

## Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and western hemlock canopy

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**Summary** We examined needle-level light response of photosynthesis across a vertical light gradient within 45–55-m-tall western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees growing in a 400–500-year-old mixed species stand. We determined: (1) whether light-saturated photosynthetic rates, light compensation points, and respiration rates varied from the upper to the lower canopy, and (2) if light-saturated photosynthetic rates, light compensation points, and respiration rates varied between Douglas-fir and western hemlock. Over a 25-m gradient from the canopy top to the lower canopy, mean light-saturated photosynthetic rates, light compensation points, and respiration rates declined in overstory Douglas-fir and western hemlock needles, paralleling a 65% decline in the mean daily photosynthetic photon flux density (PPFD). At the canopy top, increasing light-saturated photosynthetic rates relative to lower canopy needles increased carbon uptake at high PPFD. In the lower canopy, reduced respiration rates relative to upper canopy needles increased carbon uptake at low PPFD by reducing the light compensation point. At all canopy positions, western hemlock had lower mean light-saturated photosynthetic rates, light compensation points and respiration rates than Douglas-fir. As a result, western hemlock had higher net photosynthetic rates at low PPFD, but lower net photosynthetic rates at high PPFD compared with Douglas-fir.

**Keywords:** carbon assimilation, leaf irradiance, light compensation point, photosynthesis, *Pseudotsuga menziesii*, respiration, *Tsuga heterophylla*.

### Introduction

Light utilization is a primary factor determining plant ecosystem productivity (Monteith 1977, Jarvis and Leverenz 1983, Medlyn 1998), and is a function of light interception by the plant canopy and the response of photosynthesis to irradiance. Increasing leaf mass per unit ground area increases light interception by the canopy and is positively correlated with net primary productivity across a range of ecosystems (Webb et al.

1983). However, the cumulative interception of light through the canopy causes light limitation of photosynthesis in the lower canopy. To maximize canopy-level carbon uptake, changes in photosynthetic light response that maximize leaf-level carbon uptake under prevailing light conditions should occur through the tree crown (Givnish 1988). In conifers, acclimation to prevailing light conditions involves physiological as well as morphological changes at both the needle and shoot levels, including changes in needle dimensions and specific leaf area (e.g., Tucker and Emmingham 1977, Jordan and Smith 1993, Niinemets and Kull 1995a, Sprugel et al. 1996), and the distribution and orientation of needles on shoots (e.g., Carter and Smith 1985, Oker-Blom 1985, Wang et al. 1990, Niinemets and Kull 1995b).

In contrast to the relatively extensive literature on morphological acclimation to light availability in conifer crowns, few studies have examined needle-level changes in photosynthetic light response through a mixed species canopy. Studies on leaf-level light acclimation in the crowns of broad-leaved species have shown higher light-saturated photosynthetic rates, light compensation points, and respiration rates in leaves grown in sun rather than in shade (Hollinger 1989, Marek et al. 1989, Ellsworth and Reich 1993, Bassow and Bazzaz 1998). Similar shoot-level changes in photosynthetic light response have been observed within the crowns of overstory conifers grown in monoculture (Leverenz and Jarvis 1979, Troeng and Linder 1982, Kull and Koppel 1987, Brooks et al. 1996). One important difference between shoot-level measurements and needle- or leaf-level measurements is that photosynthetic rates of conifer shoots are strongly affected by shoot morphology (Carter and Smith 1985, Leverenz and Hinckley 1990, Oker-Blom et al. 1992, Wang and Jarvis 1993). In particular, conifer shoot morphology alters the convexity of the light response curve, affecting net photosynthetic rates at low and intermediate irradiances (Leverenz and Jarvis 1979, Leverenz 1987), and may affect light-saturated photosynthetic rates (Jarvis and Leverenz 1983). As a result, the relative magnitude of needle-level changes in physiology through the crown may differ from changes inferred from shoot-level measurements

of photosynthetic light response.

Physiological adjustments to a given light environment may also vary between co-occurring tree species (Marek et al. 1989, Bassow and Bazzaz 1998). Shade-intolerant species often maintain higher light-saturated photosynthetic rates and respiration rates than co-occurring shade-tolerant species across a range of light environments (Björkman 1981, Marek et al. 1989, Bond et al. 1999). However, shade-intolerant species may have lower net photosynthetic rates under low irradiances than co-occurring shade-tolerant species (Marek et al. 1989, Niinemets 1997). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) co-occur extensively in the Pacific Northwest, and Douglas-fir is classified as less shade-tolerant than western hemlock (Franklin and Dyrness 1988). Douglas-fir generally has higher branch-level light-saturated photosynthetic and respiration rates than other co-occurring conifers when grown under similar light conditions, whereas western hemlock has lower light-saturated photosynthetic and respiration rates (Krueger and Ruth 1969, Fry and Phillips 1977, Carter and Klinka 1992, Leverenz 1995, Bond et al. 1999). Differences in shoot morphology contribute to branch-level differences in photosynthetic light response between these species (Leverenz 1995), but it is unclear whether needle-level differences in physiology affect photosynthetic light response through the crowns of these species.

