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ORIGINAL ARTICLE

Dynamics of coast redwood sprout clump development in variable light environments

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Abstract Post-thinning stump sprout response was assessed in a coast redwood [*Sequoia sempervirens* (D. Don) Endl.] stand from 5 to 9 years after five treatments were initiated. Nine years after treatment, leaf area index (LAI) ranged from 5.9 to 14.1 and the percent above canopy light (PACL) ranged from 0.8 to 3.9. Sprout responses included rapid self-thinning in all treatments with complete sprout mortality at low light regimes. Self-thinning of clumps increased with greater overstory LAI and poorer light regimes. Leaf area of individual sprout clumps also declined in low light regimes. The probability of sprout survival declined rapidly below 10 PACL and coincided with declining leaf area in sprout clumps. A conceptual model is presented that shows the sensitivity of redwood sprouts to light regime. Results have implications for management of multiaged stands and indicate these redwood coppice systems require relatively severe overstory treatments to provide sufficient light for sprout vigor and growth.

Keywords Coppice · Leaf area index · *Sequoia sempervirens* · Stump sprouting · Uneven-aged silviculture

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Introduction

Coast redwood [*Sequoia sempervirens* (D. Don) Endl.] is relatively unique among coniferous species because of its ability to produce stump sprouts after cutting. These sprouts are an important source of regeneration for this species because redwood typically does not reproduce reliably from seed (Olsen et al. 1990). Stump sprouts appear almost immediately after cutting and may number 100 or more per stump (Neal 1967). Over time sprout numbers decline through self-thinning and eventually only several may remain. However, this process may take decades and result in smaller stem sizes than if sprouts are artificially thinned (Cole 1983).

Stump sprout development is also important in multiaged redwood stands where the light regime is poorer. Redwood is well-suited to multiaged management systems because it is relatively shade tolerant (Baker 1949), it reproduces well vegetatively, and responds to release even after suppression (Olsen et al. 1990). It also has a relatively plastic crown form and crown development that allows it to quickly fill canopy gaps. This has implications for multiaged systems because smaller canopy gaps may be rapidly filled by existing trees and new regeneration may become suppressed. For example, projected leaf area indices (LAI) above eight may inhibit redwood sprout regeneration (O'Hara et al. 2007; Berrill and O'Hara 2009). These previous studies documented the negative effects of shade on growth; however, no information is available on mortality or self-thinning in understory redwood stump sprouts.

A redwood plantation established in 1982 and thinned in 1997 to various densities provided an opportunity to examine sprout response following overstory removal. This plantation was used to examine growth patterns of the tallest sprout in redwood stump sprout clumps in the first

5 years since thinning (O'Hara et al. 2007). This 2003 measurement documented projected LAI values as high as 14.3 and a saturating relationship between sprout height growth and light that resembled the light response relationships for seedling-origin trees growing in understory environments. In this study we continue this work by pursuing the following additional objectives through 9 years following thinning:

1. Identify trends in LAI and understory light from years five to nine in a series of young thinned redwood stands;
2. Determine sprout growth from age five through nine in a range of light environments; and
3. Examine the self-thinning and leaf area (LA) dynamics within individual sprout clumps following different overstory removal treatments.

Methods

Study area

A redwood plantation established in 1982 immediately south of Scotia in north coastal California, USA (40.461 N, 124.083 W) served as the study area. Precipitation in Fortuna (about 40 linear km distance) averages 1220 mm/year with approximately 81% occurring from November through March. Mean monthly temperature extremes range from 12 and 3°C in January to 20 and 11°C in August. The site was an alluvial flat that was historically occupied by redwood forest but had been used for pasture and a tree nursery for decades. Soils were deep Ferndale silt loams and fine sandy loams with plentiful soil moisture that typically represent the optimal conditions for redwood forest development (Stone and Vasey 1968; Noss 2000). Site index averaged greater than 45 m at 50 years (Wensel and Krumland 1986).

The plantation was established using container seedlings from local seed sources on a precise 3.05 × 3.05 m (10 ft) grid. Herbicides were used to control grasses and other herbaceous plants. Some seedlings were heavily browsed by deer in early years of the plantation but no control measures were undertaken. A small amount of seedling mortality was replaced in 1983.

Study design

The plantation was divided into 19 treatment units in 1997. These units ranged in size from 1.1 to 1.3 ha and were assigned to one of six treatments with two to five units per treatment. Treatments included a control, removing alternate rows in one direction ("alternate row" treatment), removing diagonal rows ("diagonal row"), removing every third row in one direction ("third row"), a treatment that removed alternate rows in both directions ("double alternate"), and a "free thinning" treatment. The free thinning was thinned to leave the best trees and remove approximately 60% of trees. Thinning began during the 1997 growing season and was completed before the 1998 growing season. Windthrow in 1998 occurred in the more heavily thinned treatments obscuring differences between the free and double alternate treatments and these three plots were subsequently combined and referred to as "low density" plots.

