifolia* was found only in height classes below 20 m.

Variability of diameter–height relationships

Equation 1 was well fit to the diameter–height relationship of all trees of *Thuja plicata*, *Tsuga heterophylla*, and *A. amabilis* ($r^2 > 0.90$; Fig. 2, all trees). However, the model failed to explain a large proportion of the height variation in *P. menziesii* and *Taxus brevifolia* ($r^2 = 0.524$ and 0.500 , respectively), both of which were observed over a relatively limited range of sizes compared with other species.

Residuals from the model fits tended to display increasing variance with both increasing diameter and with increasing predicted height. This biases the standard error estimates used in parametric confidence interval calculations. Therefore, bootstrap confidence intervals were calculated for each species' H_{\max} estimates. Both the 90% and 95% confidence intervals were calculated to reveal the possible skewness present in each species' bootstrap distributions of H_{\max} estimates (Fig. 3, all trees).

The uncertainty of the estimates varied widely. The greatest uncertainty was observed in *Taxus brevifolia*. Given the uncertainty associated with each estimate, we were only able to distinguish the H_{\max} estimate of *A. amabilis* as being lower than those of $\{P. menziesii, Tsuga heterophylla, \text{ and } Thuja plicata\}$.

Effects of damage and shading

Refitting eq. 1 to the diameter–height relationship for only the intact trees of each species improved the fit (increased r^2) for all species and consistently increased the predicted height for a given diameter (Fig. 2, intact only). Species differed, however, as to the trend in differences in predicted heights between the two regressions, suggesting that damage and shading have variable effects on predicted height estimates depending on the species and on tree size (Fig. 4). *Thuja plicata*, *A. amabilis*, and *Taxus brevifolia* all showed increasing differences in predicted heights with increasing diameter, although *A. amabilis* showed very small differences below 20 cm in diameter. While *Tsuga heterophylla* showed initially increasing differences in predicted heights with increasing diameter, the difference peaked around 60 cm in diameter and declined thereafter. Alternatively, *P. menziesii* showed decreasing difference between predicted

Fig. 2. Diameter–height relationships of the five most abundant tree species. Nonlinear least-squares regression fits of eq. 1 and H_{\max} estimates are shown for all trees >5 cm DBH (thin lines) and for intact trees (●) only (thick line). Damaged (x) and suppressed (▽) trees were excluded from the latter regression analysis.

