Branch and foliage morphological plasticity in old-growth *Thuja plicata*

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Summary   At the Wind River Canopy Crane Facility in southeastern Washington State, USA, we examined phenotypic variation between upper- and lower-canopy branches of old-growth *Thuja plicata* J. Donn ex D. Don (western red cedar). Lower-canopy branches were longer, sprouted fewer daughter branches per unit stem length and were more horizontal than upper-canopy branches. *Thuja plicata* holds its foliage in fronds, and these had less projected area per unit mass, measured by specific frond area, and less overlap, measured by silhouette to projected area ratio ($SPAR_{max}$), in the lower canopy than in the upper canopy. The value of $SPAR_{max}$, used as an indicator of sun and shade foliage in needle-bearing species, did not differ greatly between upper- and lower-canopy branches. We suggest that branching patterns, as well as frond structure, are important components of morphological plasticity in *T. plicata*. Our results imply that branches of old-growth *T. plicata* trees have a guerilla growth pattern, responding to changes in solar irradiance in a localized manner.

Keywords: branch morphology, foliage angle, shoot silhouette area, SPAR, STAR, western red cedar.

Introduction

Thuja plicata J. Donn ex D. Don, the only native *Thuja* species in western North America, is widespread throughout Pacific Northwest coast forests with an additional isolated interior range (Minore 1990, Trevor and Burton 1999). Although it is commercially and ecologically important, its physiology and growth have not been researched extensively (DeBell and Gartner 1997, Trevor and Burton 1999). Individuals can live 800 to 2000 years and the species is present at all stages of succession (Minore 1990). The ability to develop at each stage is attributed to *T. plicata*'s high shade tolerance (Minore 1990), which is the reason for its classification as a climax species (Minore 1990, Feller and Klinka 1998), especially at slightly dry sites (Carter and Klinka 1992). Besides its high shade tolerance, unique characteristics of *T. plicata* among old-growth species of the Pacific Northwest include an indeterminate growth pattern (Parker and Johnson 1987) and frond or fern-like foliage (Parker and Johnson 1987) made up of small scale-like leaves typical of the Cupressceae family (Laubenfels 1953).

Classification of *T. plicata* as a climax species leads to the question of how the species acclimates to the variable light environment of Pacific Northwest forests (Parker 1997). Morphological plasticity in response to light environment has been reported for *T. plicata* seedlings (Krasowski and Owens 1991, Carter and Klinka 1992, Wang et al. 1994, Khan et al. 2000) and young trees (Parker and Johnson 1987, Barclay 2001). Responses to shading include increased height to caliper ratio, increased leaf area index (Wang et al. 1994), decreased terminal growth of the main axis relative to lateral growth (Parker and Johnson 1987), decreased shoot to root mass, decreased dry mass (Khan et al. 2000) and more horizontal leaf angles (Barclay 2001). In each of these studies, the degree of response relative to other conifer species was attributed to *T. plicata*'s designation as a shade-tolerant species. However, except in Barclay's (2001) study, morphological plasticity in *T. plicata* was measured only in seedlings and young trees. It is possible that *T. plicata*, like *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Ishii and Ford 2002), exhibits variation in these responses with age. Also, possible plasticity throughout the crowns of large trees has not been considered.

Studies of old-growth needle-bearing conifer species have shown morphological plasticity with respect to light environment in individual trees (Carter and Smith 1985, Leverenz and Hinckley 1990, Sprugel et al. 1996, Stenberg et al. 1998, 1999). Examples of needle morphological plasticity in a single tree include increased needle length, decreased needle thickness (*Abies amabilis* Dougl. ex Forbes, Sprugel et al. 1996), decreased needle width, increased specific needle area (*Picea sitchensis* (Bong.) Carr., Ford 1982; *Picea abies* (L.) Karst., Stenberg et al. 1999; *Pseudotsuga menziesii*, Ishii et al. 2002) and increased silhouette area to needle area (*Picea engelmannii* Parry ex Engelm., *Abies lasiocarpa* (Hook.) Nutt. and *Pinus contorta* Engelm., Carter and Smith 1985; *Picea abies*, Stenberg et al. 1999) in needles grown in shade compared to needles grown in sun. The silhouette to area ratio is referred to as STAR or SPAR, depending on whether total foliage surface area or projected area is taken as the denominator, respectively (Stenberg 1998). A higher value of STAR, as

found in shade needles, can indicate less needle overlap and is associated with reduced needle packing (Carter and Smith 1985). There is debate as to whether needle structure is solely adapted to light capture or additionally reflects adaptation to the severity of winter weather (Sprugel 1989, Smith and Brewer 1994). Studies have shown that artificial shading can induce some of the morphological and physiological changes associated with shade foliage (*Abies amabilis*, Brooks et al. 1994). Based on these studies of foliage structure, measurements of forest productivity (Leverenz and Hinckley 1990) and studies of needle biochemistry, Leverenz (1996) hypothesized that needle architectural variation, as estimated by STAR, is more important than variation in leaf biochemistry in determining variation in growth and productivity among species. Leverenz emphasized the relative importance of architectural variation even though studies had found definite acclimation responses in needle biochemistry (Leverenz and Jarvis 1979, Brooks et al. 1994).

The unique foliage and bifurcating branch structure of *T. plicata* suggest that several characteristics may be subject to morphological plasticity in response to variation in solar irradiance. The most consistent morphological plastic responses of plants to low light availability predicted by the foraging model (Hutching and de Kroon 1994) are internode elongation and reduced branching. Because internode elongation generally takes place without a corresponding increase in foliage mass, the prediction of the foraging model is similar to that of the cost-benefit model used in Stenberg et al.'s (1999) analysis of needle structure acclimation. The cost-benefit model predicts that shade foliage limits its tissue mass relative to leaf area. Otherwise the cost of tissue would outweigh its benefit in a sunfleck light environment. Thus, the foraging model can be used to predict branching patterns and the cost-benefit model to predict foliage morphology.

To determine whether there was morphological plasticity in response to light environment in old-growth *T. plicata*, we divided our study into two parts: analysis of branching patterns and analysis of foliage structure. We predicted that responses would be evident in both parts of the study, perhaps following the predictions of the foraging and cost-benefit models. To study branching patterns, we measured lengths, intervals between branches, foliage abundance and accumulation in branches of multiple orders. We predicted that these measurements would follow the predictions of the foraging model in some combination, resulting in a relatively higher concentration of foliage in favorable light conditions. We also measured branch angles and presence of epicormic branches as these quantities can also indicate foraging. Branch angles in young *T. plicata* are more horizontal in low light conditions (Barclay 2001) and as Sprugel et al. (1991) and studies of asymmetrical canopy structure (Umeki 1997, Brission 2001) emphasize, foraging in large trees occurs in three dimensions. Epicormic branches are a reiterative structure in some trees (*Pseudotsuga menziesii*, Ishii and Ford 2001), implying that the ability to produce them is an opportunistic characteristic (Hallé et al. 1978).

To examine foliage structure, we measured specific frond area (SFA) and silhouette to projected area ratio (SPAR). We predicted that these measurements would be similar to those for needle-bearing conifers, with both measurements increasing in the lower, more shaded, section of the canopy.

