Redwood Seedling Responses to Light Patterns and Intensities[1]

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Abstract

Coast redwood (*Sequoia sempervirens* (D. Don) Endl.) seedlings were grown from seed in controlled environments with 16 hour photoperiods using three light patterns that mimicked full shade (constant light level), intermittent high light such as long duration sun flecks (low light with 15 minutes of intense light every 2 hours), and large openings (4 hours low light, 8 hours high light, 4 hours low light). Each light pattern contained three light intensity levels (33 percent, 66 percent, and 100 percent) with one intensity level in each pattern that provided 5.1 daily light integral (DLI). Among the treatments, the extremes of daily light were 1.6 DLI to 15.5 DLI.

Seedlings increased biomass accumulation with increasing light level with diminishing accumulation at the higher DLIs. The seedlings were most efficient at utilizing light in the full shade and large opening patterns with poor utilization of light in the intermittent sun fleck pattern. Within each pattern, increased light intensity resulted in increased seedling height, stem diameter, branching, branch length, leaf area, specific leaf area, leaf mass, root mass, total mass, root/shoot ratio, stomatal density and needle thickness. In general, maximum net photosynthesis increased with increased light intensity. Quantum efficiency did not vary with intensity within the full shade and large opening patterns. Within the intermittent sun fleck pattern, quantum efficiency was lower in the seedlings grown at the lowest light intensity.

With equal daily light, seedlings in all three patterns had similar branch length, total mass, and leaf mass. However, seedlings in the large opening pattern had greater height and greater stem diameter, but less specific leaf area than the full shade pattern. Seedlings in the intermittent sun fleck pattern had less height, stem diameter, total mass, leaf area, and leaf mass, but greater root/shoot ratios and specific leaf areas than seedlings in the other patterns.

Maximum net photosynthesis was greater in the seedlings grown in the large opening pattern. Quantum efficiency was not affected by light pattern. Photosynthetic light compensation points ranged from $12 \mu Em^{-2}s^{-1}$ for seedlings in the low intensity treatment of the shade pattern to $20 \mu Em^{-2}s^{-1}$ for seedlings grown at full intensity in the large opening pattern.

Needle morphology varied markedly among light treatments. Needles in the high light treatment of the large opening pattern had a regular pattern of rounded upper epidermal cells and a deeply safranin stained, elongated palisade layer. Needles in the low light treatments of both the full shade and intermittent sun fleck treatments had prismatic shaped cells in the upper epidermis and irregular, lightly safranin stained palisade layers.

Keywords: anatomy, coast redwood, ecology, growth, light, photosynthesis, *Sequoia sempervirens,* seedling, shade

Introduction

There is a poor understanding of the environmental conditions necessary for redwood (*Sequoia sempervirens* (D. Don) Endl.) seedling establishment. Redwood seedlings are found at the edge of redwood stands and on disturbed sites adjacent to redwood forests (Jacobs 1987) and the establishment of redwood seedlings has been found to be positively correlated with soil disturbance

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with seedling growth greater in open sites (Woodward 1986). The factors thought to be most detrimental to the establishment of redwood seedlings in the understory are: moisture stress, soil-borne fungi, and light (Becking 1996, Jacobs 1987, Muelder and Hanson 1961, Olson et al. 1990). These factors are inter-related; increased light was found to assist redwood seedlings in resisting both damping-off fungi and water stress (Jacobs 1987). Investigations of light conditions at redwood forest floors are somewhat limited, but they indicate that light is generally low and variable (Jacobs 1987, Pfitsch and Pearcy 1989, Powles and Björkman 1981, Waring and Major 1964, Woodward 1986). Sunflecks are present, even under a dense canopy, and may contribute a large portion of the integrated daily light available under the canopy, particularly the sunflecks of longer duration. Several studies have demonstrated that redwood seedlings can exist in low light, at least under experimental conditions (Baker 1945, Bates and Roeser 1928,). In natural conditions, shade has been described as beneficial to redwood seedling establishment provided root rot is excluded and other factors are held equal (Muelder and Hansen 1961). Shade was also found to be beneficial to redwood seedlings planted into open areas, although it was thought that the benefit was derived primarily through improved soil moisture (Fritz and Rydelius 1966). Additionally, it has been claimed that redwood seedlings can endure and grow slowly in heavy shade, but that their best juvenile growth is under full sunlight (Olson et al. 1990). More recent studies of redwood seedlings and light have demonstrated increased water potential and photosynthesis with fog exposure (Simonin et al. 2009) and increased light use and carbon gain from sun fleck use with increased moisture inputs (Santiago and Dawson 2014).

The purpose of this study was to investigate the response of redwood seedlings in a controlled environment varying only light. The primary objectives of this experiment were: 1) To determine the effect of light patterns on redwood growth, 2) to determine the effect of light intensity on redwood growth, and 3) to determine the plasticity of morphological and physiological characteristics of redwood seedlings to differing light patterns and intensities that mimic both openings and the redwood forest understory.

Methods

Three patterns of light were used with three levels of light intensity within each pattern for nine light treatments (table 1) within controlled environment growth chambers. Light intensity and integrated daily light treatments were selected based on reports of light levels in redwood forests in the studies cited above, as well as constraints imposed by the characteristics of the chambers available (Western Environmental, Inc. Napa, California, Model E-78HL). Intensity levels were obtained by partitioning the chambers using black shade cloth drapes (33 percent and 66 percent light transmittance, Stuewe and Sons, Corvallis, Oregon) as neutral density filters fitted above and around the open sides of a treatment area on the platforms holding the seedlings.