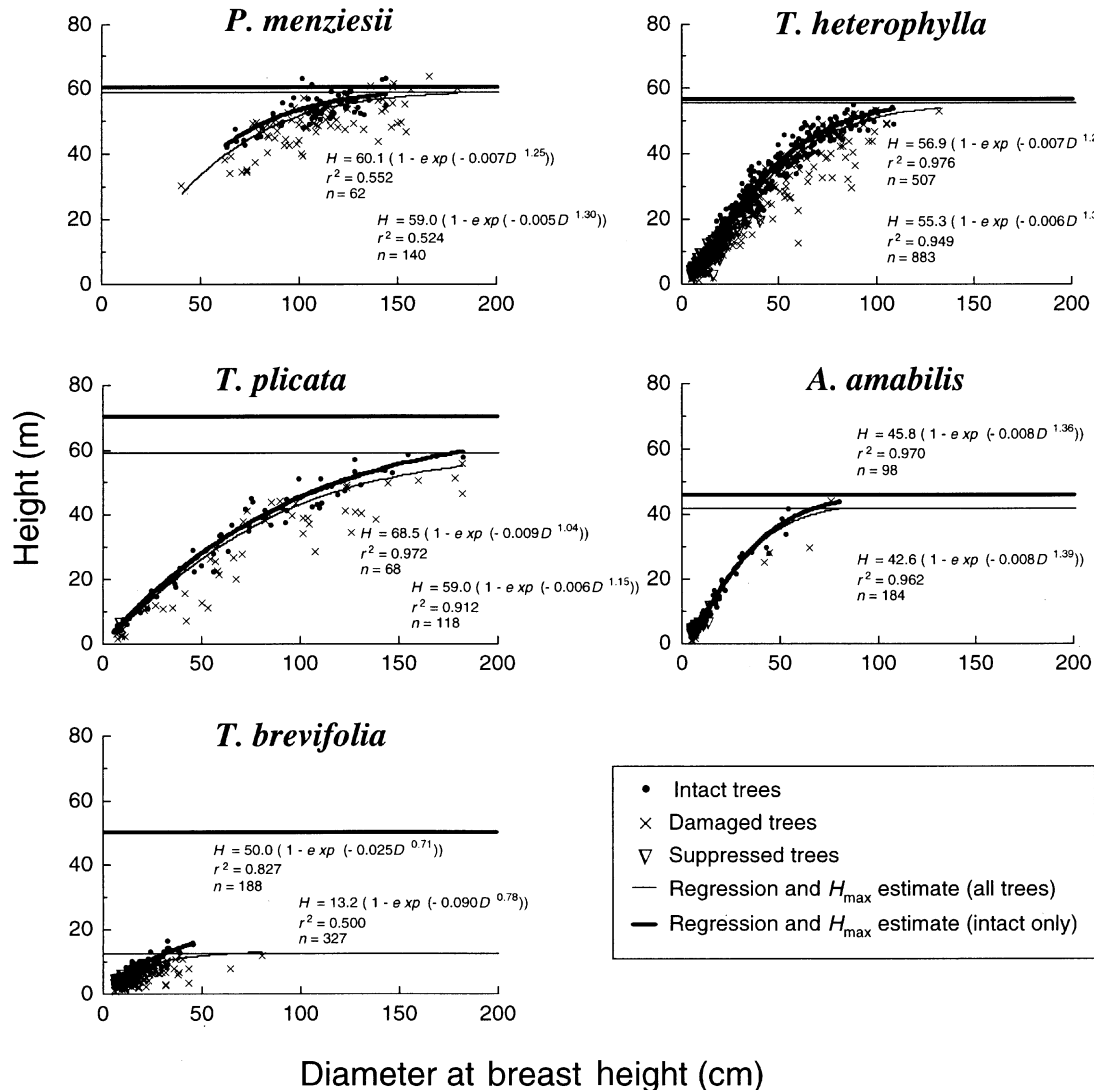
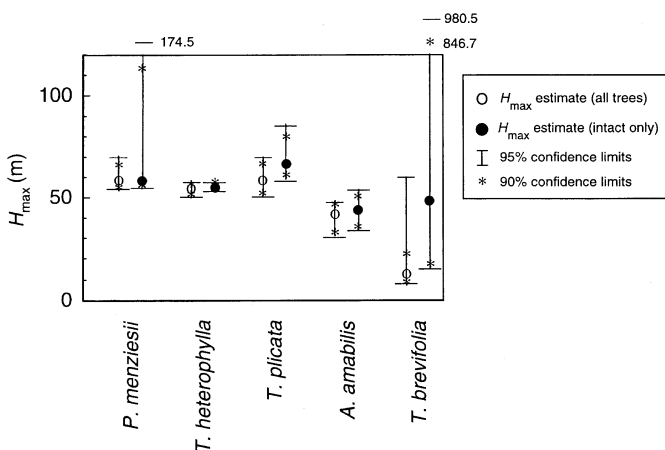


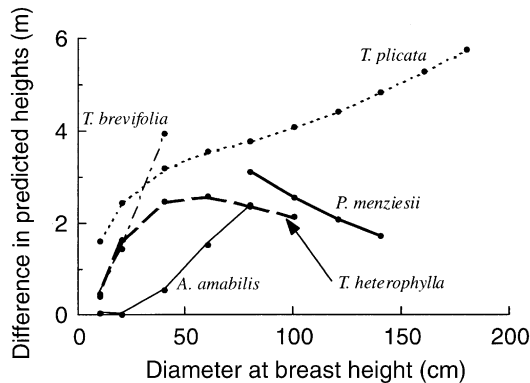
Fig. 3. Estimated H_{\max} for all trees >5 cm DBH (○) and for intact trees only (●) with 90% (*) and 95% (error bars) bootstrap confidence limits.



heights with increasing diameter. The greatest maximum differences in predicted heights between the two regressions were observed for *Thuja plicata* and *Taxus brevifolia* (5.78 and 3.99 m, respectively).

Estimates of H_{\max} also consistently increased after excluding damaged and suppressed trees (Fig. 3; intact only). The increases were considerable for *Thuja plicata* and *Taxus brevifolia* (9.5 m and 36.8 m, respectively), and relatively small for the other species. Except for *Tsuga heterophylla*, the uncertainty associated with each species' H_{\max} estimate increased. This partly resulted from the decreased sample sizes used. As a result, we were able to distinguish the H_{\max} estimate of *A. amabilis* as being lower than those of *P. menziesii* and *Thuja plicata*, and the estimate of *Tsuga heterophylla* as being lower than that of *Thuja plicata*. The unrealistically large value and large uncertainty in the H_{\max} estimate for *Taxus brevifolia* resulted from the fact that observations were limited to the smaller tree sizes, providing little information for estimating the model asymptote.