Douglas-fir and western hemlock are among the tallest tree species in the world, often attaining heights of 60–75 m in old growth stands, and individual trees may continue to grow for 400 years or more (Hermann and Lavender 1990, Packee 1990). Because these species occur as dominants in the overstory, rather than as isolated individuals, the potential aboveground biomass accumulation in old growth Douglas-fir–western hemlock stands ranks among the highest of any forest, and may exceed 1600 Mg ha<sup>-1</sup> (Waring and Franklin 1979, Franklin and Dyrness 1988). High aboveground biomass in these stands is associated with leaf area indices of 10 or more. In contrast, leaf area indices in other temperate forests generally do not exceed 6–8 (Waring and Schlesinger 1985, Larcher 1995). The height and high leaf area indices of overstory trees in these forests create larger vertical gradients in the light environment compared with most other temperate forests (Jarvis and Leverenz 1983). Associated with this light gradient is a substantial reduction in net photosynthetic rates from the top to the bottom of the canopy (Woodman 1971). Irradiances at the bottom of the canopy (Hodges 1967) may be lower than the light compensation points at the top (Leverenz 1981).

We examined variation in needle-level photosynthetic light response across a vertical light gradient within a 45–55 m tall Douglas-fir–western hemlock stand approximately 400–500 years old. We tested two hypotheses: (1) light-saturated photosynthetic rates, light compensation points, and respiration rates decrease from the upper to the lower canopy; and (2) light-saturated photosynthetic rates, light compensation points, and respiration rates vary between Douglas-fir and western hemlock.

## Materials and methods

### Study area

The study site is a Douglas-fir–western hemlock old growth forest at the Wind River Canopy Crane Research Facility (WRCCRF). The WRCCRF is located 355 m a.s.l. in the Thornton T. Munger Research Natural Area of the Gifford Pinchot National Forest in the southern Washington Cascade Range (45°49'N, 121°57'W). The forest is 400–500 years old (Franklin and DeBell 1988), and there have been no detectable major disturbances since stand initiation. The dominant overstory tree species are Douglas-fir and western hemlock. Less abundant species include Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), grand fir (*Abies grandis* Dougl. ex Forbes), western red cedar (*Thuja plicata* Donn ex D. Don), and western white pine (*Pinus monticola* Dougl. ex D. Don). The site has a temperate wet winter and a dry summer. Meteorological data from the nearby Wind River Ranger Station show a mean annual precipitation of 253 cm (less than 10% occurring between June and September), a mean annual snowfall of 233 cm, and a mean annual temperature of 8.7 °C (E. Freeman, D. Shaw, D. Ford, K. Bible, Wind River Canopy Crane Research Facility, WA, unpublished data). The canopy was accessed with a Liebherr 550 HC freestanding construction tower crane (Morrow Crane Inc., Salem, OR). The crane jib had a range of 85 m, providing access to 2.3 ha of the forest. Within the crane circle there were 1776 living trees with a diameter at breast height > 0.5 cm (E. Freeman, D. Shaw, D. Ford, K. Bible, unpublished data); 311 of these trees were accessible from the suspended gondola. The height of the tallest Douglas-fir (also the tallest tree of any species) within the crane circle was 64.7 m; the height of the tallest western hemlock was 59.6 m.

### Canopy light measurements

The canopy light environment and needle physiology were measured at three heights in the canopy: within 5 m of the tree top (upper canopy); about 12.5 m from the tree top (mid-canopy); and 25 m below the tree top, which was near the base of the tree crown in Douglas-fir (lower canopy).

The light environment within the canopy was measured with gallium arsenide phosphide photodiodes (G1116, Hamamatsu, Patterson, NJ). Pontauiller (1990) found that these sensors provide estimates of PPFD that correspond closely to measurements made with a standard quantum sensor (LI-190 SA, Li-Cor, Inc., Lincoln, NE). However, the photodiodes are not cosine corrected and likely underestimate flux densities at low incident angles. This effect is probably greater in the upper canopy because the lower canopy receives less direct light when the sun is low in the sky. As a result, differences in the light environment across the canopy may be greater than reported here. Each photodiode was calibrated with a quantum sensor (Li-Cor LI-191 SA) before use.