Fifteen rectangular plots distributed equally in five treatments were established in selected treatment units in 2003 (Table 1). Units were avoided if they were too small to include a plot without excessive edge effects or because of too much windthrow after the 1997 thinning. One plot was established in each of three units for the control, third row, alternate row, and low density treatments. Three plots were established in two units of diagonal row thinning.

The fifteen sample plots were designed to include a minimum of 20 overstory trees and ranged in size from 0.023 to 0.093 ha because of the variable densities in the treatment units. Control plots included 5 × 5 original grid points or positions of trees in the original planting. The alternate row included 5 × 10 and the diagonal row 5 × 8 or 6 × 9 original grid points. The third row included 5 × 9 grid points or six rows with trees and three thinned rows. The low density plots used a 9 × 9 or 10 × 10 grid sample. Numbers of sample trees also varied from the number of post-thinning grid points because of mortality prior to the 1997 thin and the multiple stems formed by many seedlings. Plots therefore included 20–30 grid points.

Table 1 Mean PACL for 2003 and 2007 or 5 and 9 years after thinning

Treatment	Date	*n*	Mean PACL (SE)	Min.–Max. PACL
Control	2003	3	0.62 (0.08)	0.54–0.77
	2007	2	0.89 (0.07)	0.82–0.95
Third row	2003	2	2.99 (1.48)	1.51–4.47
	2007	3	1.32 (0.12)	1.15–1.54
Alternate row	2003	3	6.12 (0.73)	4.78–7.27
	2007	2	1.88 (0.27	1.61–2.14
Diagonal row	2003	3	1.75 (0.17)	1.51–2.07
	2007	2	1.24 (0.07)	1.17–1.32
Low density	2003	3	26.86 (8.98)	10.26–41.11
	2007	1	3.94	–

Only the alternate row treatment had a significant difference between 2003 and 2007 ($P = 0.021$)

Although the study was intended to last for many years, the owner of the plantation, Scotia Pacific Lumber Company, thinned one control plot and one diagonal row plot in 2004 reducing the number of plots in these treatments to two each. In 2007, facing bankruptcy, Scotia Pacific Lumber Company decided to thin most of the remaining plots. The remaining plots were therefore remeasured in 2007 immediately prior to the thinning.

The diameter at 1.37 m (dbh), total height, and height to the crown base (lowest live branch) were measured on all overstory trees in 2003 and 2007. In both years, each tree was cored on the west side or as close to the west side as possible on multiple stem trees. To estimate LA, cores were measured for sapwood width using color and translucence to differentiate the sapwood/heartwood boundary. Bark thickness was measured adjacent to the core extraction points.

Tallest sprout development

Nearly all stumps produced sprouts following the 1997 thinning although some clumps were dead by 2003. In 2003, 15 sprout clumps per plot were randomly selected for measurement. A sprout clump was defined as a group of sprouts originating from one original grid point (i.e. tree stump) where a tree had been cut. If less than 15 living sprout clumps per plot were present, all were measured. For each of these sprout clumps the tallest or dominant sprout was measured for total height and caliper (diameter) at the base in both 2003 and 2007. Sampling intensities would have ranged from 20% in the low density to 100% in the third row treatments without mortality: actual sampling intensities of live clumps were 100, 73, 72 and 27% based on 2003 living sprout clumps for the third row, alternate row, diagonal row, and low density treatments, respectively.

Sprout clump dynamics

A random sample of four sprout clumps per thinning plot were selected for more intensive measurement. Some plots, in the third row treatment, had only three surviving sprout clumps in 2003 so all were sampled. The largest 20 sprouts/clump were tagged and measured for both height/length, caliper at the base, and dbh if they were equal or greater than 1.37 m tall. If the clump had greater than 20 sprouts, the remainder were counted but not tagged.