Five seed sources from Del Norte and Humboldt counties were used to allow for a gradient in both latitude and elevation. Eight seedlings from each of the five seed sources were used in each of the nine light treatments for a total of 360 seedlings. To allow for the observance of plasticity and avoid the confounding factor of observing and correcting for acclimation, germinated seeds with a radicle less than 2 cm were placed in 3 liter pots (10 X 10 cm top, 7.5 X 7.5 cm bottom, 30 cm height). The pots were filled with a 1:1 peat/perlite mix. Replacement planting was carried out until all treatments had a full complement of seedlings that reached 40 days in age. Temperature, moisture, and nutrient availability were held as constant as possible. Air temperature was held at 25 °C during periods of light and 15 °C during darkness. Seedlings were watered to field capacity daily and humidity was not controlled. Seedlings were fertilized three times with an application of 4 ml of Osmocote® 17-6-10 Plus Minors (Grace Sierra Horticultural Products Co., Milpitas, California) applied at the emergence of each seedling’s cotyledons and at 40 and 80 days after the initial application.

Table 1—Experimental design, Light patterns and intensity treatments. All treatments had a 16-hour photoperiod with 8 hours of darkness between photoperiods. Values given as PPFD ($\mu Em^{-2} s^{-1}$) or DLI ($Em^{-2} day^{-1}$). Note that within each Light Pattern one treatment had an integrated daily light level of 5.1 DLI

	Light intensity treatment		
	33%	66%	100%
Shade Pattern: constant light			
PPFD	29	57	87
DLI	1.6	3.3	**5.1**
Sun Fleck Pattern: low light interrupted by 15 min high every two hrs			
Low light PPFD	20	40	60
High light PPFD	275	550	825
DLI	2.7	**5.1**	8.2
Large Opening Pattern: 4 hrs low light, 8 hrs high light, 4 hrs low light			
Low light PPFD	12	25	38
High light PPFD	165	330	500
DLI	**5.1**	10.2	15.5

Harvest of seedlings was delayed until most seedlings were large enough to have amble foliage for measurement of photosynthesis in a 5 liter cuvette. However, there was a disparity between the times allowed for growth of seedlings in different light treatments (table 2). At harvest, the largest seedlings were too tall to control their light levels within the growth chambers and to use the photosynthesis cuvette while the smallest seedlings were too small for the measurement of net photosynthesis. Proceeding with the harvest of the largest seedlings before those of smaller seedlings introduced a bias in the sampling.

Net photosynthesis was measured at harvest as the difference between CO_2 concentration in air entering the cuvette and that of air passed through the cuvette with the use of a Non-Dispersive Infrared Analyzer (Model 865, Beckman Industrial Corp., Fullerton, California). Light levels used for measuring, in order of measurement, were 0 (respiration) 11, 33, 100, 300, 600, and 1000 photosynthetic photon flux density (PPFD). Leaf characteristics were measured on 10 adjacent needles from mid-length of a branch that was at the mid-length of the seedling. One of these needles was randomly selected for the measure of stomatal density. Three needles for microscopic examination were taken from the mid-length of another branch opposite of the branch selected for needle characteristics. Height and stem diameter at the root collar were measured and the seedling partitioned into root, shoot, and leaf. Leaf area was measured with a Delta-T area measuring device (Delta-T Devices, Cambridge, England) and all parts dried at 80 °C for 12 hours.

Analysis of variance was performed using BMDP (BMDP Statistical Software, Inc., Los Angeles, California). Program 7D was used for two-way analysis and their associated contrasts. Contrasts were weighted by sample size. To control type I errors, contrasts were limited by using linear contrasts only when a significant difference in the main effect was detected in the analysis of variance. Program 2V was used for the three-way analysis of variance of photosynthesis. Schéffé's procedure for the unplanned contrast of the time allowed for seedling growth was performed using NCSS (5.X series 1992 J.L. Hintze, Kaysville, Utah). Fisher's least significant difference was used for the planned comparisons of net photosynthesis. Regression of photosynthesis data to determine quantum efficiency was performed using BMDP program 1R.

Table 2—Mean values for variables and sample size. (Asterisk* = a significant contrast ($p < 0.05$) between 33% and 100% intensity within a light pattern; within equal light treatments, values that are significantly different ($p < 0.05$) are followed by a different letter)