Diurnal measurements of the canopy light environment were made during two mostly sunny days in August 1997. Photodiodes were attached horizontally to the ends of the Douglas-fir branch tips on which physiological measurements were made. The sensor data were logged with a battery pow-

ered data logger (CR10, Campbell Scientific, Logan, UT). Sensors were sampled once per minute, and averages were recorded at 10-min intervals. Means were calculated for each canopy level (top, middle, bottom). Integrated daily PPFD values did not vary substantially among sensors at any one height, although differences in the instantaneous values of PPFD were observed over the photoperiod.

#### Physiological measurements

Leaf physiology measurements were performed during the third weeks of September 1996, and April and July 1997 on four dominant trees 45–55 m in height, including two Douglas-fir and two western hemlock (Table 1). Leaf gas exchange rates were measured on intact, fully expanded needles with infrared gas analyzers built into a leaf cuvette in an open-flow gas exchange system (Li-Cor LI-6400). Needles were arranged in the cuvette to minimize self-shading and all needles were parallel to the plane of the leaf chamber. In this way, effects of species- and height-related differences in needle orientation on photosynthetic light response were eliminated. The LI-6400 light source was used to control photosynthetic photon flux density (PPFD). The airstream entering the cuvette was maintained at  $360 \mu\text{mol mol}^{-1} \text{CO}_2$  with a computer-controlled  $\text{CO}_2$  mixing system supplied with the LI-6400. Needle, cuvette, and air temperatures were measured with thermocouples linked to the LI-6400 computer. Cuvette air was maintained at the desired temperature ( $18^\circ\text{C}$  in September 1996 and April 1997, and  $24^\circ\text{C}$  in July 1997) with a computer controlled Peltier module mounted on the cuvette. These temperatures reflected mean ambient air temperatures during the measurement periods. Data were not corrected for differences in temperature between measurement periods. The leaf-to-air vapor pressure deficit in the chamber was maintained at approximately 1.3 kPa in September and April, and at approximately 2.0 kPa in July by regulating the air flow rate, and by using desiccant to scrub incoming air as necessary. Corresponding mean stomatal conductances ( $\pm$  SE) in September, April and July were  $0.11 \pm 0.01$ ,  $0.17 \pm 0.02$ , and  $0.12 \pm 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$ , respectively. All gas exchange parameters were calculated according to Field et al. (1989). Projected sur-

face area of the measured needles was estimated by counting all needles in the cuvette and using measurements of needle length and width on a subsample of those needles. Calculating surface area by multiplying needle length by needle width measured at a point two thirds of the distance from the needle base closely approximates the projected surface area (C. Wise, U.S. Environmental Protection Agency, Corvallis, OR, unpublished data). Total leaf area in the cuvette for a given measurement was typically  $3.0\text{--}4.0 \text{ cm}^2$  for western hemlock and  $4.0\text{--}5.0 \text{ cm}^2$  for Douglas-fir.

At each measurement period, net photosynthetic rate versus irradiance curves were measured at three heights on both the north and south sides of each tree (Table 1). The same, or adjacent, branches were used at each measurement period. Because photosynthesis varies with needle age in conifers (Hom and Oechel 1983, Teskey et al. 1984, Sheriff et al. 1986, Brooks et al. 1994), all measurements were made on first-year needles. Measurements were made on fully expanded needles from the 1996 needle cohort for the first two measurement periods. Measurements in July 1997 were made on needles from the 1997 cohort. For each light response curve, needles were equilibrated at saturating PAR before initiation of the light response curve. Each light response curve consisted of measurements at 6–11 PPFDs, from 10 to  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Needles were allowed to equilibrate at each PPFD (typically requiring  $\leq 5$  min and not exceeding 20 min) before measurement. Needles were considered equilibrated if net photosynthetic and transpiration rates were stable for 1 min. Light response curves were typically completed within 30 min. Measurements were initiated 1 hour after sunrise.

#### Statistical analyses

Photosynthetic light response curves were individually analyzed with the non-rectangular hyperbolic model (Prioul and Chartier 1977, Leverenz and Jarvis 1979, Marshall and Biscoe 1980):

$$\Theta A^2 - A(\Phi \text{PPFD} + A_{\text{sat}}) + \Phi \text{PPFD} A_{\text{sat}} = 0, \quad (1)$$

Table 1. Tree reference number, aspect, and tree and branch heights for each branch measured. Tree reference numbers are the identification number assigned by the Wind River Canopy Crane Research Facility. Tree height is the distance from ground level to the highest point on the tree. Branch height is the distance above ground level, calculated using the crane base as ground level. Measurements of daily patterns of photosynthetic photon flux density were made on the same or adjacent branchlets as physiological measurements.