Light measurements

In both 2003 and 2007, photosynthetically active radiation was measured as photosynthetic photon flux density in μmol m^{-2} s^{-1} at designated points in sample plots. Light measurements followed procedures of Parent and Messier (1996) and Gendron et al. (1998). Measurements under the canopy were taken using a LI-COR system (Li-250 light meter with a Li-190SA quantum sensor attached; LI-COR Environmental Division, NE, USA) and compared with measurement from an AccuPAR ceptometer (model PAR-80; Decagon Devices, WA, USA) measuring simultaneously in an adjacent opening with full light exposure. To ensure compatibility of the readings taken by the sensors of the different instruments in the open and under canopy, an additional Li-190SA quantum sensor was attached to the ceptometer and monitored during some of the measurements. Percent above canopy light (PACL) represents the ratio of below to above canopy measurements. Within the plot, a single measurement was taken with the sensor held directly above the top of the dominant sprout in each clump with a telescoping height pole if necessary and leveled with a bubble level. The time of the sensor reading was noted for comparison with simultaneous "above canopy" measurements. This process was repeated in 2003 and again in 2007 within several hours of noon under cloudy conditions with the solar disk invisible. If the sprout clump was dead or missing, a measurement was made above the grid point. In the control plots, the sensor was held at equal distances from four grid points at an approximate height of 1 m throughout the interior of the plot resulting in 16 measurements per plot. Fourteen plots received light measurements in 2003: one-third row plot was flooded and not accessible at the time of sampling. In 2007, light measurements were completed in all of the remaining plots except one "low density" plot. Three light measurements from plot 4 were removed from the analysis because of a spike in radiation measured by the ceptometer in the opening.

Leaf area estimation

Leaf area was estimated from sapwood thickness on increment cores for larger individual trees. Sapwood cross-sectional area was calculated from dbh, bark thickness, and sapwood thickness. For trees with crown base above 1.37 m, a sapwood taper model for redwood (Stancioiu and O'Hara 2005) was used to estimate sapwood cross-sectional area at crown base. Projected LA was estimated from sapwood cross-sectional area at crown base using a ratio of 0.57 m^2:cm^2 (Stancioiu and O'Hara 2005). Leaf area of small trees was estimated from cross-sectional area of the stem at the base and using the 0.57 m^2:cm^2 LA:sapwood area ratio. Stand LAI was the sum of individual tree and stump sprout LAs divided by plot size (m^2/m^2). Leaf area of stump sprout clumps was the sum of LAs of all sprouts within a clump.

Analysis

A linear regression was fitted to the LAI–PACL relationship after a natural logarithmic transformation of PACL. Analysis of variance was used to compare LAI by treatment with a Holm–Sidak multiple comparison test to identify means with significant differences. Mean PACL was compared by measurement year using *t*-tests. An alpha of 0.05 was used for all tests. Logistic regression was used to estimate the probability of survival of the tallest sprout in each clump based on PACL. Linear and nonlinear regression were used to fit a variety of model forms to the relationship between sprout growth or percent survival and PACL. Models were compared in terms of goodness of fit using the Akaike information criterion (AIC) (Burnham and Anderson 2002) and the ecological basis of the model form.

Results

Stand LAI in 2003 and 2007 remained at similar levels in the control and third row treatments but tended to increase during the 4-year period in the more heavily thinned treatments (Fig. 1). However, only the alternate row treatment had a significant increase in 2007 ($P = 0.032$) because of the loss of one diagonal row plot and high variance in the low density treatment. In 2007, 25 years after planting and 10 years after thinning, no significant differences in overstory cohort LAI were observed except in the low density plots, where LAI was significantly lower than for all other treatments. In 2003, LAI for the control treatment was significantly greater and that for the low density treatment significantly less than for the other treatments (Fig. 1).

Percent above canopy light based on plot-level averages appeared to decline in the thinning treatments despite no significant change in LAI but increased in the control from 2003 to 2007 (Table 1). However, the combination of loss of plots and our inability to get light measurements before the harvest treatments reduced sample sizes so that only the decrease in the alternate row treatment was statistically significant ($P = 0.021$). The relationship between LAI and PACL in 2007 was a negative exponential form: $\mathrm{LAI} = 19.56 - 3.05 \times \ln\ (\mathrm{PACL}_{2007} \times 10)$ (adjusted $R^2 = 0.69$; SE = 0.89 m^2; $n = 10$). The coefficients for this model did not differ significantly from coefficients for an earlier 2003 model presented by O'Hara et al. (2007) that included a greater data range and more data points. Because these new data were assumed to validate the previous model, we developed a new model with both datasets that applies to thinned and unthinned stands 21–25 years old (Fig. 2).

Logistic regression models using light to predict survival of the tallest tree per clump demonstrated the importance of light to tree survival. The probability of survival approached 100% at only 10 PACL_{2003} but declined rapidly at lower light levels (Fig. 3). A 50% probability of survival was achieved with a PACL_{2003} of approximately 5.9% and a 10% probability of survival was achieved with a PACL_{2003} of approximately 2.4%.