Materials and methods

Basic structure of T. plicata

Thuja plicata has a bifurcating branch system with multiple orders (Figures 1a and 1b). New branches are formed one at a time, on alternating sides of each terminal bud. A series of branches of more or less equal length is produced rather than whorls of branches as in other coniferous species (Parker and Johnson 1987). Branches would occur in a single plane were it not for the bending and twisting that occurs during growth (Parker and Johnson 1987). The over-wintering bud does not contain fully preformed shoots. At each order, there is some photosynthetic tissue, and in a centrifugal ordering system, the lower orders (i.e., closest to the main stem axis) have the least photosynthetic tissue (Briand et al. 1992). The photosynthetic tissue consists of small scale-like leaves (Minore 1990). These fall into Laubenfels's (1953) Type III grouping, where Cupressaceae is further classified as having flattened lateral leaves in the mature branches that differ from facial leaves. *Thuja plicata*'s leaves are cupressoid scale leaves with the adaxial surface predominantly adpressed to the shoot. Leaves are in pairs at right angles to each other and stem leaves are usually in whorls of four leaves and occasionally in whorls of three leaves (Trevor and Burton 1999). This structure makes it potentially inaccurate to determine age without destructive sampling, especially when examining individuals in a single season as was done in this study. It also makes it potentially inaccurate to use branching order to measure age.

Our objective was to compare functionally equivalent terminal ends of main branches in three contexts: within the upper canopy, within the lower canopy and between these two sections of the canopy. Therefore, we developed a branch nomenclature (Figures 1a and 1b) similar to the centrifugal ordering system used by Briand et al. (1992) for *Thuja occidentalis* L. Unlike the young trees studied by Briand et al. (1992), however, old-growth *T. plicata* has large terminal branches in the lower canopy that can be anywhere from two to six orders away from the trunk. Accordingly, the branch typing used in this study was centrifugal but with a lateral branch, or main axis, as Branch Type I instead of the trunk used by Briand et al. (1992). For upper-canopy branches, Branch Type I was always the lateral branch extending from the bole. For lower-canopy branches, Branch Type I was two or three orders away from the bole but always the lowest-order branch associated with a terminal end.

An alternative branch nomenclature is provided by the Stahler method, in which orders are numbered in the direction of the bole instead of away from it, so the lateral branches have similar orders. In our study, this method would have led to comparisons within the canopy positions between branches
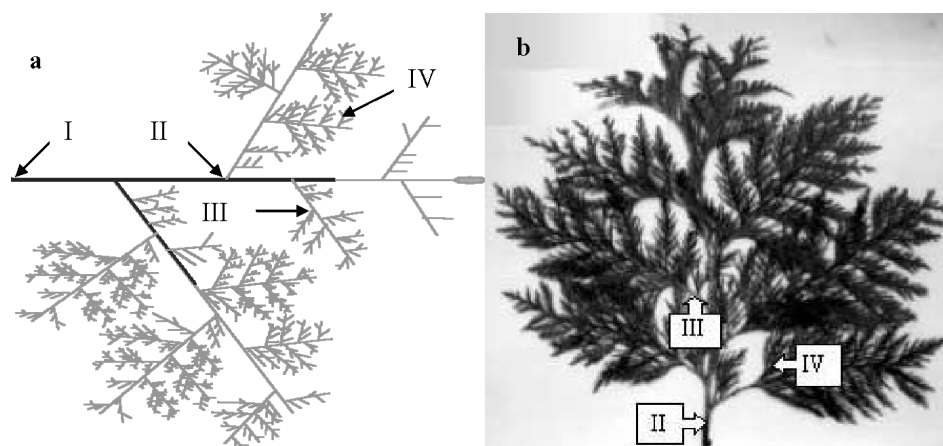
Figure 1. *Thuja plicata*'s branching structure. Branch Types in *T. plicata* were ordered centrifugally, with Branch Type I representing a lateral branch main axis. The labels in (a) the illustration (not drawn to scale) and (b) the photograph are positioned at the branching points of each of the branch types.

that were not functional equivalents. This is because, as time passes, a given shoot of *T. plicata* accumulates additional orders of branching. However, at any given age of the original shoot, it appears that the newest shoots are at the highest orders. Therefore, when examining a large set of branches, counting backward from the most terminal branch would mean that a main axis would be assigned a different order depending on the shoot from which one started (Figure 1a).

With our nomenclature, Branch Types I to V are similar to Briand et al.'s (1992) orders II to VI. Green foliage is found mainly on Branch Types III to V, with a substantial amount on Branch Type II and a small amount at the tip of Branch Type I. The nomenclature does not imply an exact foliage status nor does it predict size, although all the individual Branch Type IIs tended to be smaller than the Branch Type Is from which they branched and Type IIIs were smaller than Type IIs, and so forth.

Study site

The study was conducted at the Thorton T. Munger Research Natural Area of the Wind River Experimental Forest in Gifford Pinchot National Forest, an old-growth forest in southwestern Washington State (45°49′ N, 121°57′ W; altitude 355 m). The stand is about 500 years old and has experienced little human disturbance (Franklin and DeBell 1988). It is dominated by *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) in terms of basal area. *Thuja plicata*, *Abies amabilis* (Pacific silver fir) and *Taxus brevifolia* Nutt. (Pacific yew) are also abundant (Franklin and DeBell 1988). The old-growth trees at the site were accessed with an 87-m tall Biebherr construction crane operated by the Wind River Canopy Crane Research Facility (WRCCRF).

Sampling

We chose three old-growth *T. plicata* trees of similar height (mean height 47.4 m) with abundant new and 1-year-old cones. Measurements were made mainly between mid-July and mid-August 2000, and in summer 2001. On each tree, we examined six Branch Type Is, three from the upper canopy

(2.6–3.1 m from the tree top) and three from the lower canopy (19.5–32.1 m from the tree top) (Table 1). All upper-canopy branches were in the estimated bright zone of the crane circle determined by Parker (1997) based on photosynthetically active radiation and UV-B. Access to lower-canopy branches was restricted to those on the outer parts of the crowns. One of the lower-canopy branches in Tree 1 was located in what Parker (1997) designated the dim zone, whereas the rest of the lower-canopy branches were in Parker's estimated transition zone. Radiation at different wavelengths was measured at each sampled branch, as discussed below.

Nondestructive sampling was limited by crane time. Six to 10 Branch Type IIs were measured on the 18 selected Branch Type Is. The first Branch Type II measured was Number 14 from the tip of the Branch Type I and then every third branch in the direction of the tip was examined with substitutions made

Table 1. Branch Type I locations. The three study trees were of similar height (mean height 47.4 m) and on each tree, we studied six Branch Type Is. Branch heights are approximations based on the canopy crane's location at the branch and are accurate to within 1 m. The distances from treetops are based on tree heights gathered by the WRCCRF.

Tree number	Branch number	Canopy position	Height (m)	Distance from treetop (m)
1 (*Thuja* 137)	1–3	Upper	45.7	2.8
	1	Lower	21.5	27.0
	2	Lower	16.4	32.1
	3	Lower	11.8	26.7
2 (*Thuja* 3096)	1–3	Upper	42.9	2.6
	1	Lower	20.1	25.4
	2	Lower	20.1	25.4
	3	Lower	15.7	29.8
3 (*Thuja* 3228)	1–3	Upper	45.2	3.1
	1	Lower	26.5	21.8
	2	Lower	27.5	20.8
	3	Lower	28.8	19.5

for damaged branches. A total of 64 upper-canopy Branch Type IIs and 53 lower-canopy Branch Type IIs were measured. The Thorton T. Munger Natural Research Area restricts the amount of material that may be sampled destructively. To ensure that we had enough foliage for analysis, we excised five upper-canopy and four lower-canopy Branch Type IIs of similar length (mean length 34.5 ± 1.9 cm), rather than similarly numbered from the tip. On each clipped Branch Type II, all Branch Type IIIs were measured with the destructive and nondestructive protocols described below. Additionally, on one clipped Branch Type II from the upper canopy and one from the lower canopy, we examined one and three Branch Type IIIs, respectively, measuring all the Branch Type IVs to explore the possibility of preserved patterns throughout the orders of branching.