Species	Tree no.	Aspect	Height (m)	Diameter (cm)	Measurement height (m)		
					Top	Mid	Low
Douglas-fir	1373	North	56.8	129.0	55.0	40.5	30.1
		South			51.8	35.8	25.5
	1376	North	55.7	109.6	54.3	37.7	23.2
		South			54.1	36.3	28.2
Western hemlock	0260	North	50.5	92.5	47.6	37.5	25.5
		South			47.8	37.5	24.6
	1184	North	46.4	75.1	45.4	34.7	24.3
		South			45.6	35.2	20.4

where PPFD is the incident photosynthetic photon flux density,  $A$  is the photosynthetic rate,  $\Phi$  is the maximum apparent quantum yield (the initial slope of the curve),  $\Theta$  is the convexity of the light response curve, and  $A_{\text{sat}}$  is the light-saturated gross photosynthetic rate. Curves were fit to this equation with the aid of the NLIN function in the SYSTAT software package Version 5.2 (1992, Systat, Inc., Evanston, IL). To obtain a correct intercept on the y-axis, an additional term was added to the photosynthetic rate. This term was used as an estimate of the non-photorespiratory respiration rate ( $R_d$ ). For some curves, the model fitted the curve poorly at low irradiances. For these curves,  $\Phi$  and  $R_d$  were calculated by linear regression analysis of data below a PPFD of  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The light compensation point ( $\Gamma$ ) was calculated as the PPFD at which the net photosynthetic rate equaled zero for each curve. The PPFD required for saturation of photosynthesis was estimated by calculating the PPFD at which  $A = 0.9 A_{\text{sat}}$ . It is not possible to calculate the PPFD when  $A$  first equals  $A_{\text{sat}}$  because  $A$  approaches  $A_{\text{sat}}$  asymptotically.

Spatial patterns in needle physiology were analyzed by repeated measures analysis of variance with species as the between-subjects factor, and height in canopy (top, middle, bottom), measurement aspect (north, south), and period (September, April, July) as the within-subjects factors. In general, one light response curve was performed at each sampling location per measurement period. Because the tree was the experimental unit for this analysis, multiple measurements from a sampling location at a given measurement period were combined and the mean value used in the analysis. Analyses were performed with the MGLH function in SYSTAT. Results from univariate analysis are shown where results from univariate, multivariate and polynomial analyses with one degree of freedom were similar. Measurement aspect did not significantly affect any parameter, and there were no significant interactions between measurement aspect and other factors. As a result, data from the north and south aspects were grouped together in all analyses. Additionally, measurement period did not significantly affect  $A_{\text{sat}}$ , and there were no interactions between measurement period and other factors on  $A_{\text{sat}}$  ( $P \geq 0.21$  in all cases). As with aspect, data were grouped across measurement periods for all analyses.

## Results

Histograms of photosynthetic photon flux density under mostly sunny conditions over a full diurnal cycle at the top-, mid- and low-canopy positions are shown in Figure 1. Branchlets at the canopy top spent 90% of the light cycle at photosynthetic photon flux densities (PPFD) above  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and 80% of the light cycle at PPFD above  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In contrast, branchlets at the lowest measurement height spent 40% of the light cycle at PPFD below  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and 75% of the light cycle at PPFD below  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Mean daily photon flux densities were 39.2, 24.4, and  $14.1 \text{ mol m}^{-2} \text{ day}^{-1}$  at the top-, mid- and low-canopy positions, respectively.

Representative photosynthetic light response curves measured in July 1997 at three canopy heights are shown in Fig-

ure 2, along with parameter values calculated from each curve with Equation 1. These curves reflect the mean light-saturated photosynthetic rate ( $A_{\text{sat}}$ ), the convexity of the light response curve ( $\Theta$ ), the apparent quantum yield ( $\Phi$ ), and the non-photorespiratory respiration rate ( $R_d$ ). Across aspects and measurement periods, the PPFD required for 90% saturation of photosynthesis was significantly lower in western hemlock than in Douglas-fir ( $P = 0.003$ ; Table 2), and in both species it was significantly lower in the low-canopy position than in the high-canopy position ( $P = 0.003$ ). Based on the estimated PPFD for 90% saturation of photosynthesis and the PPFD measured over a full diurnal cycle at each canopy level, the time during which needles were in saturating light can be estimated. This estimate assumes that all needles on a branch were unshaded and oriented perpendicular to the sun. Differences in needle distributions on branches through the canopy and between species affected the time individual needles were exposed to photosynthetically saturating irradiance. Based on these calculations, Douglas-fir needles in the upper