The growth of surviving sprouts also showed strong sensitivity to light levels. PACL was averaged for 2003 and 2007 to represent average light for the growth period. Height growth of surviving trees—among the 20 largest sprouts sampled for growth in each clump—was strongly

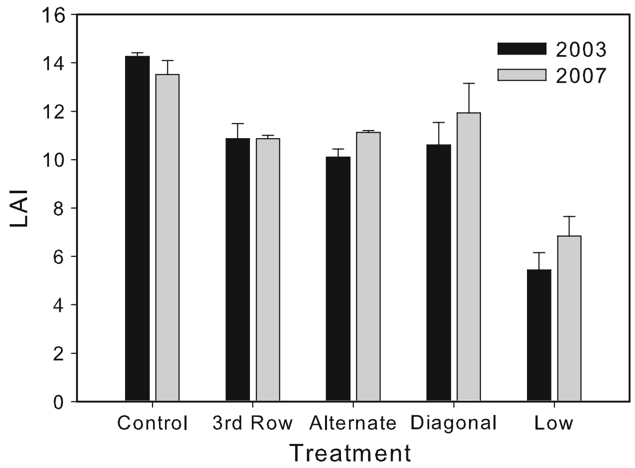

Fig. 1 Mean LAI for each treatment in 2003 and 2007 with one standard error. Means are based on three plots each in 2003, three plots in the third row, alternate, and low treatments in 2007, and two plots in the control and diagonal treatments

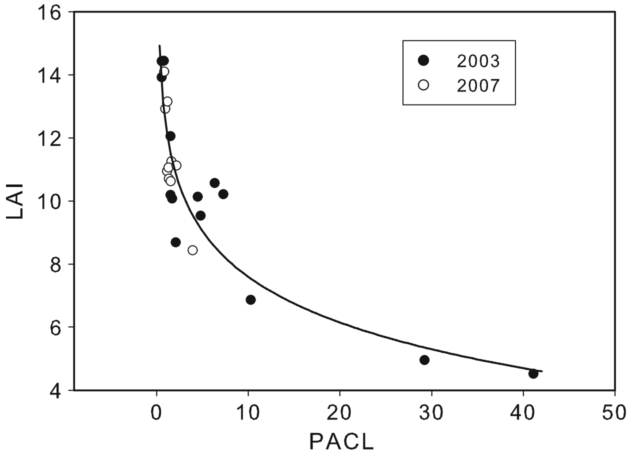

Fig. 2 Relationship between LAI and PACL using combined 2003 and 2007 data. Model was of the form: $\mathrm{LAI} = 17.21 - 2.09 \times \ln\ (\mathrm{PACL} \times 10)$, (adj. $R^2 = 0.81$, $P < 0.001$, SE = 1.15 m^2/m^2, $n = 24$)

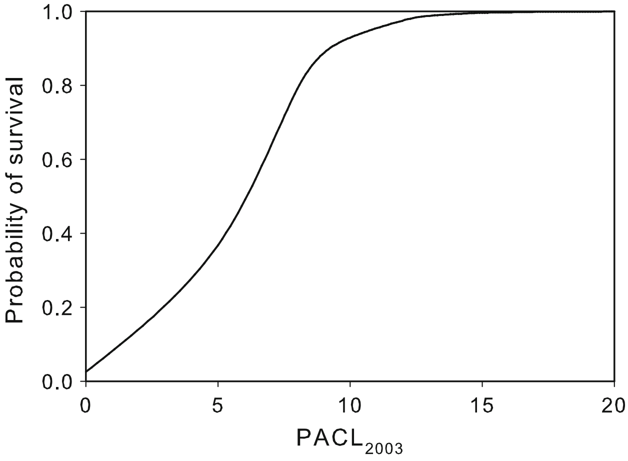

Fig. 3 Logistic model to predict the probability of survival of the tallest sprout in redwood sprout clumps. Model shown was probability of survival $P = e(-3.657 + 0.623\ \mathrm{PACL}_{2003})/(1 + e(-3.657 + 0.623\ \mathrm{PACL}_{2003}))$, (Wald statistics: constant = 21.657, $\mathrm{PACL}_{2003} = 22.229$; significance: constant < 0.001, $\mathrm{PACL}_{2003} < 0.001$; $n = 99$)