Nondestructive measurements

On each Branch Type II sampled, we measured distances between attachment points and lengths of all Branch Type IIIs. We measured angles to the horizon of each Branch Type II, and to account for branch curvature (noted by Barclay 2001), we took three measurements: one at the point of connection to the Branch Type I, one at the estimated midpoint, and one at the tip. The angle measurement protocol was repeated in summer 2001 for Branch Type IIIs on Branch Type IIs on one upper-canopy and one lower-canopy Branch Type I per tree. Each branch was chosen at random from those already measured at that station and four to six Branch Type IIs were measured on each Branch Type I. Additional observations on Branch Type IIs included amount of deviation from the alternating pattern of branch development, as well as presence of cones and epicormics. Epicormics are shoots that originate from dormant preventitious buds and secondary daughter buds that proliferate from them (Kozlowski 1971, Ishii and Ford 2001). For the nondestructive measurement sample set for each branch type, we compared branches that were similarly numbered from the tip of the previous order.

Destructive measurements

Silhouette to projected area ratio (SPAR) and specific frond area (SFA) were measured for all Branch Type IIIs. Silhouettes were measured with a Cohu solid-state camera with a Nikon 28-mm lens and analyzed with the Optimus 3.01 image analysis system. The middle of the Branch Type II was pinned to a rotator and silhouette area was measured starting at 0° to the camera and then in increments of 30° (cf. Stenberg et al. 1998). Unlike the procedure used by Stenberg et al. (1998), our measurement at 0° was taken when the shoot was parallel to the direction of view (camera) with the tip pointed toward the lens. At 90° the branch axis was perpendicular to the direction of view, and at 180° the branch axis was again parallel to the direction of view, but now with the point of connection pointed toward the lens.

The measurement at 90°, $SPAR_{90}$, was used as the maximum value for the rotator measurements. The value of $SPAR_{90}$ was similar to the maximum values reported in other studies (e.g., Stenberg et al. 1999). In our study, $SPAR_{max}$ was calculated with an additional measure of silhouette area where the Branch Type II was placed on a flat surface without flattening (cf. plane of the leaf; Barclay 2001). We used this silhouette measurement because of the flatness of the frond and the floppiness of the branches pinned to the rotator.

Projected frond area was measured with the camera and image analysis system used to determine SPAR. To determine foliage area, the upper side of a planar frond's surface area was measured as described by Ishii et al. (2002) (cf. Leverenz and Hinckley 1990). Foliage was weighed after drying to constant mass at 70 °C. The results from the destructive sample set were compared on the basis of branches of similar length (mean length 34.5 ± 1.9 cm). That is, the excised upper-canopy Branch Type IIs were farther away from the tip of Branch Type I than the lower-canopy Branch Type IIs (see the section Sampling above).

Light measurements

Our objective was to estimate differences between sampled branches in the quantity of visible radiation intercepted and its red/far red ratio, both of which affect morphology (Gilbert et. 2001). Radiation at 400, 500, 600, 660 and 730 nm was measured with an LI-1800 (Li-Cor, Lincoln, NE). First, measurements were made above each tree by cycling through the wavelengths for three replicates. Then measurements were made at the three sample branches at one canopy position on one tree, again cycling through the wavelengths three times for each branch. Above-tree measurements were repeated, followed by measurements at another branch in a different tree and canopy position. Measurements above trees were used to calculate changes in the diurnal radiation pattern. Reduction ratios (branch irradiation/above-canopy irradiation) for the sample branches were calculated based on a time-corrected mean for above-canopy radiation. Red/far red ratios were calculated by comparing the 660 nm measurements to the 730 nm measurements at each of the branches and reduction ratios were calculated in the same manner for these comparisons.

Data analysis

In general, mean values between upper- and lower-canopy measurements were compared by paired *t*-tests ($n = 3$; *P*-value = P_t). However, because the power may be low for an effective test, we also performed an unpaired test in which all the data were analyzed as replicates ($n \approx 100–2000$ depending on branch type; *P*-value = P_f). In cases where there was a possibility of between-tree differences at both canopy positions, an analysis of variance (ANOVA; *P*-value = *P*) was used to determine whether there was a within-canopy-position tree effect in addition to a possible canopy position effect; i.e., upper canopy versus lower canopy.

Results

Branching patterns

Branch Type II lengths   Branch Type IIs were longer in the lower canopy than in the upper canopy (Table 2a). There was

no significant within-canopy-position tree effect (upper canopy and lower canopy $P > 0.10$). In the lower and upper canopy, length of Branch Type IIs increased linearly with number from the tip of Branch Type I (Figures 2a and 3). Thus, foliated shoots extended at a constant rate relative to each other and the rate was greater in the lower canopy than in the upper canopy (Figure 2a).

Branch Type II foliage abundance and foliage accumulation
Upper-canopy Branch Type IIs had more Branch Type III branches per unit length, i.e., greater foliage abundance, than lower-canopy Branch Type IIs (Table 2b). In addition, ANOVA revealed a significant within-canopy-position tree effect for both the lower-canopy and upper-canopy Branch IIs (upper canopy $P < 0.001$; lower canopy $P < 0.006$) for foliage abundance.

For Branch Type IIs, the relationship between length and amount of Type III branches that they supported was linear (Figure 2b). Furthermore, the slope of the relationship was greater in the upper canopy than in the lower canopy. Linearity was preserved when length on the *x*-axis was replaced by amount of Branch Type II from the tip of its parent Type I. However, there was no significant difference in these slopes, called foliage accumulation slopes, between the upper and lower canopy (Figure 2c) for the destructively sampled data set. Nonetheless, examination of the foliage accumulation slopes of the 18 Branch Type IIs indicated that the slope tended to be greater in the lower canopy than in the upper canopy, as seen in the significant difference between the mean foliage accumulation slopes (Table 2c).

Branch Type II angles　Upper-canopy Branch Type IIs had significantly greater angles (mean angle 123.8°) from the vertical than lower-canopy Branch Type IIs (mean angle 114.0°) when measurements at the node, midpoint and tip were averaged (Table 3). There were similar differences (upper > lower) for measurements at points along the branch (Table 3), except for measurements at the node (Table 3). This indicates that,

Table 2. Upper- and lower-canopy means and associated statistics for each characteristic studied. The intervals are 95% confidence intervals. The fourth column contains *P*-values for an unpaired *t*-test with individual branches as replicates; numbers in parenthesis are the degrees of freedom (df). The last column contains paired *t*-test results with mean tree values as replicates ($n = 3$, because the test pairs the upper- and lower-canopy results on each of the three trees). Significant values ($P < 0.05$) are in bold.