Fig. 4. The difference in predicted heights between the regression using all trees and the regression using intact trees only. Predicted heights were calculated at 20-cm intervals within the range of DBH observed for each species.



Main causes of damage and relative distribution of damage by height class differed among species (Fig. 5). For *P. menziesii*, resprouted or forked main stem and top die-back were the main causes of damage, over 85% of trees in the 30–40 m height class showed evidence of past breakage, and damage in general increased with decreasing height class (K–S test, $P < 0.01$). For *Tsuga heterophylla*, resprouted or forked main stem was the main cause of damage, and the relative height distribution of damaged trees could not be distinguished from that of the intact trees (K–S test, $P = 0.19$), suggesting that damage was not size dependent in this species. For *Thuja plicata*, resprouted or forked main stem and top die-back were the main causes of damage, over 35% of trees in the tallest height class (50–60 m) showed top die-back, but damage in general was not size dependent in this species (K–S test, $P = 0.58$). For *A. amabilis*, resprouted or forked main stem and top die-back were the main causes of damage, and damage in general increased with increasing height class (K–S test, $P = 0.06$). For *Taxus brevifolia*, leaning and resprouted or forked main stem were the main causes of damage. Leaning was more common in height classes below 4 m, while resprouted or forked main stem was more common in the 4- to 12-m height classes, and damage in general increased with decreasing height class (K–S test, $P = 0.01$). Suppression due to shading increased with decreasing height class in all species (K–S test, $P < 0.01$ for all species), suggesting, not unexpectedly, that the effects of shading on tree height was skewed toward shorter trees.

Current height-growth rates

Terminal shoot elongation rates of intact, nonsuppressed trees displayed a decreasing trend with increasing tree height for *P. menziesii* and *Thuja plicata* (Fig. 6, $r = -0.50$, $P = 0.02$, and $r = -0.52$, $P = 0.03$, respectively). Terminal shoot elongation rates ranged from 2.9 to 10.6 cm/year for *P. menziesii*, and 3.9 to 34.0 cm/year for *Thuja plicata*. Terminal shoot elongation rates showed an increasing and then decreasing trend with increasing tree height for *Tsuga heterophylla*. Minimum terminal shoot elongation rate for this species was 4.2 cm/year, and maximum terminal shoot elongation rate was 34.7 cm/year observed around 30 m in

Fig. 5. Relative frequency distributions by height class for each species' intact (open bars), damaged (hatched bars) and suppressed (solid bars) trees. Note different height classes for *Taxus brevifolia*.

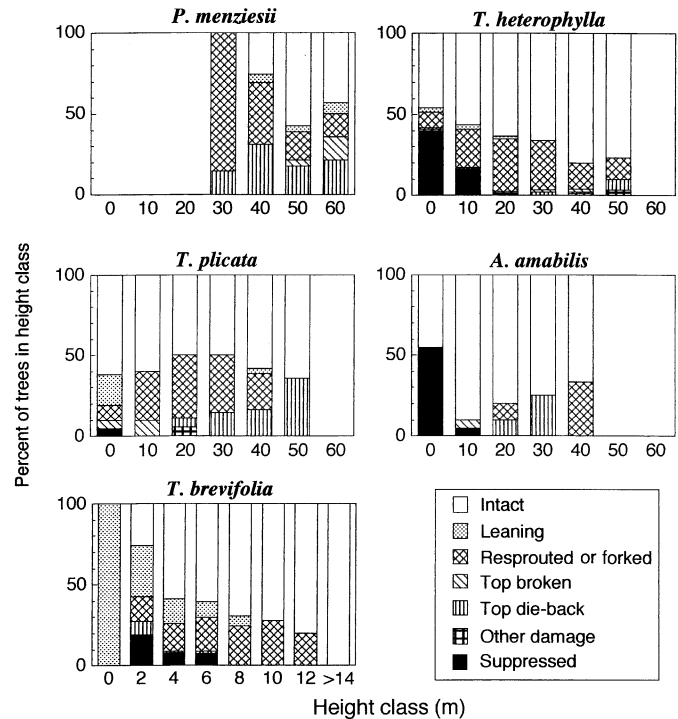
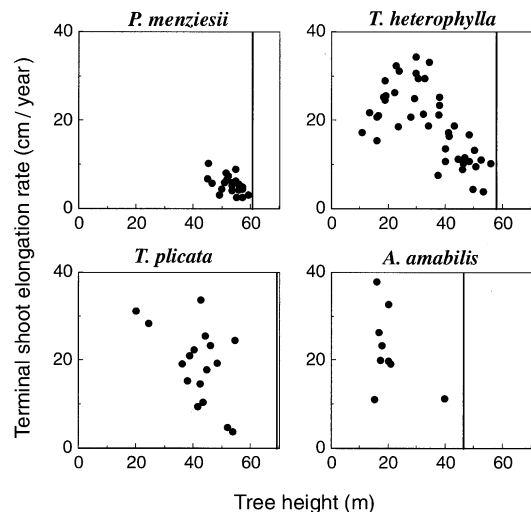