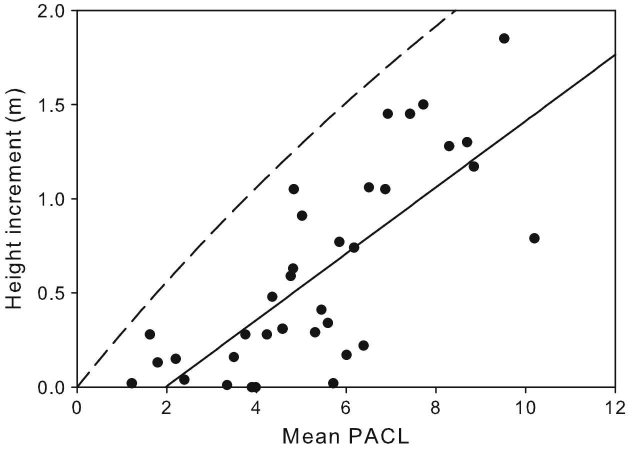

Fig. 4 Data and model of tallest sprout increment and mean PACL from 2003 to 2007. The linear model for 2003–2007 was of the form: HT Incr. = 0.044 mean PACL −0.087 (adj. $R^2 = 0.58$, $P < 0.001$, SE = 0.086 m/year, $n = 63$). The Michaelis–Menten model for data from 1999 to 2003 is also shown (*dashed line* data not shown; O'Hara et al. 2007)

related to average light. A linear model for 2003–2007 predicts less height growth per unit of PACL than the Michaelis–Menten model developed for the 1999–2003 data from this same trial. The 2003–2007 model indicates that sprout height growth ceases when average PACL falls below 2 (Fig. 4).

Sprout clumps comprised 1–50 individual sprouts in 2003, 5 years after the initial harvest treatment. In 2007 these numbers had declined dramatically in all treatments (Table 2). Percent survival of all sprouts within clumps from 2003 to 2007 in the low density treatment averaged approximately 44%. In the three lighter thinning treatments, within-clump survival of individual sprouts ranged from only 6.7 to 9.6%. Mortality of entire sprout clumps leading up to the 2007 assessment was strongly correlated with thinning treatment and the resulting light environment. All clumps were alive in 2007 in the low density treatment, but only 9.1% were alive in the third row treatment (Table 2).

Mean LA per sprout clump increased from 2003 to 2007 in the low density treatment but declined in the three less severe thinning treatments (Fig. 5). Mean PACL declined in all treatments between 2003 and 2007 (Fig. 5). However, the reduction in the diagonal row treatment was only from approximately 1.6–1.4%. PACL in the low density treatment was 6.4% in 2007, down from 16% in 2003 (Table 2).

Percent survival from 2003 to 2007 was related to PACL in 2003 through an asymptotic exponential function (Fig. 6). A similar model without an intercept produced a slightly lower AIC (209.185 vs. 209.380) but was not used because the non-zero intercept in the selected model accounted for the clumps with no survivors but with PACL up to approximately 7%. Additionally, the model in Fig. 6 had the lowest residual standard error. This model predicted 80% survival at a light level of 40 PACL, the upper limit of light intensity immediately above sprout clumps selected for investigation of within-sprout dynamics.

Discussion

The dynamics of redwood stump sprout clumps are primarily a function of their overstory light regime. These clumps exhibit three primary responses:

1. A reduction in growth with decreasing light and advancing age (Fig. 4). This is a common observation with seedling regeneration of many species (Helms and Standiford 1985; Lieffers et al. 1999; Stancioiu and O'Hara 2006) including understory redwood in multiaged stands (Berrill and O'Hara 2007), and confirms previous results from this study site with redwood stump sprouts (O'Hara et al. 2007).
2. Redwood stump sprouts, which may initially include over 100 stems per stump, self-thin rapidly in shade and self-thin at increasing rates in poorer light environments (Figs. 3, 5, 6). The notion that understory redwoods do not self-thin (Thornburgh et al. 2000) is not correct. Instead, densities of sprout clumps decline rapidly and may self-thin at rates similar to those of sprout clumps in full sunlight. Unlike self-thinning in full sunlight, which is the result of within-clump competition as dominant sprouts suppress

Table 2 Sprout survival, and mean leaf area, and PACL by treatment

Treatment	Percent survival of sprouts within clumps	Percent survival of clumps	Mean leaf area/clump 2003 (m^2)	Mean leaf area/clump 2007 (m^2)	Mean clump PACL 2003	Mean clump PACL 2007
Third row	6.7	9.1	2.8	0.3	3.0	1.4
Alternate row	9.6	71.4	5.0	2.1	8.5	3.1
Diagonal row	8.5	42.9	11.8	0.9	1.6	1.4
Low density	43.9	100.0	34.4	49.2	16.5	6.4