| Characteristic	Upper mean	Lower mean	P_f (df)	P_t ($n = 3$)
a. Branch Type II lengths (cm)	23.07 ± 2.22	61.01 ± 10.25	**< 0.001** (100)	**0.013**
b. Branch Type II foliage abundance (amount of IIIs/length of II (cm))	0.814 ± 0.064	0.402 ± 0.031	**< 0.001** (100)	0.066
c. Branch Type II foliage accumulation regression slopes	2.19 ± 0.251	3.18 ± 0.650	**0.026** (14)	0.091
d. Branch Type III lengths (from Branch Type IIs of similar numbers) (cm)	6.38 ± 0.248	14.23 ± 0.62	**< 0.001** (2075)	**0.002**
e. Branch Type IIIs lengths	11.91 ± 1.39	12.36 ± 1.53	0.679 (121)	0.145
f. Branch Type III intervals (from Branch Type IIs of similar numbers) (cm)	1.44 ± 0.12	3.22 ± 0.18	**< 0.001** (2203)	**< 0.001**
g. Branch Type III intervals (from Branch Type IIs of similar lengths) (cm)	1.78 ± 0.16	2.75 ± 0.256	**< 0.001** (111)	**0.008**
h. Branch Type III foliage abundance (from Branch Type IIs of similar lengths) (amount of IVs/length of III (cm))	1.66 ± 0.11	1.47 ± 0.142	**0.041** (109)	**0.025**
i. Branch Type IV lengths (cm)	4.94 ± 0.74	6.04 ± 0.66	0.076 (90)	
j. Branch Type IV increments (cm)	0.80 ± 0.13	0.98 ± 0.08	**0.022** (90)	
k. Branch Type III total foliage area (cm^2)	534.3 ± 587.5	506.8 ± 333.5	0.9334 (4)	
l. Branch Type III SFA (cm^2 g^{-1})	34.77 ± 0.073	50.76 ± 3.04	**< 0.001** (107)	0.091
m. Branch Type III SPAR$_{90}$	0.768 ± 0.035	0.821 ± 0.043	0.070 (72)	0.398
n. Branch Type III SPAR$_{max}$	0.879 ± 0.017	0.917 ± 0.018	**0.003** (56)	0.122
o. Branch Type IV SFA (cm^2 g^{-1})	39.92 ± 3.86	50.56 ± 1.67	**< 0.001** (68)	
p. Branch Type IV SPAR$_{90}$	0.901 ± 0.024	0.849 ± 0.018	**0.008** (62)	
q. Branch Type IV SPAR$_{max}$	0.928 ± 0.056	0.914 ± 0.012	0.450 (62)	
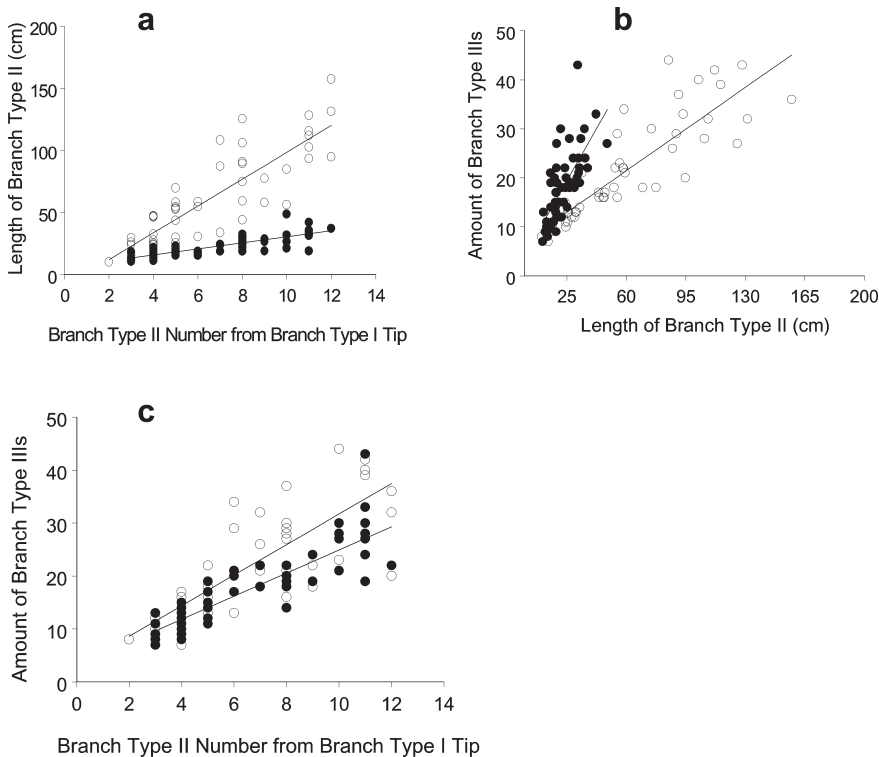
Figure 2. Branching patterns for Branch Type IIs. Upper canopy Branch Type IIs (●) are compared with lower-canopy Branch Type IIs (○) in the relationships between (a) length of Branch Type II and Branch Type II number from the Branch Type I tip (upper $r^2 = 0.67$; lower $r^2 = 0.73$), (b) amount of Branch Type IIIs and length of Branch Type II (upper $r^2 = 0.50$; lower $r^2 = 0.74$), and (c) amount of Branch Type IIIs and Branch Type II number from the tip of Branch Type I (upper $r^2 = 0.73$; lower $r^2 = 0.65$). All relationships are linear ($r^2 > 0.05$) and linear regression estimates of the slopes are (a) upper = 2.43 ± 0.47, lower = 10.79 ± 1.92; (b) upper = 0.61 ± 0.17, lower = 0.24 ± 0.04; and (c) upper = 2.18 ± 0.38, lower = 2.88 ± 0.62.

compared with lower-canopy Branch Type IIs, upper-canopy Branch Type IIs drooped more, but not because of differences in the angle at the point of attachment to Branch Type I.

Branch Type III lengths Similar to Branch Type IIs, lower-canopy Branch Type IIIs were longer than upper-canopy Branch Type IIIs on Branch Type IIs with the same number (numbers 3–14 from the tip of the parent Branch Type I) (Table 2d). However, there were some differences between the patterns at the two orders. First, ANOVA showed a significant within-canopy-position tree effect for Branch Type III lengths in the upper and lower canopy (upper canopy $P < 0.001$; lower canopy $P = 0.002$). Mean Branch Type III lengths in the upper canopy of Trees 1 to 3 were 4.7, 6.7 and 7.7 cm, respectively, and corresponding mean lengths in the lower canopy were 13.5, 16.1 and 16.1 cm. Second, the linear relationship between Branch Type II length and its number from the tip of its parent Branch Type I, which was observed in all 18 Branch Type Is, was found in just more than half of Branch Type IIIs on Branch
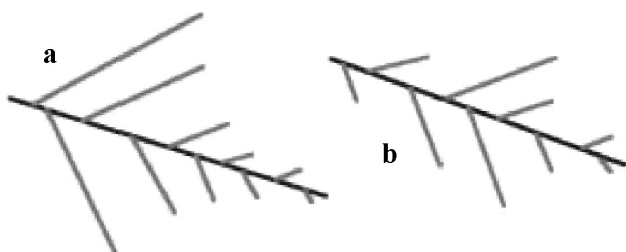
Type IIs (upper canopy = 60.9%; lower canopy = 63.4%). The Branch Type IIs for which the Branch Type III length showed a nonlinear relationship generally followed a pattern in which the lengths were shorter at both the tip and the point of attachment of the Branch Type II, with maximum lengths in the middle of the branch (Figure 3). Within a Branch Type I, the Branch Type IIs with a linear length pattern of Branch Type IIIs tended to be those farther away from the tip of the Branch Type I, followed by a switch to a nonlinear length pattern closer to the tip of the Branch Type I. Eight out of nine of the upper-canopy Branch Type Is and seven out of nine of the lower-canopy Branch Type Is exhibited this switch, indicating similarity between canopy positions.

In several cases, there was cycling of alternating Branch Type III lengths (Figure 4). That is, one side of the branch had longer branches than the other side. Cycling occurred in 41% of the lower-canopy Branch Type IIs, but in only 13% of the upper-canopy Branch Type IIs.

A comparison of destructively sampled Branch Type IIIs taken from Branch Type IIs of similar length showed no significant difference in Branch Type III lengths between the upper and lower canopy (Table 2e). However, to obtain Branch Type IIs of similar length (mean length 34.5 ± 1.9 cm), those sampled from the upper canopy had higher branch numbers than those sampled from the lower canopy, which is in agreement with the Branch Type II length results (Table 2a, Figure 2a) obtained from the nondestructive measurements. Therefore, Branch Type IIs at the same branch number from the tip of the Branch Type I had longer daughter branches in the lower canopy than in the upper canopy. However, when Branch Type IIs

Figure 3. Illustration of linear (a) versus nonlinear (b) length patterns in Branch Type IIIs (not drawn to scale).