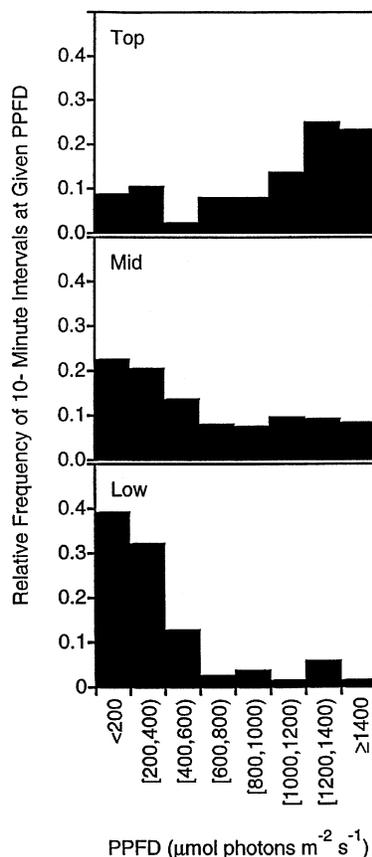


Figure 1. Histograms of photosynthetic photon flux density (PPFD) over a full diurnal cycle in August 1997 at the top-, mid- and low-canopy positions. Each bar represents the relative frequency of 10-min intervals during which the mean PPFD was within the range indicated. Measurements were made under mostly sunny conditions on Douglas-fir branchlets used for physiological measurements, and are averaged across measurement positions for each height in the canopy ( $n = 2-4$  measurement positions).

canopy were light saturated for about 55% of the light cycle on a midsummer day, whereas western hemlock needles were light saturated for about 70% of daylight hours. In the low canopy position, Douglas-fir needles were light saturated for, at most, 40% of the time, whereas western hemlock needles were light saturated for about 55% of the time.

Across all measurement periods and aspects, the light-saturated photosynthetic rate declined 27 and 36% in Douglas-fir and western hemlock, respectively, between the upper canopy and the lower canopy (Figure 3), whereas respiration rate (calculated as the y-intercept of the light response curve) and the light compensation point declined about 35 and 55% in Douglas-fir and western hemlock, respectively. In contrast, the convexity of the light response curve increased 25–30% between the upper and lower canopy (Table 2). Apparent quantum yield was similar in the upper and lower canopies, but was significantly higher in the mid-canopy. A comparison across canopy positions indicated that the light-saturated photosynthetic rate ( $P = 0.049$ ), respiration rate ( $P = 0.003$ ),

and light compensation point ( $P = 0.045$ ) were significantly higher in Douglas-fir than in western hemlock. Apparent quantum yield and the convexity of the light response curve did not differ significantly between species ( $P \geq 0.643$  for both parameters), and there were no significant interactions between species and measurement height on any parameter ( $P \geq 0.543$  in all cases).

Relationships between the light-saturated photosynthetic rate and respiration rate, respiration rate and light compensation point, and the light-saturated photosynthetic rate and light compensation point are shown in Figure 4. Relationships between parameters were similar in both species. Across species, the respiration rate was significantly correlated with the light-saturated photosynthetic rate ( $R_d = 0.082A_{\text{sat}} + 0.153$ , adjusted  $r^2 = 0.299$ ,  $P < 0.001$ ). For this relationship, the y-intercept value did not differ significantly from zero ( $P = 0.284$ ). When reanalyzed with the constant term set equal to zero, the relationship between the light-saturated photosynthetic rate and respiration rate was:  $R_d = 0.097A_{\text{sat}}$  (adjusted  $r^2 = 0.861$ ,  $P < 0.001$ ). The light compensation point was significantly

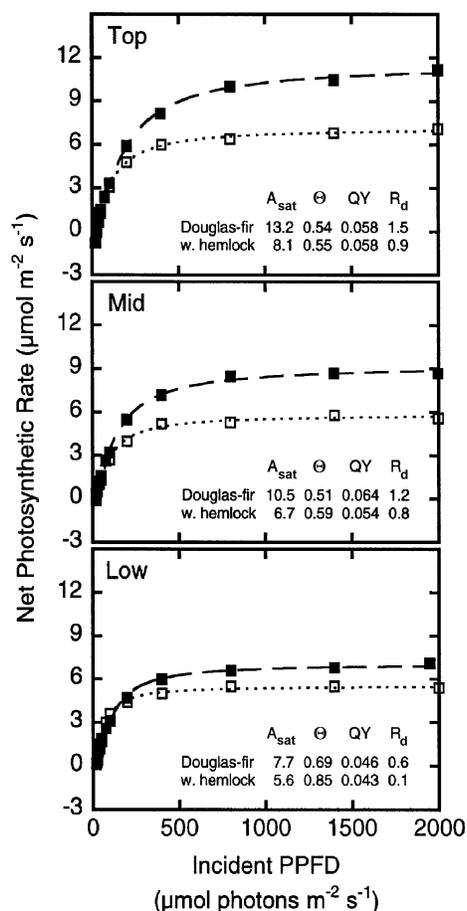


Figure 2. Representative light response curves at three heights in the canopy for Douglas-fir (■) and western hemlock (□) needles. Each curve was fit with Equation 1, and corresponding parameter values are shown. For all curves,  $r^2 \geq 0.98$ . Measurements were made in July 1997, at ~50 (top), 35–40 (mid) and ~25 m (low) above the forest floor, respectively.