Survival data show the change from 2003 to 2007

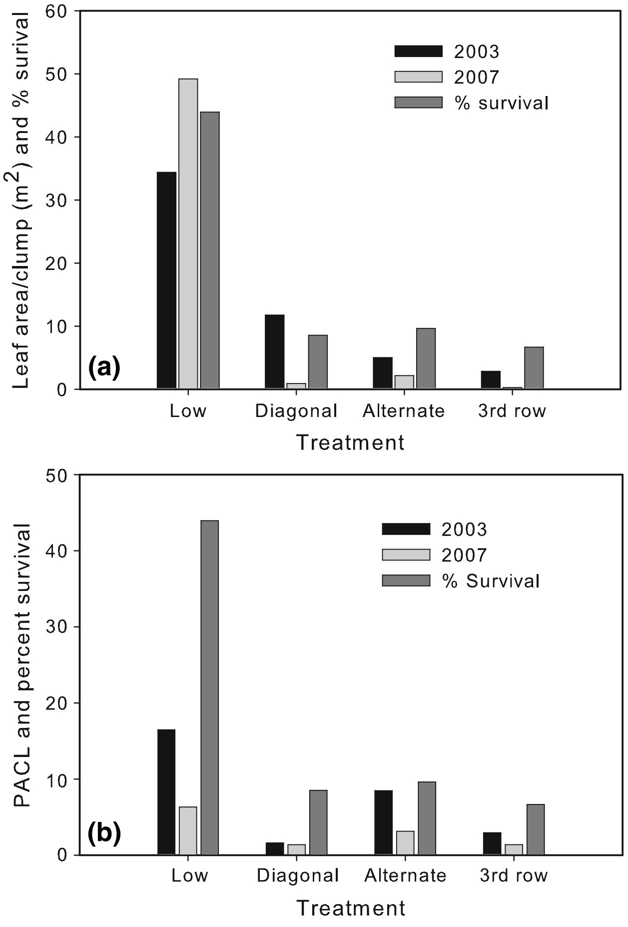

Fig. 5 Leaf area per clump in 2003 and 2007 by treatment (**a**). PACL in 2003 and 2007 by treatment (**b**). Both figures also show percent survival until 2007 by treatment

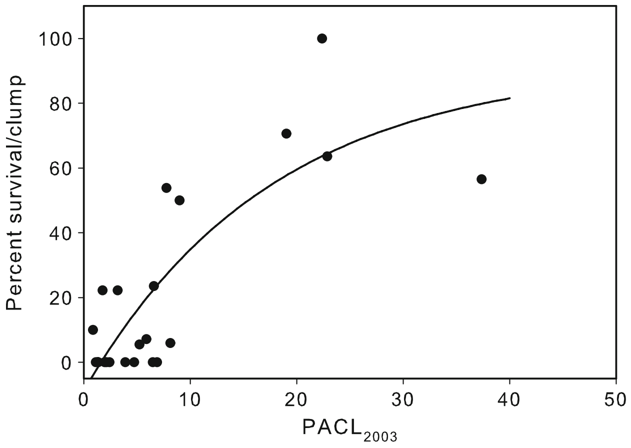

Fig. 6 Light regime and sprout mortality within clumps. Exponential model predicts percent of surviving sprouts per clump and PACL in 2003. Equation: $\text{percent survival} = -8.791 + 100.688(1 - \exp(-0.057\text{PACL}))$; ($P < 0.001$, SE = 17.17%, $n = 24$)

slower sprouts, the self-thinning in these sprout clumps in poor light environments seems to be a result of attrition in which all sprouts may eventually die.

3. Mortality of entire redwood sprout clumps becomes highly probable at light regimes below a PACL of 10 (Figs. 3, 5, 6). This mortality is evident in both reductions in numbers of sprouts per clump and mortality of entire stump sprout clumps. Light levels had fallen below this PACL threshold in all treatments by 9 years following thinning and within 5 years in the three less severe treatments.

This study was hampered by low survival of sprout clumps and the second partial harvest treatments that altered the light environment in some plots and hastened the final measurements of others. The rapid reduction in numbers of individual sprouts/clump and living clumps caused by competition was unexpected. After only 4 years since the study was initiated, approximately 85% of sprouts had died, and approximately 50% of sprout clumps were completely dead. Given these high rates of mortality, sample sizes should have been larger. Harvesting in 2004 resulted in the loss of two plots: one from the control, the other from the diagonal row treatments. This resulted in a reduction in the sample size. The 2007 remeasurement was unexpected and rushed because of impending harvest plans. As a result, not all light measurements were completed.

