Growth and development of ponderosa pine on sites of contrasting productivities: relative importance of stand density and shrub competition effects[1]

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Abstract: Effects of stand density and shrub competition on growth and development were compared across a gradient of study sites. Challenge, the most productive site, is located in the foothills of the Sierra Nevada, northern California. Pringle Falls is of intermediate productivity in the rain shadow of the central Oregon Cascades. Trough Springs Ridge is the poorest site with minimally developed soils in California's North Coast Range. Treatments included a minimum of four stand densities, from 150 to 2700 trees·ha^{-1}, in combination with at least no or full shrub removal. Challenge produced almost twice as much tree volume as Pringle Falls, and about three times the volume of Trough Springs Ridge. Regardless of site quality, growth was significantly greater in full shrub removal plots for stand densities <2000 trees·ha^{-1}. After 26–36 years, stand volumes were 25–67 m^3·ha^{-1} (11%–38%) greater at Challenge, 30–33 m^3·ha^{-1} (25%–52%) greater at Pringle Falls, and 27–41 m^3·ha^{-1} (115%–326%) greater at Trough Springs Ridge when shrubs were removed. Periodic volume growth declined substantially during the last 10 years at Challenge and Pringle Falls, regardless of treatment, because of confounding effects of mortality, drought, inter-tree competition, and insect defoliation. Further, the importance of shrub control on growth increment was not evident during the last 10 years at both sites, as tree–shrub competition likely switched to tree–tree competition. On the low quality site, shrub control is critical for stand development.

Résumé : Les effets de la densité du peuplement et de la compétition des arbustes sur la croissance et le développement ont été comparés le long d'un gradient de stations expérimentales. Challenge, la station la plus productive, est situé dans les contreforts de la Sierra Nevada, dans le nord de la Californie. Pringle Falls dont la productivité est intermédiaire est situé dans l'ombre pluviométrique des Cascades, dans le centre de l'Oregon. Trough Springs Ridge, qui est la station la plus pauvre avec des sols à peine développés, est situé dans la partie nord de la chaîne côtière en Californie. Les traitements incluaient au moins quatre densités de peuplement, de 150 à 2700 tiges·ha^{-1}, combinées avec au moins l'élimination complète ou non des arbustes. À Challenge, le volume des arbres était presque deux fois plus élevé qu'à Pringle Falls et environ trois fois plus élevé qu'à Trough Springs Ridge. Peu importe la qualité de la station, la croissance était significativement plus forte dans les parcelles avec une densité de moins de 2000 tiges·ha^{-1} où les arbustes avaient été complètement éliminés. Après 26–36 ans, le volume du peuplement était 25–67 m^3·ha^{-1} (11 % – 38 %) plus élevé à Challenge, 30–33 m^3·ha^{-1} (25 % – 52 %) plus élevé à Pringle Falls et 27–41 m^3·ha^{-1} (115 % – 326 %) plus élevé à Trough Springs Ridge lorsque les arbustes avaient été enlevés. La croissance périodique en volume a diminué de façon importante au cours des 10 dernières années à Challenge et Pringle Falls, peu importe le traitement, à cause de la confusion créée par la mortalité, la sécheresse, la compétition interspécifique et la défoliation causée par les insectes. De plus, l'importance de la suppression des arbustes sur l'augmentation de la croissance n'était pas évidente durant les 10 dernières années dans les deux stations étant donné que la compétition entre les arbustes et les arbres a probablement été remplacée par la compétition entre les arbres. L'élimination des arbustes est critique pour le développement du peuplement dans la stations de qualité inférieure.

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Introduction

The successful establishment of plantations depends on a wide variety of factors including sufficient site preparation and competition control. Studies have shown that controlling competing vegetation is critical for the survival and growth of seedlings and consequently for stand establishment (Lanini and Radosevich 1986; Smith et al. 1997). In ponder-

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Table 1. Site characteristics for the three studies investigating the influence of stand density and shrub competition on growth of ponderosa pine.

	Challenge Experimental Forest	Pringle Falls Experimental Forest	Trough Springs Ridge
National Forest	Plumas NF	Deschutes NF	Mendocino NF
County, State	Yuba, California	Deschutes, Oregon	Colusa, California
Latitude	39°29′N	43°44′N	39°17′N
Longitude	121°13′W	121°36′W	122°40′W
Elevation (m)	810	1340	1280
Slope	S or SE 2%–10%	E 10%	E 20%
Site index (m at age 50 years)	34	24	17
Annual precipitation (mm)	1730	610	1040
Annual mean temperature (°C)	12.3	7.0	8.8
July average high temperature (°C)	30.0	26.0	28.0

osa pine (*Pinus ponderosa* P. & C. Lawson var. *ponderosa*) forests of Oregon and California, shrubs and trees are aggressively competing for natural resources such as water and nutrients (Riegel et al. 1991, 1995). After partial or complete stand-replacement disturbance, these sites are rapidly recolonized with early succession shrubs, such as *Arctostaphylos* and *Ceanothus*. If competing vegetation is not controlled, tree seedlings can be suppressed for decades (Conard and Radosevich 1982; Powers et al. 2004). Therefore, it is often important to control competing vegetation if trees are to occupy the dominant position in the plantation community.