Table 3. Upper- and lower-canopy mean declination angles and associated statistics. The intervals are 95% confidence intervals. The fourth column contains *P*-values for an unpaired *t*-test with individual branches as replicates; numbers in parenthesis are the degrees of freedom (df). The last column contains paired *t*-test results with mean tree values as replicates (*n* = 3, because the test pairs the upper- and lower-canopy results on each of the three trees). Angles were measured at the node or point of attachment, midpoint and tip and averaged for each branch. For Branch Type IIs, with the exception of the measurement at the node, the lower-canopy branches were more horizontal than the upper-canopy branches. This was also true at the node of the Branch Type IIIs, but the difference was not significant for the mean at this order. A dash indicates that no data were available.

	Upper-canopy mean	Lower-canopy mean	P_f (df)	P_t ($n = 3$)
Branch Type II				
Node	87.6 ± 5.9	94.2 ± 8.9	0.231 (90)	0.510
Midpoint	123.4 ± 8.6	99.4 ± 9.7	< 0.001 (89)	–
Tip	159.9 ± 3.6	142.4 ± 8.1	0.005 (53)	0.008
Mean	123.8 ± 3.6	114.0 ± 6.3	0.014 (90)	0.164
Branch Type III				
Node	136.7 ± 3.6	128.5 ± 4.5	0.005 (484)	0.375
Mean	144.2 ± 3.0	143.9 ± 3.9	0.657 (467)	0.616

of the same length (but different branch number) were compared between upper and lower canopy there was no difference in length of the Branch Type IIIs they supported.

Intervals between Branch Type IIIs The distance between Branch Type IIIs along their parent Branch Type II was significantly greater for lower-canopy branches than for upper-canopy branches, when comparing mean Branch Type III intervals on Branch Type IIs of similar branch number and when comparing Branch Type IIs of similar length (Table 2f and 2g). However, the difference in mean values of Branch Type III intervals between the upper and lower canopy was greater when

comparing similarly numbered Branch Type IIs (1.78 cm) than when comparing Branch Type IIs of similar length (0.97 cm). There was a significant within-canopy-position tree effect in the upper canopy ($P < 0.0001$), but not in the lower canopy ($P > 0.10$). The upper-canopy mean intervals for Trees 1 to 3 were 0.98, 1.44 and 1.46 cm, respectively.

Foliage abundance on Branch Type IIIs When comparing Branch Type IIIs on Branch Type IIs of similar length, the Branch Type IIIs from the upper canopy had more Branch Type IVs per unit length than Branch Type IIIs from the lower canopy (Table 2h).
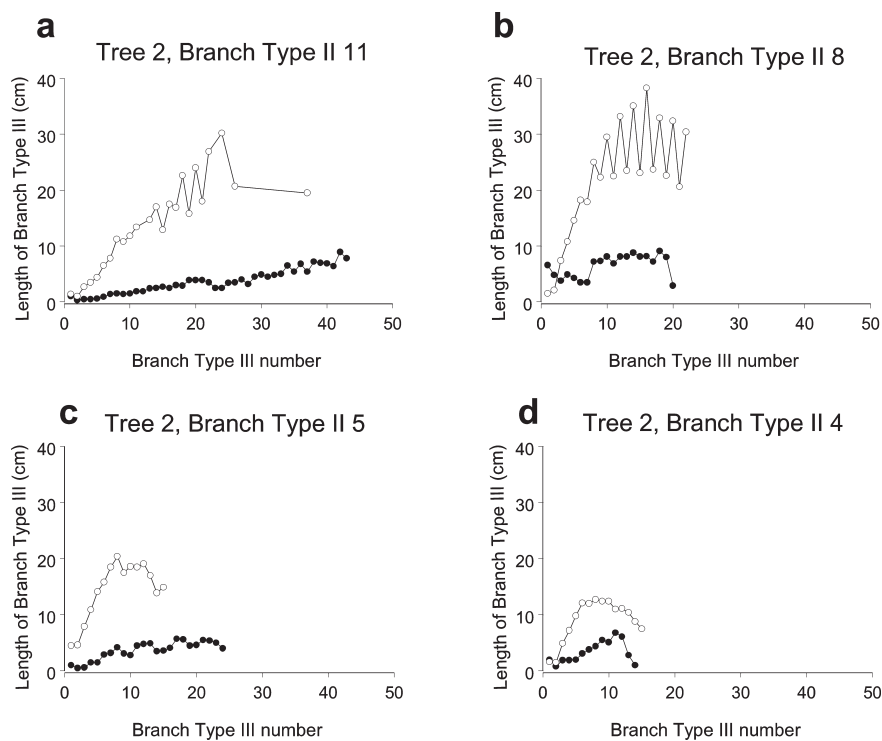
Figure 4. Eight examples of upper-canopy (●) and lower-canopy (○) Branch Type III lengths versus branch number from the tip of their parent Branch Type II. These Branch Type IIs are on two different Branch Type Is: upper- and lower-canopy branches of the same tree. As the branch number decreases, the Branch Type II becomes closer to the tip of the Branch Type I. Note the progression from linear to nonlinear length patterns (Figures 5a–5d) as the Branch Type II becomes closer to the tip of its parent Branch Type I. Also note the cycling, which is when one side of the branch has longer branches than the other side. This is most evident in the lower-canopy Branch Type II 8.

Branch Type III angles Unlike Branch Type IIs, which drooped more in the upper canopy than in the lower canopy, Branch Type III mean angles did not differ significantly between the upper and lower canopy (Table 3). However, at the node where the Branch Type III was joined to the Branch Type II, upper-canopy Branch Type IIIs were angled more toward the ground than lower-canopy Branch Type IIIs (Table 3). Also, Branch Type III angles cycled in a manner similar to Branch Type III lengths. Of the 33 Branch Type IIs for which Branch Type III angles were measured, seven out of 17 upper-canopy Branch Type IIs showed some cycling in Branch Type III mean angles, whereas in the lower canopy, nine out of 16 did. On 10 of the branches with angle cycling, length cycling was also present. On eight of these 10 branches the side with greater declination was the side with greater lengths. Observations indicate that this pattern is repeated throughout the tree, where the branch appears to be twisted to one side and the side that it twists toward has longer Branch Type IIIs.

Branch Type IVs The intervals between Branch Type IVs on Branch Type IIIs were greater in lower-canopy branches than in upper-canopy branches (Table 2j), indicating a possible concordance in patterns of spacing differences between the upper and lower canopy for all branch types. However, there was no significant difference in lengths of the Branch Type IVs between the upper and lower canopy (Table 2i).

Epicormic branches Epicormic branches of *T. plicata* appear more horizontal, or squat, than regular branches and are present at the nodes of branches, even though that branch may have died or fallen from the tree (Figure 5). Epicormic branches were present on Branch Type Is in the upper and lower canopy, as well as on lower-canopy Branch Type IIs. Number of epicormic branches on lower-canopy Branch Type IIs increased with Branch Type II length (Figure 6; $r^2 = 0.85$).

Figure 5. Epicormic shoots are produced from suppressed epicormic buds on older parent branches. In *Thuja plicata* they form at the node of normal branches whether they are alive or dead. The first of these is seen in this picture in the lower left hand corner and the rest are nodes where the Branch Type II has died.
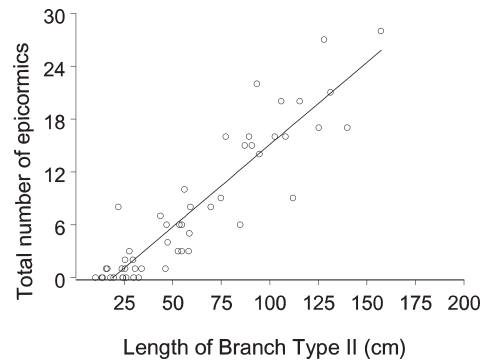

Figure 6. Total number of epicormics on lower canopy Branch Type IIs versus Branch Type II length. Total epicormics refers to epicormics at the node of the Branch Type II and at the nodes of dead or living Branch Type IIIs. Only lower-canopy Branch Type II data is given because there were no epicormics on Branch Type IIs on the upper-canopy Branch Type Is that we measured. This may have been related to length, for the Branch Type IIs were longer in the lower canopy (Table 2a) and, as this graph demonstrates, there is a linear relationship between length and number of epicormics ($r^2 = 0.85$).