The study site had very high site productivity with site index in excess of 45 m (50 year, Wensel and Krumland 1986), and mean annual increment over 40 m^3/ha/year in control plots. The LAIs on this very productive site approached 14 and were high by any standards. Their effect on the understory was to intercept more light than would be typical of an average redwood site. These results probably represent a worst-case for suppression by the overstory and crown closure after thinning. However, the resulting sprout growth and mortality are indicative of light levels that may be less common, but could occur on most redwood sites. Whereas the LAIs may not have been representative across the range of redwood, the sprout response relationships that include a range of light intensities are probably representative of the broader redwood range.

Studies in redwood and other species have found the number of stump sprouts is unaffected by overstory cover and more a function of age and size of the parent tree (Wiant and Powers 1966; Solomon and Blum 1967; Neal 1967). The physiological reserves at time of cutting may therefore affect initial sprout numbers but subsequent sprout growth, vigor, and mortality may be more a function of light levels. For example, in a study of sprouting of potted redwood seedlings, sprouting was lower in poorer light environments (Finney 1993): hence at extremes the number of sprouts may be affected. Wiant and Powers (1966) described a "physiological equilibrium" for redwood stump sprouting where photosynthetic production equals carbohydrate requirements. Once a sprout clump exceeds the equilibrium, the system is self-sustaining and subsequent sprout growth is primarily a function of the light regime (Fig. 4, O'Hara et al. 2007). These results are consistent with previous studies in redwood (Boe 1975; Lindquist 1979, 2004; Barrett 1988) but quantify overstory competition with LAI and the light regime rather than basal area. The developing sprout clump continues to benefit from the existing root system (Bond and Midgley 2001). Post-equilibrium sprout growth in redwood can be very rapid and typically exceeds growth of seedlings (Fritz 1959; Jameson and Robards 2007) as with other sprouting species (Oliver and Larson 1996). Seedlings establishing in the understory may have light requirements different from those of stump sprouts, because they have smaller root systems to sustain. Sprouts originating from stumps in thinned clumps (where some existing stems were retained and maintain LA) may share resources with existing stems and therefore have light requirements different from those of sprouts originating from stumps where photosynthesis was halted by removal of all live stems.

Sprout height growth between 2003 and 2007 per unit of PACL was lower than earlier growth predicted by the Michaelis–Menten model developed for the 1999–2003 data from this same trial (Fig. 4). A Michaelis–Menten model is often used to represent growth of small trees in varying light environments (Pacala et al. 1996; Coates and Burton 1999; Drever and Lertzman 2001). The 2007 sprout growth and PACL data were best described by a linear model that performed slightly better than a Michaelis–Menten model based on AIC scores (48.7 for linear and 50.8 for Michaelis–Menten). The 1999–2003 model included data ranging to over 70 PACL and height increments up to approximately 1.6 m/year, whereas the more recent data had a narrower range and slower average growth (Fig. 4). This finding could reflect maturation in the aging stump sprouts, but also suggests that as sprouts develop they need more light to sustain height growth (of larger, older stems) or become more dependent on light as stored energy reserves in the established root system become depleted.

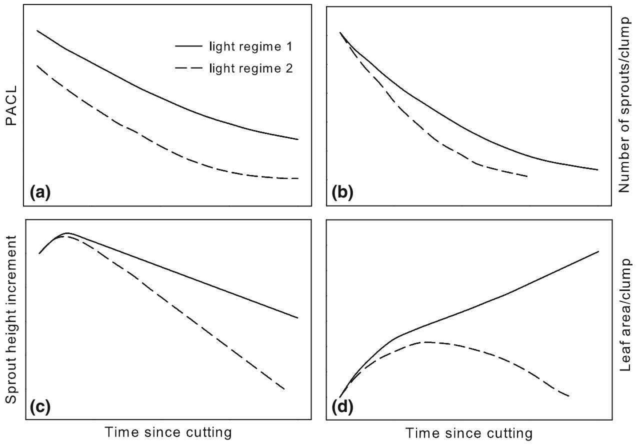

Fig. 7 Conceptual model for change in environment under a redwood canopy and the effect on stump sprout development for two different light regimes resulting from (*1*) heavier or (*2*) lighter overstory removal

Whereas number of sprouts following cutting is a function of pretreatment vigor and stump size, numbers of sprouts soon begin to self-thin relatively in full sunlight (Barrette 1966; Boe 1975). Self-thinning occurs more rapidly in poorer light environments (Figs. 5b, 6) and complete mortality of sprout clumps can occur in low light environments (Fig. 3). Hence the term "self-thinning" may not be as appropriate as a simple decline in density, because overstory competition appears to play a dominant role in affecting sprout mortality.