Fig. 6. The relationship between tree height and terminal shoot elongation of intact, nonsuppressed trees. Vertical lines are H_{\max} estimates from diameter–height relationships of intact trees.



tree height. No clear trend in terminal shoot elongation rates was found in *A. amabilis*.

For both *P. menziesii* and *Tsuga heterophylla*, terminal shoot elongation rates reached minimum values near the H_{\max} estimated from the diameter–height relationship of intact trees. While the tallest trees of *Thuja plicata* were still more than 10 m shorter than the estimated H_{\max} of 68.5 m, and their terminal shoot elongation rates were more variable. The wide range of terminal shoot elongation rates observed

above 40 m in height for *Thuja plicata* may be due to annual variation, as measurements were only made for 1 year's growth in this species.

Discussion

The amount of variation around the diameter–height regression and the degree of uncertainty in the H_{\max} estimates reflected differences among species in their relative abundance and size structure. The greatest variation and uncertainty were found for *P. menziesii*, a shade-intolerant, early successional species, whose size range was limited to large trees, and for *Taxus brevifolia*, an extremely shade-tolerant, late-successional species, whose size range was limited to small trees. Other species showed less variation and uncertainty as a result of their high abundance and wide range of tree sizes. Note that, while limited observation ranges need not translate into larger uncertainties in linear regression, it can have extreme impact in fitting nonlinear models (Draper and Smith 1981).

Species differences in variation and uncertainty associated with the diameter–height relationship reflected well the transitional succession stage of this stand. Differences among species in their relative abundance and size structure are characteristic of forests in transitional stages of succession (Stewart 1986b). As a consequence of the long life-spans of trees, species succession in the coniferous forests of the Pacific Northwest proceeds at a much slower rate than in other forest types where more rapid, seral replacement of species is observed (Spies et al. 1990). Sprugel (1991) pointed out that old-growth forests in this region are still at a transition stage in succession and have been so for centuries. It is likely that species composition and structure of the forest has changed over time and will continue to do so for the next several hundred years (DeBell and Franklin 1987; Franklin and DeBell 1988). Constant changes in growth conditions result in changes in species composition and differential development of individual trees, making it difficult to interpret diameter as a surrogate for tree age (Stewart 1986b). It is likely that the variation and uncertainty associated with diameter–height relationships of the species in this stand will continue to change over time and that such changes will have an effect on our ability to infer height-growth patterns from static diameter–height relationships.

Excluding damaged and suppressed trees from the static diameter–height relationship consistently increased predicted heights and H_{\max} estimates in all species. In addition, uncertainties around the H_{\max} estimates increased in all but one species. The largest increase in both predicted height and H_{\max} estimates were observed in *Thuja plicata* and *Taxus brevifolia*. The negative impact of environmental factors such as wind and snow damage leading to stem breakage and die-back have been reported for various forest types (Goto and Nitta 1990; Everham 1995; Nykanen et al. 1997). Shaded trees have been shown to have reduced growth in comparison with open-grown trees of the same species (Kohyama 1980; O'Connell and Kelty 1994). Of the total number of trees in this study, 44.1% showed evidence of damage or suppression of terminal shoot growth.