		Shade			Sun fleck			Large opening			Equal light treatments		
Time	Variable	33%	66%	100%	33%	66%	100%	33%	66%	100%	Shade	Sun fleck	Large opening
40 days	Height (cm)	2.8*	3.6	3.7	3.1*	3.1	4	3.8*	3.3	3.1	3.7^{a}	3.1^{b}	3.8^{a}
80 days	Height (cm)	6.4*	9.3	10	7.2*	8.2	11	11.1	11.3	11	10.0^{a}	8.2^{b}	11.1^{a}
	Stem diameter (mm)	0.8*	1.2	1.5	0.8*	1	1.3	1.4*	1.8	2	1.5^{a}	1.0^{b}	1.4^{a}
	Branches/cm stem	0.12*	0.37	0.59	0.05*	0.21	0.4	0.58*	0.75	0.84	0.59^{a}	0.21^{b}	0.58^{a}
	Longest branch (cm)	3.5*	6.3	8.4	2.3*	4.3	6.4	8.1*	8.9	9.6	8.4^{a}	4.3^{b}	8.1^{a}
120 days	Height (cm)	10.9*	21.2	22.3	12.7*	15.6	24.5	26.3*	31.8	33.9	22.3^{a}	15.6^{b}	26.3^{c}
	Stem diameter (mm)	1.3*	2.1	2.5	1.3*	1.8	2.4	2.7*	3.5	3.9	2.5^{a}	1.8^{b}	2.7^{a}
	Branches/cm stem	0.35*	0.57	0.68	0.35*	0.6	0.61	0.59	0.58	0.66	0.68^{a}	0.60^{ab}	0.59^{b}
	Longest branch (cm)	7.8*	13.9	16	7.1*	10.3	13.8	15.1*	18	19.9	16.0^{a}	10.3^{b}	15.1^{a}
Harvest	Sample size	28	37	37	35	34	35	35	34	35	37	34	35
	Time (days)	270*	237	223	283*	241	220	220	209	213	223^{a}	241^{b}	220^{a}
	Height (cm)	28.0*	45.9	49.6	29.3*	40.8	51.2	56.9	64	62.6	49.6^{a}	40.8^{b}	56.9^{c}
	Stem diameter (mm)	2.6*	4	4.3	2.5*	3.7	4.4	4.8*	6.1	6.1	4.3^{a}	3.7^{b}	4.8^{c}
	Leaf area 1000 cm^2	0.22*	0.58	0.79	0.21*	0.53	0.64	0.78*	1.1	1.15	0.79^{a}	0.53^{b}	078^{a}
	Leaf mass (g)	0.82*	2.51	3.74	0.75*	2.33	3.11	4.01*	7.45	7.73	3.74^{a}	2.33^{b}	4.01^{a}
	Specific leaf area $cm^2\ g^{-1}$	268*	230	219	270*	236	210	201*	154	155	219^{a}	236^{b}	201^{c}
	Mass (g)	1.35*	4.24	6.04	1.19*	3.84	5.56	6.87*	13.32	13.39	6.04^{a}	3.84^{b}	6.87^{a}
	Root mass (g)	0.17*	0.61	0.89	0.14*	0.68	1.08	1.07*	2.78	2.81	0.89^{a}	0.68^{a}	1.07^{a}
	Root/Shoot	0.14*	0.16	0.17	0.13*	0.21	0.23	0.18*	0.24	0.25	0.17^{a}	0.21^{b}	0.18^{a}
	Stomatal density	2.58*	3.05	3.22	2.61*	2.95	3.19	3.43*	3.67	4.09	3.22^{a}	2.95^{b}	3.43^{c}
	Needle length (mm)	20	23	21.9	17.9*	22.9	22.8	24.5	24.2	23.3	21.9^{a}	22.9^{b}	24.46^{c}
	Needle width (mm)	1.9*	2.3	2.4	1.9*	2.2	2.2	2.2	2.3	2.2	2.35^{a}	2.15^{b}	2.2^{ab}
	Needle thickness (mm)	0.16*	0.21	0.24	0.16*	0.21	0.25	0.22*	0.28	0.29	0.24^{a}	0.21^{a}	0.22^{a}
	Needle width/thickness	12.5*	11.2	10.3	11.9*	10.6	8.9	10.5*	8.4	8.3	10.3^{a}	10.3^{a}	10.5^{a}

Results and Discussion

Seedling height, stem diameter, and biomass increased with greater light intensity within all light patterns (table 2). The differences in growth were striking (fig. 1) with higher light intensity promoting growth in nearly all treatments. The results may have been even more distinct had it been possible to harvest the seedlings simultaneously. The exception was the seedlings of the 66 percent and 100 percent intensity treatments of the Large Opening Pattern which had similar growth. The heights of seedlings grown in these two light intensity treatments compared closely with the mean height of 53.6 cm at 168 days for seedlings grown in somewhat similar conditions (Hellmers 1966).

Figure 1—Representative seedlings from each treatment at 192 to 198 days old. Treatments and DLI from left to right : Shade 33 percent (1.6) , Sun Fleck 33 percent (2.7), Shade 66 percent (3.3), Shade 100 percent (5.1), Sun Fleck 66 percent (5.1), Large Opening 33 percent (5.1), Sun Fleck 100 percent (8.2), Large Opening 66 percent (10.2), and Large opening 100 percent (15.5). Bar in background is 25 cm in length.

Higher light intensity, regardless of pattern, resulted in greater total seedling mass, root mass, leaf mass, and increased leaf area (table 2). The increase in root mass with increased light was proportionally greater than the increase in shoot mass and resulted in increased root/shoot ratios in each light pattern. Additionally, increased light resulted in a proportionally greater increase leaf mass than leaf area and a subsequent lower specific leaf area (cm^2 g^{-1} leaf tissue) in each pattern. This decrease in specific leaf area was consistent with the response in other conifers (Del Rio and Berg 1970, Klinka et al. 1992, Lassoie et al. 1985, Tucker and Emmingham 1977). Increased light increases thickening and structural changes, such as increased stomatal density, in needles while the seedling total leaf area also increased (table 2). The increase in total leaf area of seedlings exposed to increased light may have had a high cost in carbon consumption; however, these same seedlings were also able to place a higher proportion of their biomass into the development of roots and conductive tissue as measured by stem diameter (table 2). Conversely, seedlings from the 33 percent intensity treatments of the Sun Fleck and Shade Patterns did not construct as extensive root systems and conductive tissues as seedlings in higher light treatments. Seedlings grown in lower light prioritized leaf area rather than root or stem diameter growth which is consistent with observations of Baker (1945). A decline in root development in low light is probably a consistent pattern in conifers as shading is also known to increase carbon allocation to the shoot in *Psuedotsuga menziesii* (Mirb.) Franco (Brix 1967, Drew and Ferrell 1977, Krueger and Ruth 1969) and *Picea sitchensis* (Bongard) Carrière and *Tsuga heterophylla* (Raf.) Sarg. (Krueger and Ruth 1969).