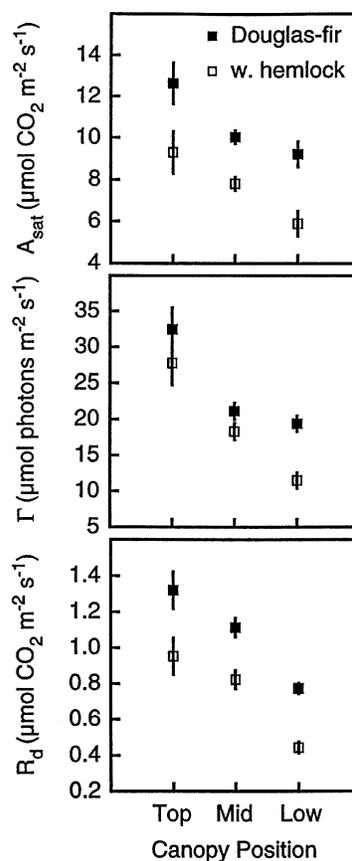


Figure 3. Effects of vertical position in the canopy on mean ( $\pm$  SE) light-saturated photosynthetic rate ( $A_{\text{sat}}$ ), light compensation point ( $\Gamma$ ) and dark respiration rate ( $R_d$ ) in Douglas-fir and western hemlock needles. All three parameters significantly decreased with decreasing height in the canopy, and were significantly higher in Douglas-fir needles compared with western hemlock needles. Results are summed across all aspects and measurement periods ( $n = 12$ ).

Table 2. Effect of measurement height on least-squared means ( $\pm$  SE) for the PPFD at which  $A = 0.9 A_{\text{sat}}$ , the convexity of the light response curve ( $\Theta$ ), and apparent quantum yield ( $\Phi$ ). Apparent quantum yield was significantly higher at the mid-canopy position than at the top-or low-canopy positions ( $P = 0.041$ ). Results are summed across all aspects and measurement periods ( $n = 12$ ).

Parameter	Species	Canopy position (m)		
		Upper	Middle	Lower
Light saturation point ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Douglas-fir	$364 \pm 46$	$327 \pm 30$	$626 \pm 92$
	Western hemlock	$200 \pm 18$	$252 \pm 49$	$363 \pm 47$
Convexity (dimensionless)	Douglas-fir	$0.63 \pm 0.12$	$0.67 \pm 0.03$	$0.81 \pm 0.04$
	Western hemlock	$0.67 \pm 0.12$	$0.74 \pm 0.03$	$0.84 \pm 0.04$
Apparent quantum yield ( $\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$ )	Douglas-fir	$0.045 \pm 0.006$	$0.054 \pm 0.001$	$0.043 \pm 0.003$
	Western hemlock	$0.043 \pm 0.006$	$0.053 \pm 0.001$	$0.042 \pm 0.003$

correlated with the respiration rate ( $\Gamma = 18.760R_d + 4.810$ , adjusted  $r^2 = 0.427$ ,  $P < 0.001$ ). In addition, the light compensation point was significantly correlated with the light-saturated photosynthetic rate ( $\Gamma = 1.357A_{\text{sat}} + 9.351$ , adjusted  $r^2 = 0.092$ ,  $P = 0.006$ ); however, differences in the light-saturated photosynthetic rate accounted for less than 10% of the variation in the light compensation point.

## Discussion

We observed significant changes in the light response of photosynthesis in overstory Douglas-fir and western hemlock needles along a 25-m vertical light gradient extending from the canopy top to lower branches. Area-based, light-saturated photosynthetic rates, light compensation points and respiration rates declined significantly along this gradient, paralleling a 65% reduction in mean daily photosynthetic photon flux density. Such changes in photosynthetic light response and light availability through the canopy are consistent with the expectation that the potential daily carbon uptake should be

higher for needles in the upper canopy relative to needles in the lower canopy (e.g., Woodman 1971, Watts et al. 1976, Schulze et al. 1977, Beadle et al. 1985). Additionally, the observed changes in photosynthetic capacity, light compensation point, and respiration rates are consistent with physiological differences associated with acclimation of sun and shade leaves (Boardman 1977, Björkman 1981, Givnish 1988). Higher photosynthetic capacity in the upper canopy relative to the lower canopy may result from greater allocation of resources, such as nitrogen, to needles in the upper canopy (Field 1983, Jarvis and Leverenz 1983, Givnish 1988, Pearcy and Sims 1994) or changes in chloroplast organization (Oya and Laisk 1976, Terashima and Saeki 1985) or needle morphology (Brooks et al. 1996).