The growth of individual trees in Pacific Northwest forests is affected continuously by environmental and competi-

tive factors over their long life-span, resulting in widely varied growth patterns among individual trees and across species (Edmonds et al. 1993). We observed variable effects of damage and shading on predicted height estimates depending on the species and on tree size. Predominant damaging agents and size dependency of damage also differed among species. These results emphasized the importance of considering differential effects of various damaging agents and competitive interactions in studies of height-growth pattern.

Measurements of terminal shoot elongation rates revealed trends in current height-growth rates with tree height for *P. menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. Maximum terminal shoot elongation rate in *P. menziesii* was about one third that of *Tsuga heterophylla* and *Thuja plicata* and considerably lower than maximum height-growth rates reported by Ritchie and Hann (1986) for younger *P. menziesii* (18–137 years old, growth rates ranging from 0.67 cm/year to 1.10 cm/year). Values for minimum terminal shoot elongation rate were more constant across species. The decline in terminal shoot elongation rate with increasing height found for *P. menziesii* and *Thuja plicata*, and for *Tsuga heterophylla* above 30 m in height, may lead to reduced apical control and result in “multiple tops” or “flat tops,” characteristic of trees that are said to be near their maximum attainable height (Brown et al. 1967). Many of the intact, nonsuppressed trees of *Tsuga heterophylla* below 20 m in height were growing in gaps. Their low height-growth rates may be the result of low light conditions at the bottom of gaps. Coniferous forests have low gap-size ratios (deep, narrow gaps) and low incident angles of sunlight, resulting in low-light environments at the bottom of gaps (Canham et al. 1990; Spies et al. 1990; Easter and Spies 1994). Increased crown closure and low incident light have been shown to result in reduced rates of height growth (Ritchie and Hann 1986; Hann and Ritchie 1988). For short trees growing in gaps, height-growth rate is likely to increase as tree height increases, as a result of the positive feedback between improved light conditions and accumulation of foliage area. The changes in height-growth rate with tree height observed for *Tsuga heterophylla* may also characterize other shade-tolerant species in this stand, such as *A. amabilis*. Additional information on the three-dimensional position of these trees in the stand may provide a more accurate explanation of the height-growth patterns observed (Ritchie and Hann 1986; Hann and Ritchie 1988).

The results of the diameter–height relationships, effects of damage and shading and current height-growth rates were combined to infer future development of the forest canopy. High incidence of damage in height classes below 50 m and declining height-growth rates with increasing tree height suggested that the *P. menziesii* population as a whole may be near their maximum attainable height. The *Tsuga heterophylla* population had abundant understory trees that have the potential for further height growth as damage was not size dependent in this species. Current height-growth rates for *Tsuga heterophylla* also suggested that trees ranging in height from 20 to 35 m have the potential to grow considerably in height. As a result, the *Tsuga heterophylla* population as a whole has the potential to increase in height. The *Thuja plicata* population also had several understory trees that have the potential for further height growth as damage

was also not size dependent in this species. Although terminal shoot elongation rates for *Thuja plicata* showed a declining trend with increasing tree height, most trees were still far from the predicted maximum attainable height, and some tall trees showed relatively high height-growth rates. The *A. amabilis* population also had abundant understory trees. However, the maximum attainable height estimate for this species was more than 10 m shorter than the other canopy-level species. In addition, damage increased with increasing height class suggesting that damage may also be a factor limiting the maximum attainable height of the population. *Taxus brevifolia* is empirically known as an understory to lower canopy species with adult heights in this region usually ranging from 7 to 15 m (King 1991) with maximum height around 25 m (Sudworth 1967; Arno and Hammerly 1977). We also found that height growth of understory trees of this species may be limited, as damage increased with decreasing height class.

Our results suggest that the future development of the forest canopy would involve a slow invasion of the upper canopy by *Tsuga heterophylla* and *Thuja plicata*, while *A. amabilis* and *Taxus brevifolia* continue to survive in the lower canopy. However, at current height-growth rates of 4 to 5 cm/year for the tallest trees of *Tsuga heterophylla*, it would take them nearly 100 years to reach heights comparable with the dominant trees of *P. menziesii*. Although some of the tallest trees of *Thuja plicata* showed relatively high height-growth rates, this species had low relative abundance in the upper canopy. In their population dynamics study of the same area, Franklin and DeBell (1988) predicted that, if current mortality rates continue, *P. menziesii* would continue to persist in this forest for 755 more years. Given their long life-span of nearly 1200 years (Franklin and Hemstrom 1981), it is likely that *P. menziesii* will continue to maintain its dominant status in the upper canopy for at least another century.

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