The limit of the positive effect of light on seedling growth may have been approached in the 66 percent and 100 percent intensity treatments of the Large Opening Pattern. Height at 40 days was less in the 100 percent intensity of light intensity on seedling growth peaked near the intensities provided by the 66 percent and 100 percent intensity treatments. Conversely, the lower light limit for redwood seedlings was likely approached in the 33 percent intensity treatment of the Shade Pattern. In addition to the poor growth within this treatment, there was greater mortality. Twelve seedlings died after the 40 days within this treatment (table 2) and all displayed symptoms of infection by damping off fungi.

Within each light pattern, higher light intensity resulted in greater maximum photosynthesis (figs. 2A, 3A, and 4A) and greater respiration (figs. 2B, 3B, and 4B). The exception was the response curves for seedlings in the 66 percent and 100 percent Large Opening Pattern (figs. 4A and 4B) which were similar in respiration and maximum photosynthesis. Photosynthetic light compensation points ranged from 12 PPFD for seedlings in the low intensity treatment of the shade pattern to 20 PPFD for seedlings grown at full intensity in the large opening pattern (figs. 2B, 3B, and 4B). In the Sun Fleck Pattern, quantum efficiency was significantly lower in seedlings grown in the 33 percent intensity treatment (fig. 4B) but in all the other light patterns intensity treatments did not affect quantum efficiency.

Comparing responses within the Equal Light Treatments, seedlings in the Sun Fleck Pattern were smaller than those in the Shade or Large Opening Patterns (table 2). Seedlings in the Shade and Large Opening Patterns were similar in size at 40 and 80 days, but seedlings in the Large Opening Pattern had greater height at 120 days and harvest and larger stem diameter at harvest (table 2). The specific leaf area of the seedlings differed among the three patterns with the highest specific area in the Sun Fleck Pattern and the lowest in the Large Opening Pattern (table 2). Specific leaf area is known to decrease from low light to high light in conifers (Del Rio and Berg 1970, Klinka et al. 1992, Lassoie et al. 1985, Tucker and Emmingham 1977, Tucker et al. 1987). It appears that, for redwood seedlings, specific leaf area is affected by both light intensity and pattern and is not controlled simply by integrated light, or by the highest instantaneous light level to which seedlings were exposed.

There were no differences in root mass among light patterns in the Equal Light Treatments (table 2); however, the root/shoot ratio was greater in seedlings of the Sun Fleck Pattern. It could be speculated that allocation of carbon to roots in intermittent light is a mechanism that compensates for possible water stress that may occur during sun flecks. An alternate explanation is that root growth is strongly determined by integrated light whereas top growth is affected by light pattern.

Needle morphology varied markedly among light treatments. Needles from seedlings grown in high light treatments had a regular pattern of rounded upper epidermal cells and a deeply safranin-stained, elongated palisade layer (fig. 6) whereas needles from seedlings grown in low light treatments of both the full shade and intermittent sun fleck treatments had prismatic shaped cells in the upper epidermis and irregular, lightly safranin-stained palisade layers (fig. 7). This response is not unlike sun and shade leaves in western hemlock reported by others Tucker and Emmingham (1977).

In summary, both light intensity and light pattern affected the growth and morphological characteristics of redwood seedlings (table 2). The DLI had the greater, but not exclusive, effect on seedling characteristics. In general, the higher the DLI the larger the seedling grew. Given equal DLI, seedlings in the Large Opening and Shade Patterns generally had similar size and characteristics and seedlings in the Sun Fleck Pattern were smaller. The seedlings in the Sun Fleck Pattern were unable to effectively use the periods of high light provided, but this lack of growth may have been the result of the particular intermittent light pattern of light chosen. Other patterns of intermittent light, such as shorter, more frequent sun flecks or longer duration sun flecks, may be utilized by redwood seedlings in a more efficient manner. Other than a lower quantum efficiency of seedlings within the lowest light intensity of the Sun Fleck Pattern and the expected increases in respiration and maximum photosynthesis of seedlings within the high light treatments, photosynthetic characteristics did not radically differ between seedlings grown in different intensities or patterns.