The observed vertical gradients in leaf physiology are consistent with the hypothesis that carbon uptake will tend to be optimized at the canopy level (Mooney and Gulmon 1979, Field 1983). Increases in light-saturated photosynthetic rates will have the greatest effect on carbon uptake at the high irradiances (Sharkey 1985) in the upper canopy. Area-based, light-saturated photosynthetic rates were 30–40% higher in the upper canopy relative to the lower canopy. Studies on the relative change in light-saturated photosynthetic rates within the crowns of individual coniferous trees with increasing height in the canopy have shown increases ranging from 10 to 290%, with an average increase of approximately 50% (Leverenz and Jarvis 1979, Leverenz and Jarvis 1980, Troeng and Linder 1982, Kull and Koppel 1987, Brooks et al. 1996, Bond et al. 1999). Similar increases have been observed between the lower and upper canopies of broad-leaved trees (DeJong and Doyle 1985, Hollinger 1989, Marek et al. 1989, Ellsworth and Reich 1993). As irradiance decreases with depth in the canopy, lower light compensation points will increase net carbon uptake per unit leaf area more than will increased photosynthetic capacity (Boardman 1977, Björkman 1981, Givnish 1988). Light compensation points for Douglas-fir and western hemlock needles decreased 35 and 55%, respectively, from the upper canopy position to the lower canopy position. These physiological adjustments to the prevailing light environment should lead to significant gains in total canopy carbon uptake relative to canopies where photosynthetic light response is uniform through the canopy (Givnish 1988).

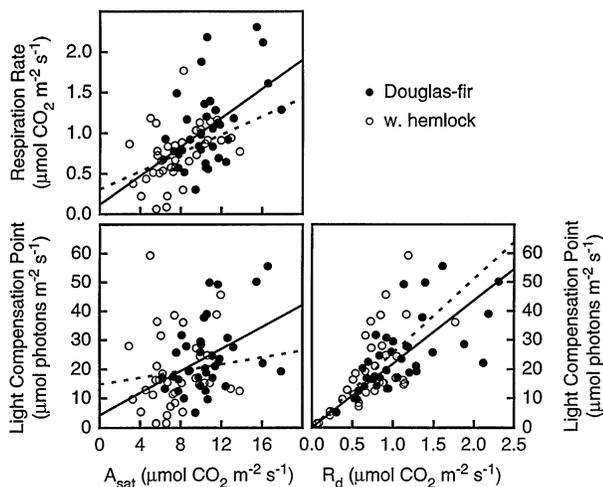


Figure 4. Relationships between light-saturated photosynthetic rate and respiration rate, light-saturated photosynthetic rate and light compensation point, and respiration rate and light compensation point for Douglas-fir (—) and western hemlock (---).

Acclimation to the prevailing light environment has been associated with higher convexities of photosynthetic light response curves in shade-acclimated leaves relative to sun-acclimated leaves (Leverenz and Jarvis 1979, DeLucia et al. 1991, Ögren 1993). Consistent with this pattern, light response curve convexity increased between the upper and lower canopy, suggesting that photosynthetic efficiency at low and intermediate irradiances was higher in needles from the lower canopy relative to needles from the upper canopy. Increasing convexity with increasing depth in the canopy indicates that the light response curve saturated at lower PPFD, all other parameters being equal (Ögren 1993), and is consistent with differences in the light saturation point inferred from the light response curves at the different measurement heights (Figure 2). Reductions in the light saturation point are commonly seen during shade acclimation (Boardman 1977, Björkman 1981). Convexity values for sun needles in this study were lower than those reported in studies on conifers grown in shade houses or growth chambers under lower PPFD conditions (Leverenz 1988, Wang and Jarvis 1993, Leverenz 1995). However, convexity values for shade needles were similar to or somewhat higher than values calculated for conifers grown in shade houses or growth chambers. This suggests that differences in convexity among studies on needle-level photosynthetic light response of conifers may partially reflect acclimation of needles to the light environment during growth.