Shorter Branch Type IIs in the upper canopy (Table 2a) may have contributed to the absence of epicormic branches in the upper-canopy Branch Type IIs. In the lower canopy, there was also a linear relationship between number of epicormic branches on Branch Type IIs and number of Branch Type IIIs, though the relationship was weaker than for length ($r^2 = 0.59$).

Frond structure

To compare similarly foliated branches, the following comparisons were made between Branch Type IIs of similar length (mean length = 34.5 ± 1.9 cm) and their daughter Branch Type IIIs.

Branch Type II total foliage area Total foliage area on Branch Type IIs did not differ significantly between the upper and lower canopy. However, the variation at each location was large (Table 2k).

Specific frond area The relationship between foliage area and mass was linear in both lower- and upper-canopy Branch Type IIIs. However, lower-canopy Branch Type IIIs had a greater rate of production of foliage area as foliage mass increased (Figure 7). Furthermore, SFAs were 1.5 times higher in lower-canopy Branch Type IIIs than in upper-canopy Branch Type IIIs. However, the difference was significant only when Branch Type IIIs rather than trees were used as replicates (Table 2l). The ANOVA indicated that SFA values varied significantly between individual trees for lower-canopy Branch Type IIIs ($P < 0.001$) but not for upper-canopy Branch Type IIIs. Lower-canopy tree means were 58.1, 50.3 and 41.6 $cm^2\,g^{-1}$ for Trees 1 to 3, respectively.

Lower-canopy Branch Type IVs had higher mean SFA values (Table 2) than upper-canopy Branch Type IVs, but the difference was smaller than for Branch Type IIIs (Table 2l). Mean SFA was slightly higher for upper-canopy Branch Type IVs than for upper-canopy Branch Type IIIs, but there was no sig-
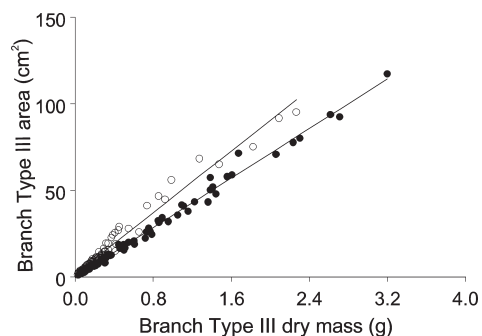
Figure 7. The relationship between Branch Type III foliage area and mass was linear for both upper canopy (●) and lower canopy (○) Branch Type IIs (upper $r^2 = 0.99$; lower $r^2 = 0.97$). The linear regression estimates of the slope are upper = 35.72 ± 1.614 and lower = 44.51 ± 0.6391.

nificant difference between these branch types for lower-canopy branches.

Measurement of SPAR Estimates of $SPAR_{90}$ for Branch Type IIIs were consistently the maximum value for measurements made with the angle rotator (Figure 8). There was no significant difference in $SPAR_{90}$ between upper- and lower-canopy Branch Type IIIs (Table 2m). However, $SPAR_{max}$ values indicated that there was more foliage overlap in the lower-canopy Branch Type IIIs than in the upper-canopy Branch Type IIIs when tested with branches as replicates (Table 2n). Additionally, there was a significant tree effect in the lower-canopy Branch Type IIIs for both $SPAR_{90}$ and $SPAR_{max}$ ($P < 0.001$). Tree 1 had higher $SPAR_{90}$ and $SPAR_{max}$ (less foliage overlap) than Trees 2 and 3, and the Branch Type II sampled from this tree was the lowest branch measured in this study (Branch 3). No significant within-canopy-position tree effect was seen in the upper-canopy Branch Type IIIs for either measurement ($P > 0.100$). The overlap estimators, $SPAR_{90}$ and $SPAR_{max}$, for Branch Type IVs yielded opposite results compared with those for Branch Type IIIs. There was no difference in mean $SPAR_{max}$ values, but the $SPAR_{90}$ values suggested that there was more overlap in the upper-canopy Branch Type IVs than in the lower-canopy Branch Type IVs (Table 2p and 2q), which may have been related to the floppiness of the branches pinned to the rotator.

Light measurements

Only Tree 2 showed clear differences in reduction ratio (branch irradiation/open irradiation) between upper- and lower-canopy Branch Type Is at all wavelengths (Figure 9), even though on average Tree 2 did not have the lowest branches (Table 1). The tree with the lowest measured branches (Tree 1) appeared to have relatively lower reduction ratios for its lower-canopy Branch Type Is compared with its

Figure 9. Reduction ratios for each tree at selected wavelengths. Reduction ratios are the ratio of irradiance measured at the branch to the "open" measurement, taken above the canopy. Symbols: ● = upper branch 1; ■ = upper branch 2; ▲ = upper branch 3; ○ = lower branch 1; □ = lower branch 2; and △ = lower branch 3.
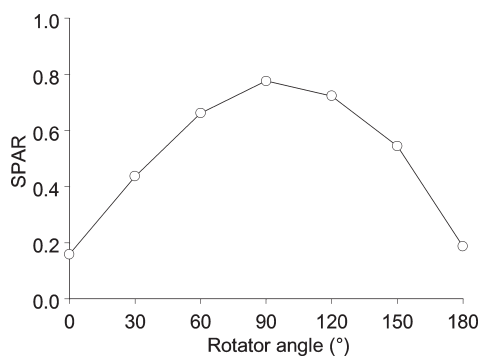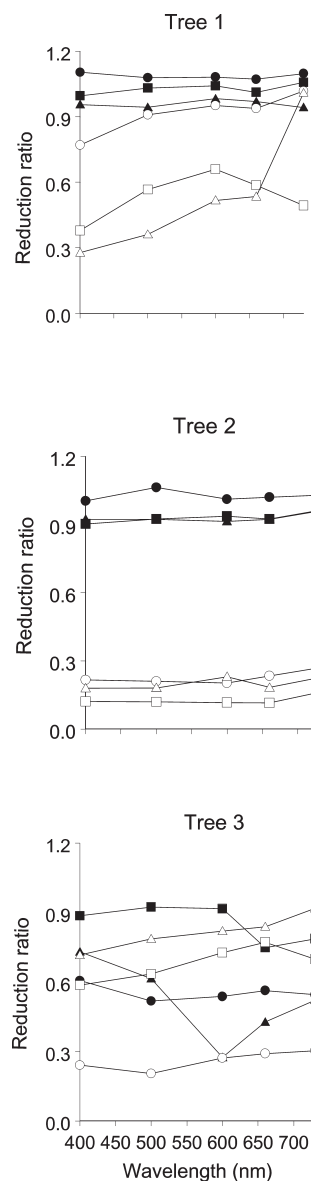

Figure 8. Example of Branch Type III silhouette to projected area ratio (SPAR) versus angle on rotator. Graphs like this were plotted for every set of Branch Type III SPAR measurements. All except a few of these graphs had a maximum at 90°.

Table 4. Red/far red reduction ratio and conditions at each of the Branch Type Is. The red/far red ratio is the ratio of irradiances at 600 and 730 nm. The differences in reduction ratios between the upper- and lower-canopy Branch Type Is were small, which may be related to the light conditions described in the third column.