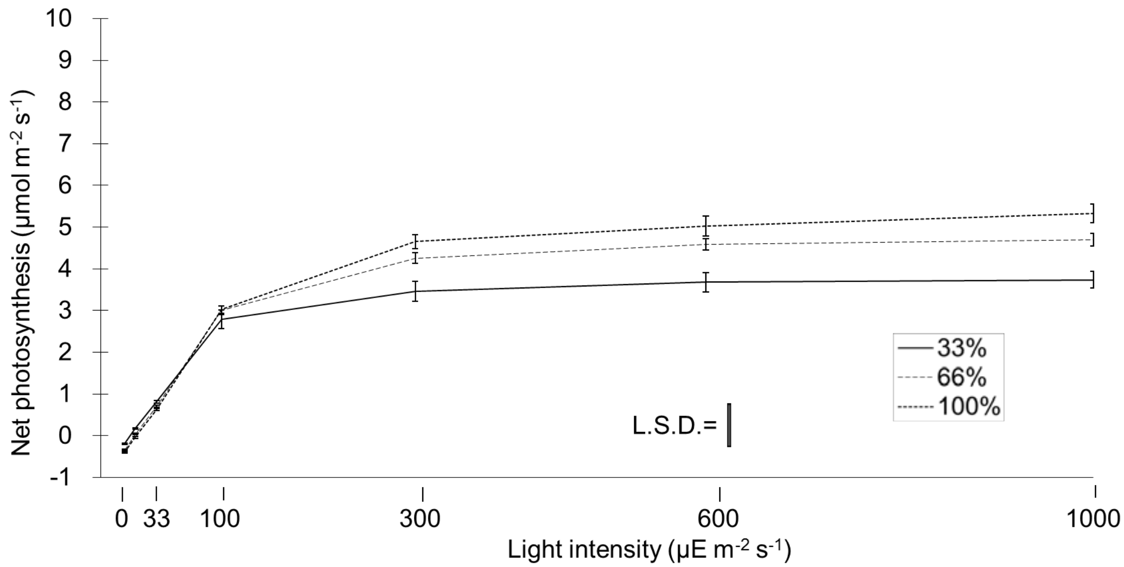

Figure 2A—Steady state net photosynthesis by redwood seedlings grown in the Shade Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$).

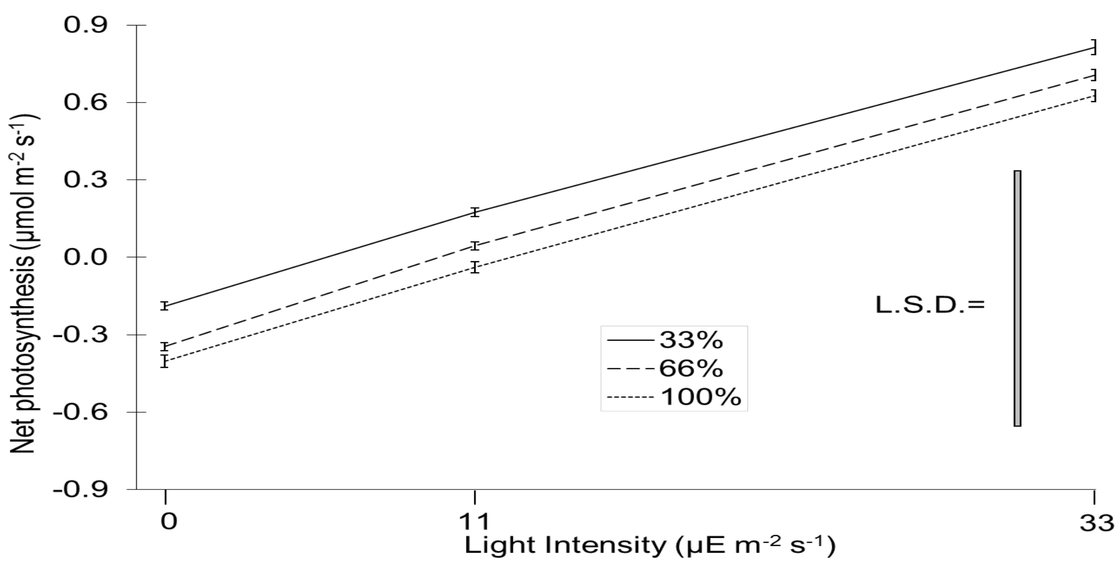

Figure 2B—Detail of steady state net photosynthesis by redwood seedlings grown in the Shade Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$). Quantum efficiency did not differ between different light intensities ($p < 0.05$).

With increased light, needles of redwood developed a palisade layer (figs. 6 and 7), increased stomatal density, and decreased specific leaf area (table 2). The seedlings grown in the treatments with higher light levels were able to develop greater leaf area, root mass, and stem tissue.

Redwood seedlings responded to low light environments by the development of needle area rather than root mass. The development of greater root mass and conductive tissue in higher light is a mechanism by which redwood seedlings grown in high light may avoid mortality from drought and perhaps, fungal infection.