The relationships in Fig. 7 represent a conceptual model for stump sprout development following partial removal of the overstory. Similar relationships are probably applicable to other stump-sprouting species. Figure 7 presents two light regimes for post-cutting sprout development. Following cutting, the light environment for the understory sprout is at its maximum. With overstory crown expansion, light penetration to the understory declines with time (Fig. 7a). Initial sprout height growth is rapid after cutting because of stored reserves in the stump and the light environment at the stump (Fig. 7b). As storage reserves become less important than photosynthesis for growth, the light regime becomes the factor determining sprout growth. In redwood, a stump may produce more than 100 sprouts (Neal 1967; Powers and Wiant 1970). Resources are therefore divided among many growth points. The growth of the tallest sprout is a function of the light regime in redwood (Fig. 4) and in broadleaf species (Clark and Liming 1953; Gardiner and Helmig 1997). Differentiation and self-thinning in a sprout clump occurs rapidly, resulting in a relatively small number of sprouts early in stand development. The tallest sprout generally remains dominant during this process: only 5 of 54 surviving sprout clumps had a change in sprout dominance from 2003 to 2007.

Management implications

These data document the sensitivity of redwood sprouts to low quality light regimes. These results do not contradict the reported high shade tolerance of redwood (Baker 1949; Olsen et al. 1990). Instead they indicate that at relatively low light levels, even redwood sprouts may succumb to insufficient light. Redwood overstories have a great potential to reclose crowns following thinning (Fig. 5). This capacity to reclose the overstory canopy resulted in sharp reductions in light after only 9 years since thinning. For example, the alternate and diagonal row treatments were reduced in density by 50% in 1997, but had only 3.1 and 1.4 PACL in 2007 (Table 2).

These results have implications for two types of management activities: thinning of sprout clumps and management of overstory light in multiaged stands. Thinning of sprout clumps is a common part of precommercial thinning recommendations in even-aged redwood stands (Olsen et al. 1990). Reducing the number of sprouts to two or three per stump concentrates growth on the smaller number of residual sprouts and results in larger trees. Thinning of sprout clumps may also be appropriate in multiaged stands, but there would seem to be no justification in stands with low light levels because of high mortality of sprouts. Cole (1983) cautioned that thinning sprout clumps in uneven-aged systems might even kill sprout clumps because of insufficient carbohydrate production to support the existing root system.

Management regimes to promote new understory cohorts in redwood will need to provide sufficient light even if this regeneration is in the form of stump sprouts or other vegetative regeneration. For survival of these sprouts, light levels of approximately 5 PACL will be needed. However, at light levels below 8 PACL, growth is very slow and many sprouts are not growing (Fig. 4). For growth averaging 0.5 m/year, sustained PACL levels greater than approximately 15 will be necessary (O'Hara et al. 2007). A 1.0 m/year growth rate will require sustained PACL levels of approximately 40. Berrill and O'Hara (2009) recommended reducing basal area by at least 45% at each cutting cycle in multiaged stands to sustain sprout growth and vigor over longer cutting cycles. The effect of these 45% removals would, of course, be dependent on the pretreatment basal area levels. Successful multiaged silviculture in redwood requires replacement regeneration trees. Redwood trees, as with all species, require sufficient light to survive and grow. Multiaged silviculture is a balancing process between overstory and understory: too much overstory results in understory loss of vigor or death (O'Hara 1998). The tendency in redwood silviculture has been to under-harvest multiaged stands because of the ease of obtaining stump sprout regeneration and the redwood's high shade tolerance. However, the combination of rapid crown closure and requirements for minimal light levels indicate light management is essential to multiaged silviculture in redwood. This is no different than for other species, but becomes more urgent in redwood because of the rapid reductions in understory light following harvest treatments. Managers will need to control stocking to maintain sufficient understory light levels for understory survival and growth over the entire cutting cycle.

Conclusions

Responses to variable overstory removal in coast redwood indicated that:

1. Vigorous canopies expanded very rapidly after harvest and resulted in rapid reductions in understory light levels.
2. At higher light levels, stump sprout clumps can expand LA and grow rapidly in height forming a vigorous understory cohort.
3. At lower light levels, stump sprouts were less vigorous, as was evident from declining LA/clump and heavy clump mortality.
4. All sprout clumps exhibited a decline in number, or self-thinning, of sprouts. In high light environments this process occurred at a slower rate resulting in more sprouts per clump present at the time of measurement. In low light environments, the self-thinning process was rapid and was characterized by very low numbers of surviving sprouts and high rates of complete sprout clump mortality.

Management to encourage understory cohorts requires substantial overstory reductions to maintain sufficient understory light levels through an entire cutting cycle.

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