Branch Type I number	Reduction ratio	Conditions
Tree 1 (Thuja 137)		
Upper-canopy branch 1	0.9710	Bright sun
Upper-canopy branch 2	0.9500	Bright sun
Upper-canopy branch 3	1.0212	Bright sun
Lower-canopy branch 1	0.9169	Bright sun, in gap
Lower-canopy branch 2	2.6013	Partial shade/sunflecks
Lower-canopy branch 3	0.5470	Shade/sunflecks
Tree 2 (Thuja 3096)		
Upper-canopy branch 1	0.9919	Partially cloudy
Upper-canopy branch 2	0.9601	Partially cloudy
Upper-canopy branch 3	0.9629	Partially cloudy
Lower-canopy branch 1	0.8703	Partially cloudy
Lower-canopy branch 2	0.7147	Partially cloudy
Lower-canopy branch 3	0.8111	Partially cloudy
Tree 3 (Thuja 3228)		
Upper-canopy branch 1	0.9982	Partial shade
Upper-canopy branch 2	0.9036	Partial shade
Upper-canopy branch 3	0.8173	Partial shade
Lower-canopy branch 1	0.8167	Partial shade/sunflecks
Lower-canopy branch 2	1.1900	Light partial shade
Lower-canopy branch 3	0.9055	Direct sun, in gap

upper-canopy Branch Type Is. The difference in radiation between the upper and lower canopy was not as large as expected. However, the lowest individual branch on Tree 1, Branch 3, had relatively lower reduction ratios except at 730 nm. This branch was the only branch of the 18 Branch Type Is that was located in the WRCCRF dim zone as designated by Parker (1997). The red/far red reduction ratios showed similar patterns to the wavelength reduction ratios and variable light environments were observed in the lower canopy (Table 4).

Discussion

Although the reduction in radiation in the lower canopy of *T. plicata* was less than might have been expected in a forest plantation (Leverenz and Hinckley 1990, Stenberg et al. 1999), the characteristics seen in *T. plicata* fit well into the framework of the foraging and cost-benefit models for light adaptation. The foraging model applies to the branching pattern. Lower-canopy branches in their variable, and at times limited, light environment must forage for light differently than upper-canopy branches. The cost-benefit model helps explain the difference in foliage structure between the upper and lower canopy. It predicts how lower-canopy foliage develops more photosynthetically efficient morphological structures than upper-canopy foliage.

Application of the foraging model

The predictions of the foraging model apply to *T. plicata*'s morphological plasticity in branching structure (summarized in Table 5). The model predicts two responses to increased irradiance: reduced spacer length and increased branching intensity. These responses result in a concentration of foliage in those areas with more light to maximize light interception (Hutchings and de Kroon 1994). The opposite response in low light environments makes it possible for plants to forage for light. Elements of the foraging model are seen in *T. plicata* seedlings; they demonstrate an opportunistic growth pattern, where the shoots are capable of rapid responses to short-term environmental changes (Wang et al. 1994). The first predicted response of decreased spacer length in more favorable light conditions corresponds to our interval results for multiple orders (Table 2f and 2j) and types of comparison (Table 2g). Similarly, *T. plicata* seedlings respond to shade conditions by increased height through an increase in mean length and not number of stem units (Krasowski and Owens 1991). The foliage abundance estimates of Branch Type IIs and Branch Type IIIs (Table 2b and 2h) indicated a greater branching intensity in the upper canopy, which concurs with the second prediction of the foraging model.

We found other characteristics associated with canopy position that are not an explicit part of Hutchings and de Kroon's (1994) description of the foraging model but that fit implications of the model (Table 5). For example, to forage for light in the varied light environment of the lower canopy, branches might grow longer to increase the individual frond's unshaded surface area per unit foliage. Additionally, greater lengths may reduce the cost of creating greater total foliage surface area per branch, because it is probably more costly for a branch to produce new foliated branches than to develop longer branches in an existing structure. However, where there were significant differences between the upper and lower canopy in the interval and foliage abundance measures in Branch Type IIIs on Branch Type IIs of similar length, there was no significant canopy position effect on the length of Branch Type IIIs (Table 2i). Thus taken altogether, the differences between the upper and lower canopy suggest that branch structure is probably not simply a result of overall differences in length of parent branches or branch age.

Branch angle results (Table 3) can be interpreted in terms of the foraging model for three dimensions. Angles of lower-canopy Branch Type IIs were more horizontal than those of upper-canopy Branch Type IIs, which probably increases light capture per unit foliage area in the reduced light environment of the lower canopy. Overall, the difference in Branch Type II angles between the upper and lower canopy is caused by differences in the midpoint and tip angles (Table 3), and it is these angles that could change as the branch grows longer. There were no differences at the node (Table 3); however, for Branch Type IIIs there was a difference between the upper and lower canopy at the point of connection (Table 3), but not in mean angle. A more detailed analysis of the development of branch curvature is required to clarify the relationship between length

Table 5. Predictive frameworks for *Thuja plicata*. The foraging model is described by Hutching and de Kroon (1994) and the cost-benefit model was derived from the study by Stenberg et al. (1998). The former model describes *T. plicata*'s response to light conditions in terms of branching patterns, whereas the latter model predicts foliage structure.

Framework and overarching theory	Predictions for favorable light conditions	Concordance between results and predictions in the upper canopy	Additional results that potentially follow the framework's overarching theory but are not included under predictions
Foraging model predicts increased foliage concentration in favorable light conditions	Decreased internode length	Smaller mean intervals at all orders studied	More vertical angles in the upper canopy
	Increased branching intensity	Greater branching intensity at all orders studied	Greater lengths of lower-canopy branches
			Possible reiteration units of mini-trees and epicormic branches in the lower canopy
Cost-benefit model predicts limited expenditure on foliage structure in unfavorable light conditions	Decreased area per unit mass (specific area)	Lower mean SFA at all orders studied	Increased difference between canopy positions in frond area with increased mass
	Decreased silhouette to projected area ratio (SPAR)	Lower mean $SPAR_{max}$ but relatively small canopy position effect and slightly varied results	

differences and branch angles between the upper and lower canopy for Branch Type IIs and IIIs. Nonetheless, changes in branch angle over time suggest continuing morphological plasticity over time in order to maintain branch angles as branch structure changes. Our branch angle results complement the study of Barclay (2001), who found that leaf angles of *T. plicata* were less randomly arranged than those of other conifers (e.g., *Abies grandis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Picea sitchensis*, *Pinus contorta*) and became less horizontal in the upper portion of taller trees (~50 years old). It appears from our study that branch angles in old-
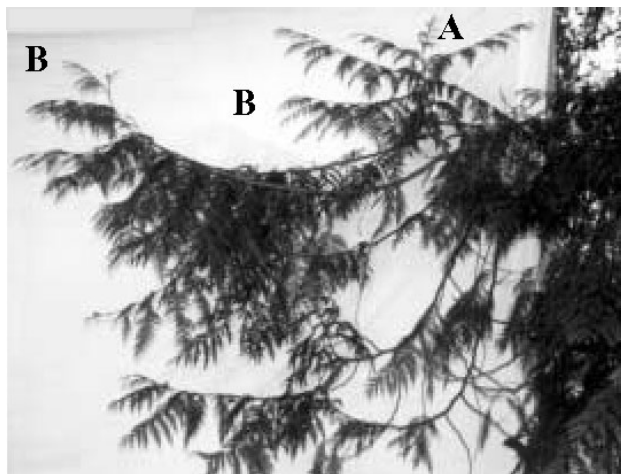

Figure 10. Photograph of a "mini-tree," a reiteration unit in the lower canopy where the main axis curves up, such that at the tip it is vertical to the horizon (A) and growth is reduced relative to its daughter branches (B). The daughter branches, then, can forage for local light resources by laterally extending in multiple directions.

growth *T. plicata* are adapted to catch light from gaps in the canopy at a more nearly vertical direction, as they are in the younger trees Barclay (2001) measured.