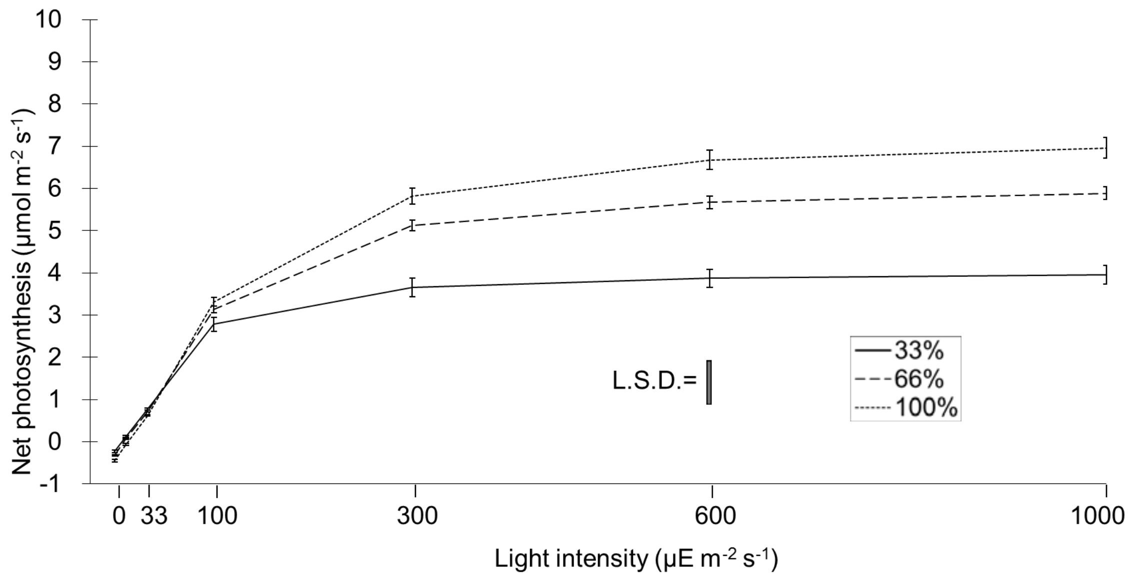

Figure 3A—Steady state net photosynthesis by redwood seedlings grown in the Sun Fleck Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$).

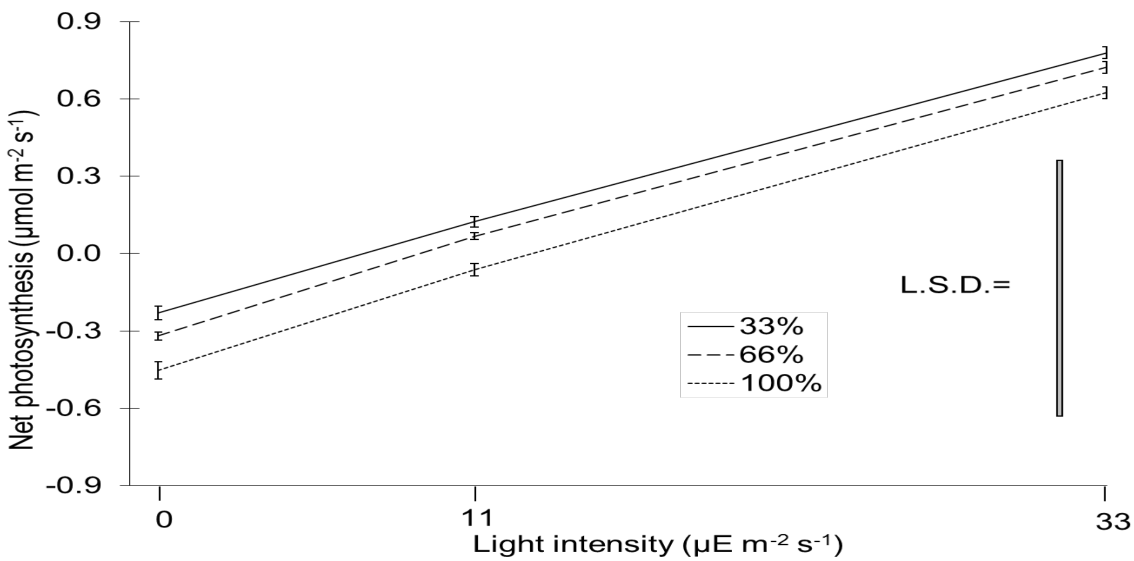

Figure 3B—Detail of steady state net photosynthesis by redwood seedlings grown in the Sun Fleck Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$). There was a significanly lower quantum efficiency of seedlings grown in the 33 percent light intensity compared to those of both the 66 percent and 100 percent intensity treatments ($p < 0.05$).

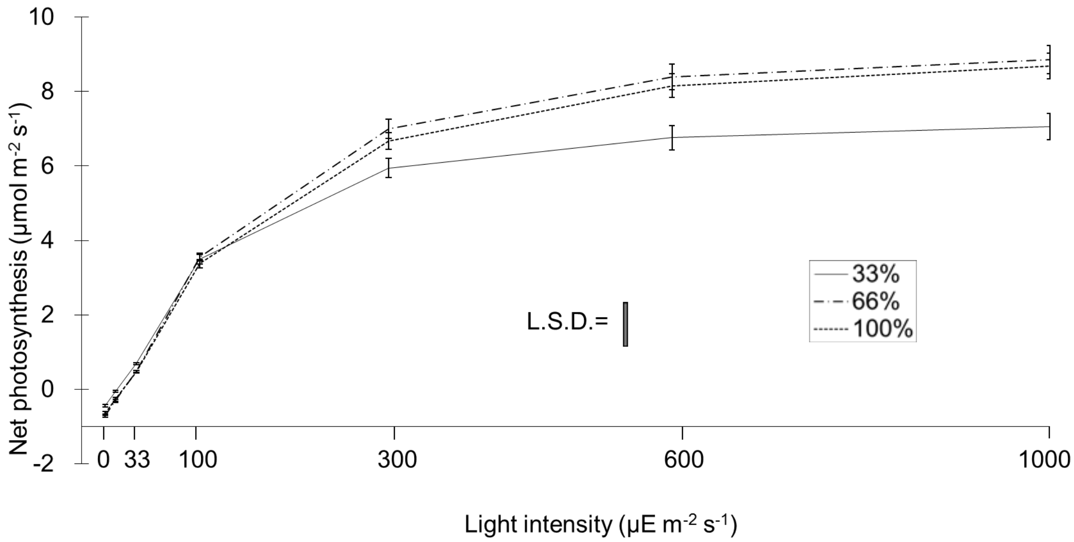

Figure 4A—Steady state net photosynthesis by redwood seedlings grown in the Large Opening Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$).