Although only a few studies have examined vertical gradients in leaf-level light compensation points within forest canopies, all of these studies show significant reductions in light compensation point from the upper to the lower canopy (Leverenz and Jarvis 1979, Marek et al. 1989, Ellsworth and Reich 1993, Bond et al. 1999). Vertical gradients in light compensation points within canopies may result from either increases in quantum yield (ratio of carbon fixed per unit quanta of light) or reductions in respiratory losses (Boardman 1977, Björkman 1981, Givnish 1988). Our results suggest that vertical gradients in the light compensation point were primarily caused by changes in leaf respiration rate rather than changes in quantum yield because apparent quantum yield was generally highest in the mid-canopy. In contrast, respiration rates were generally highest in the upper canopy and lowest in the lower canopy, paralleling vertical changes in light compensation point. A linkage between changes in the light compensation point to changes in respiration rates through the canopy is further supported by the significant correlation between these parameters. However, a study comparing Douglas-fir and western hemlock trees grown on different sites found that vertical gradients in the light compensation point were associated with changes in quantum yields, whereas respiration rates did not vary significantly through the canopy of either species (Bond et al. 1999). Thus, it is likely that changes in both respiration rates and quantum yield drive vertical gradients in light compensation points through individual crowns in these species, with genetic and environmental variation determining the relative contribution of each component.

Reductions in the light compensation point were also correlated with reductions in photosynthetic capacity. Although photosynthetic capacity is not the primary physiological factor

affecting the light compensation point, reductions in photosynthetic capacity may indirectly affect the light compensation point through effects on respiration. Photosynthetic capacity may be closely coupled with respiration in mature leaves (Givnish 1988, Brooks et al. 1991) because changes in photosynthetic capacity change protein turnover and active transport, the primary processes accounting for respiration in mature leaves (Penning de Vries 1975). The observed correlation between light-saturated photosynthetic rates and respiration rates is consistent with this linkage. The correlation is also consistent with other studies on conifers showing reductions in photosynthetic capacity and respiration rates (Leverenz and Jarvis 1979, Brooks et al. 1996) from the upper to the lower canopy or between sun and shade foliage within overstorey canopies. Thus, changes in photosynthetic capacity through the canopy may partially account for observed reductions in respiration rates and light compensation points between the upper and the lower canopy.

The species-related differences in the response of photosynthesis to irradiance provide a physiological explanation for differences in shade tolerance and, to an extent, successional changes in Pacific Northwest forests. Western hemlock is considered more shade-tolerant than Douglas-fir, based on seedling survivorship and biomass production in different light environments (Livingston and Black 1988, Carter and Klinka 1992, Gray and Spies 1997). Where the two species co-occur, Douglas-fir generally dominates early successional sites, but, in the absence of major disturbance, is gradually displaced by western hemlock as the dominant tree species (Munger 1940, Fonda and Bliss 1969, Dyrness 1973, Stewart 1986, Spies et al. 1988, Huff 1995). Consistent with this difference in shade tolerance, Douglas-fir needles had light-saturated photosynthetic rates that were 30–60% higher and light compensation points that were 15–70% higher than western hemlock needles at all measurement heights in this study. Consequently, in the high light environment of the upper canopy, Douglas-fir had higher net photosynthetic rates per unit leaf area than western hemlock. Conversely, in the low light environment of the lower canopy, western hemlock had higher net photosynthetic rates per unit leaf area than Douglas-fir. These differences in photosynthetic response to the light environment have also been observed in studies comparing Douglas-fir and western hemlock seedlings and saplings (e.g., Krueger and Ruth 1969), life stages when species differences in physiological responses to irradiances near the forest floor may differentially affect species recruitment. However, the relatively small differences between western hemlock and Douglas-fir in photosynthetic light response, particularly at low irradiances, emphasize the importance of the combined effects of physiology, morphology and phenology in regulating shade tolerance.

## Conclusions

We observed significant reductions in light-saturated photosynthetic rates, light compensation points and respiration rates in needles of overstorey Douglas-fir and western hemlock along a vertical gradient from the canopy top to the

lower branches. Although the relative reductions in physiological parameters from the upper to the lower canopy were similar in Douglas-fir and western hemlock needles, Douglas-fir had higher light-saturated photosynthetic rates as well as higher light compensation points and respiration rates throughout the canopy.

Differences in photosynthetic light response through the canopy and between species provide insights into the structure and function of the forest ecosystem. From a functional standpoint, the vertical gradients in photosynthetic light response should increase total canopy carbon uptake relative to a uniform light response through the canopy (Givnish 1988). In the high light environment of the upper canopy, net carbon uptake is increased by relatively high, light-saturated photosynthetic rates. In contrast, in the low light environment of the lower canopy, net carbon uptake is increased by relatively low, light compensation points and low respiration rates. These physiological adjustments to ambient light conditions within each vertical layer increase total canopy carbon uptake by using available resources, especially light, more efficiently.

The species-related differences in photosynthetic light response help explain differences in shade tolerance and the consequent effects on the structure of the forest community. The high photosynthetic capacity of Douglas-fir is consistent with its dominance of early successional environments, and the low light compensation point of western hemlock is consistent with its capacity to establish itself within and eventually dominate late successional environments.

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