The different lengths of Branch Type IIIs on opposite sides of the parent Branch Type II are also an indication of opportunistic growth patterns (Figure 4). This cycling was more frequent in the lower canopy than in the upper canopy, and was often accompanied by variation in angle. This may be a localized response to light, with a branch twisted to and producing more photosynthetic tissue on its least shaded side.

Another morphological change that we observed in the lower canopy was the development of "mini-trees" (Figure 10), a possible reiteration unit. This branching pattern occurs when the main axis curves up, such that at the tip it is vertical to the horizon, and the daughter branches come off as lateral branches around this axis. The growth of this "main" axis is much reduced relative to its daughter branches. The mini-tree arrangement increases the probability of sun exposure, because the daughter branches forage for sunflecks locally in multiple directions. Reiteration units are a form of opportunistic architecture and are responses to damage, environmental stress or supraoptimal conditions (Hallé et al. 1978).

Application of the cost-benefit model

We examined foliage structure by using a cost-benefit model that predicts a limit on the cost of tissue development in low-light conditions (Table 5). Greater SFA (Branch Type IV) in the lower canopy (Table 2l and 2o) means a reduced cost of light interception per unit mass (Stenberg 1999). The greater rate of production of foliage mass relative to foliage area in lower-canopy Branch Type IIIs (Figure 7) reflects this reduced cost. Upper- and lower-canopy Branch Type IIIs of the same

leaf area not only have different masses depending on their position in the canopy, but as branches gain foliage area, the difference between the foliage masses of the canopy positions increases. Thus, when comparing a lower- and upper-canopy Branch Type III, we predict that, at given foliage area, the larger that area, the greater the difference in SFA between the upper and lower canopy.

High SPAR estimates indicate less foliage overlap (Carter and Smith 1985) as was found for Branch Type IIIs in the lower canopy (Table 2n). Less overlap potentially reduces costs of tissue development in a low-light environment by using the space available effectively for increased light capture (Stenberg et al. 1998).

Although $SPAR_{max}$ is not the usual way to measure silhouette to area ratio, it may be the most accurate for this species because of the lack of rigidity of the branches (Barclay 2001). Traditionally, rotator measurements are used to quantify light exposure, because foliage can intercept light from multiple angles (Stenberg et al. 1999). The angles are not meant to represent true positioning to the tree, so given the planar nature of *T. plicata* foliage, it is reasonable to use $STAR_{max}$ in making comparisons between canopy positions. We note that the opposite difference was found for $STAR_{90}$ of Branch Type IVs (Table 2p), where $STAR_{90}$ values were significantly less in the lower canopy than in the upper canopy. This was probably a result of the confounding factor of floppiness, and indicates that the important morphological variation is how Branch Type IVs are arranged to form Branch Type IIIs. As seen in the $STAR_{max}$ results (Table 2q), the Branch Type IVs in both the upper and lower canopy had little overlap when laid flat, probably because the lengths of their daughter foliage, Branch Type V, were too short to overlap (Figure 1b). Thus, their silhouette area accounts for about 90% of their overall area in both the upper- and lower-canopy Branch Type IVs.

In addition to the large differences in various measures between the upper and lower canopy, there were smaller but statistically significant differences between trees within canopy positions. The ANOVA indicated differences in Branch Type III intervals between branches and lengths, with Tree 1 having the longest lengths in the upper and lower canopy, and also the greatest intervals in the upper canopy compared with Trees 2 and 3.

However, differences between trees were largely overshadowed by differences between the upper and lower canopy, which were highly significant in both types of *t*-test. Within-canopy-position tree effects of SFA and SPAR in the lower canopy were of interest because paired *t*-tests indicated no significance difference between the upper and lower canopy. The lower canopy of Tree 1, whose samples were deepest in the canopy, had the largest mean values of SFA, $STAR_{90}$ and $SPAR_{max}$ and the lowest red/far red ratio (Table 4). These within-canopy-position tree effects suggest the possibility of a reaction norm (Sterns 1989), in which there is not one type of foliage structure in the lower canopy in juxtaposition to one in the upper canopy, but rather a continuum between the two positions, and possibly between light environments. Continuums

in specific needle area and silhouette to area ratios have been seen in conifers such as *Abies amabilis* (Stenberg et al. 1998) and *Picea abies* (Stenberg et al. 1999), and there is a direct relationship between these measures and loss of canopy openness.

Silhouette to area ratios are one of the ways sun and shade needles have been defined in recent literature, and we found some significant differences in SPAR. The differences in SPAR between canopy positions were not large when compared with responses in other conifers (Table 6). This may be because radiation differences between the upper- and lower-canopy branches that we accessed from the canopy crane were not as large as differences in other studies. If the tree effect indicates a plastic continuum of SPAR values within the lower canopy, the difference in SPAR that we observed between the upper and lower canopy may not be as large as is possible for *T. plicata*, because the lower branches that we studied were not the most shaded within this old-growth canopy (Figure 8) and therefore did not have the highest SPAR values. Alternatively, the small difference in SPAR values between the upper and lower canopy could be a result of the alternately branched, planar structure, which makes it less likely for foliage overlap to occur within a branch, especially in the upper-canopy Branch IIIs where their daughter branches are shorter.

We conclude that for studies of within-canopy plasticity for species with frond-like foliage, branching structure must be considered in addition to foliage overlap. From only SPAR re-

Table 6. Values of silhouette to total area ratio ($STAR_{max}$) or silhouette to projected area ratio ($SPAR_{max}$) in sun and shade for various conifer species.

Species	Sun	Shade
Picea engelmanni[1]	0.12 ± 0.03	0.18 ± 0.03
Abies lasiocarpa[1]	0.15 ± 0.04	0.31 ± 0.05
Pinus contorta[1]	0.13 ± 0.02	0.14 ± 0.03
Sequoia sempervirens[2]		0.98 ± 0.03
Abies grandis[2]		0.99 ± 0.04
Pseudotsuga menziesii[2]		0.87 ± 0.08
Abies amabilis[2,3]		0.87 ± 0.1
Tsuga heterophylla[2]		0.85 ± 0.02
Picea abies[2,3]		0.84 ± 0.01
Picea orientalis[2]		0.82 ± 0.08
Picea sitchensis[2]		0.74 ± 0.08
Abies procera[2]		0.73 ± 0.06
Abies lasiocarpa[2]		0.67 ± 0.08
Pinus sylvestris[2,4]		0.54 ± 0.05
Pinus contorta[2]		0.50 ± 0.1

[1] Maximum $STAR_{max}$ = 0.5 (denominator was total surface area) (Carter and Smith 1985).
[2] Measurement = R_{max}; maximum = 1.0; denominator was projected area (similar to SPAR) (Leverenz and Hinckley 1990).
[3] Known to have decreased $STAR_{max}$ or $SPAR_{max}$ with canopy openness (STAR, *Abies amabilis*, Stenberg et al. 1998; SPAR, *Picea abies*, Stenberg et al. 1999).
[4] Known to have decreased STAR with canopy openness (Stenberg et al. 2001).

sults we might have concluded that *T. plicata* showed little plasticity between the upper and lower canopy. However, the measurements of length, distance between branches and angle suggest that *T. plicata* has a guerilla-like growth pattern (Harper 1985) with less apical dominance than other conifer species of the *Pinaceae*. The guerilla growth pattern, where apical meristems can have localized responses, enables grass species to exploit patchy environments more efficiently (Schmid 1985, Sutherland and Stillman 1988). As Sprugel et al. (1991) suggested, there is a need to explore foraging in the three-dimensional space in which trees vie for light. Branches of conifer species show different types and degrees of plasticity in response to competition (Cannell et al. 1984) and neighbors (Franco 1986), and studies of asymmetrical canopy structure consider those facts (Umeki 1997, Brission 2001).

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