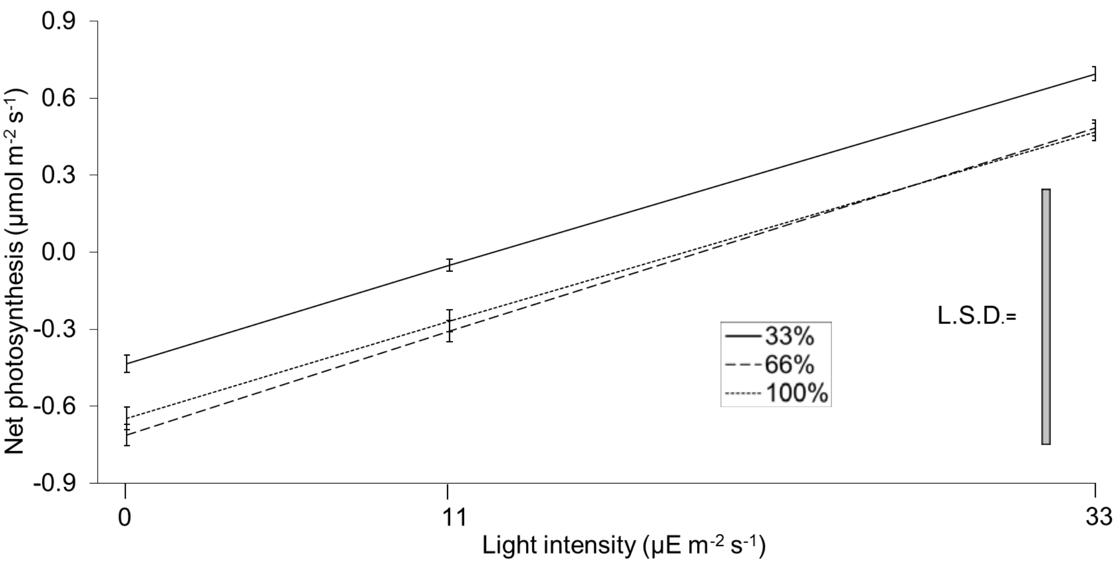

Figure 4B—Detail of steady state net photosynthesis by redwood seedlings grown in the Large Opening Pattern. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$). Quantum efficiency (slope) did not differ between different light intensities ($p < 0.05$).

It would appear that redwood is indeed plastic, or somewhat plastic, in its response to light. Classifications of redwood generally describe it as a tolerant tree implying it is a facultative shade species that can thrive in high light. Under the conditions of this experiment, redwood seedlings did thrive in the higher light treatments, especially with a relatively consistent light pattern. However, the seedlings also displayed methods of adjustment to low light. Given that redwood seedlings thrive in high light, but display methods of adjusting to low light, it may be accurate to consider redwood seedlings as facultative sun plants rather than as facultative shade plants.

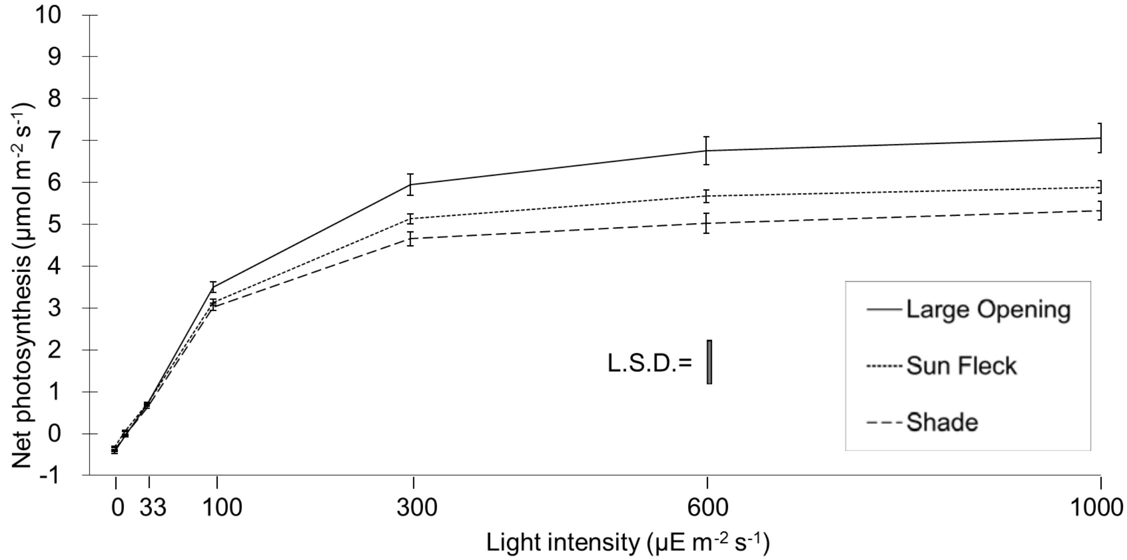

Figure 5A—Steady state net photosynthesis by redwood seedlings grown in the Equal Light Treatments. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$).

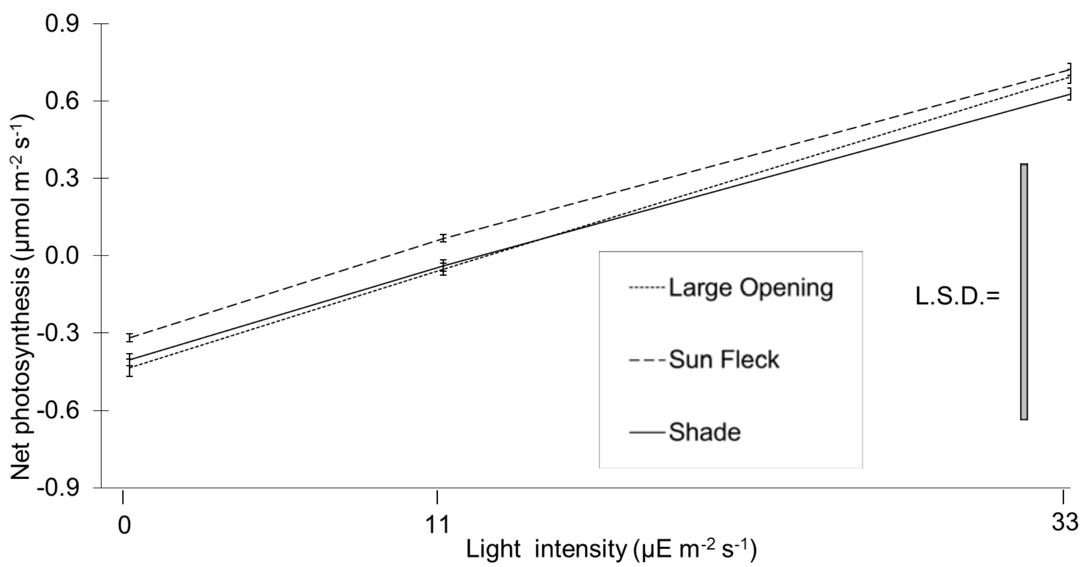

Figure 5B—Detail of steady state net photosynthesis by redwood seedlings grown in the Equal Light Treatments. Bars indicate standard error of the mean and LSD bar indicates Fisher's least significant difference among means ($p < 0.05$). There was no difference in quantum efficiency of seedlings grown in the different light patterns. Quantum efficiency (slope) did not differ between different light patterns ($p < 0.05$).

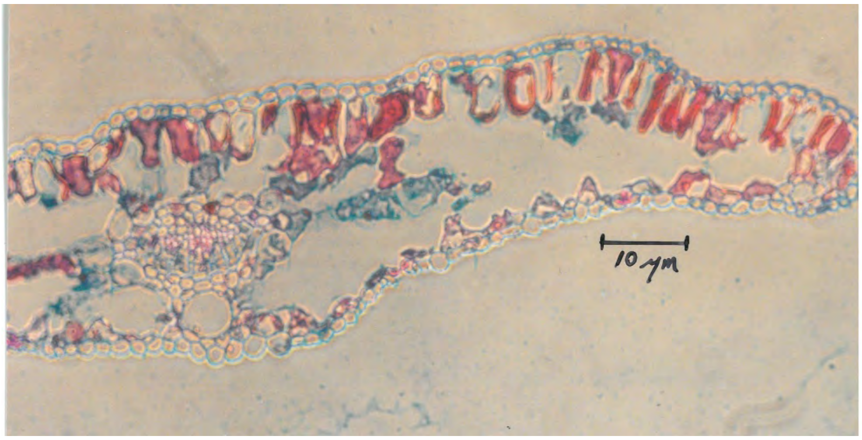

Figure 6—Needle cross section from a seedling grown in the 100 percent light intensity treatment of the Large Opening Pattern.

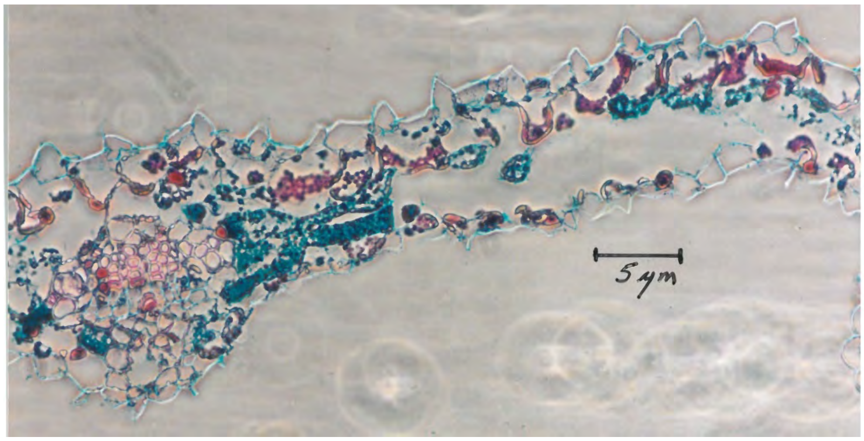

Figure 7—Needle cross section from a seedling grown in the 33 percent light intensity treatment of the Shade Pattern.

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