Over the past decades, many investigators sought to quantify increases in productivity because of the control of competing vegetation. In a review of the literature, Wagner et al. (2006) found that the magnitude of increase by controlling competing vegetation was between 30% and 300% depending on the species, site quality, and stand age. McDonald and Oliver (1984) reported that 20%–30% woody shrub cover retarded pine seedling and sapling growth for a range of tree spacings in northern California. McDonald and Powers (2003) found that average stem volumes varied between 1 $m^3 \cdot ha^{-1}$ when a heavy shrub understory was present to 126 $m^3 \cdot ha^{-1}$ where shrubs were absent on a poor site after 40 years of stand development. Powers and Reynolds (1999) showed that the 10-year response to vegetation control interacted with site quality and water availability; the significance of shrub competition diminished as site quality improved. Nonetheless, most understory vegetation control studies are short-term, before canopy closure, and (or) only planted to a single density commonly used at the time of study establishment. Because a switchover process from a tree–shrub competition to an inter-tree competition occurs most likely after canopy closure that varies with stand densities, the interaction between competing vegetation and stand density could be very useful information for managing plantations as well as natural stands.

In this paper, we summarize results from three long-term studies of stand density and vegetation control that were established on different site qualities more than 30 years ago. The specific questions that we address are the following: (*i*) what are the long-term effects of shrub control on stand growth and development? (*ii*) Is there an interaction between stand density and shrub control? (*iii*) Is the pattern observed at each site the same?

Methods

Study sites and field design

The three long-term experiments are an initial spacing and understory competition study on the Challenge Experimental Forest, a thinning and understory removal study on advanced regeneration after release from old-growth trees on the Pringle Falls Experimental Forest, and a spacing and brush competition study established in an existing plantation on Trough Springs Ridge (Table 1). Detailed site descriptions and experimental design were provided in the earlier reports (Barrett 1965; Oliver 1979, 1984, 1990; Busse et al. 1996; Cochran and Barrett 1999). A brief description follows.

Challenge

The test was established from planted seedlings near the lower edge of the mixed-conifer forests, on the west slope of the northern Sierra Nevada. Soil, a Xeric Haplohumult (Aiken series), is more than 1.5 m deep. Dominant shrub species are whiteleaf manzanita (*Arctostaphylos viscida* C. Parry), deerbrush (*Ceanothus integerrimus* Hook. & Arn.), squaw carpet (*C. prostratus* Benth.), Indian manzanita (*A. mewukka* Merriam), small numbers of Sierra gooseberry (*Ribes roezlii* Regel), and sprouts of California black oak (*Quercus kelloggii* Newberry) and tanoak (*Lithocarpus densiflorus* [Hook. & Aan.] Rehd.).

In March 1966, seedlings (1–0) were planted in two randomized blocks within a clear-cut area after a standard site preparation. Each block contains five plots that were planted at square spacings of 1.8, 2.7, 3.7, 4.6, and 5.5 m to achieve a density of 2745, 1329, 746, 479, 331 trees per hectare (TPH). Each plot was split into two subplots. On one subplot, shrubs were completely killed by 2,4,5-T (2,4,5-trichlorophenoxy acetic acid) applied by hand sprayer in the 2nd and 4th years after planting. Subsequent shrub seedlings were removed by hand for about 5 more years. On the other subplot, shrubs were allowed to develop naturally. The average shrub crown cover was 125% in 1976 and 97% in 1986. Each subplot contained 12 measurement trees that were buffered from adjacent plots by at least 7 m, minimally two rows of trees. Because the same number of trees was used among plots, subplot size with buffer varied among treatments, covering 0.05 ha for 1.8 m spacings to 0.15 ha for 5.5 m spacings.

Pringle Falls

This experiment was established in a stand of 40- to 70-year-old suppressed saplings released from an old-growth overstory averaging 49 stems per ha and a tree diameter of 65 cm. It is located in the rain shadow of the central Oregon Cascades. Before the study was initiated, average diameter of understory trees was 2.5 cm, average height was 2.4 m, and average density was 17 300 stems per ha. The soil is a Xeric Vitricryand developed on 84 cm of dacite pumice from the eruption of Mount Mazama (Crater Lake). Dominant shrub species were antelope bitterbrush (*Purshia tridentata* (Pursh) DC), greenleaf manzanita (*A. patula* Greene), and snowbrush (*C. velutinus* Dougl. ex Hook.) with scattered Ross sedge (*Carex rossii* Boott).

The experiment was installed in the fall of 1958. Thirty 0.08 ha plots were selected within a 65 ha area. Each 24.1 m × 32.2 m plot is surrounded by a 10 m buffer strip. Five square spacings of 2.0, 2.8, 4.0, 5.7, and 8.0 m (2470, 1236, 618, 309, and 154 TPH) and two shrub treatments consist of 5 × 2 factorials that were randomly assigned to each of three blocks. All understory vegetation was removed in the spring of 1959 and at successive 3 to 4 year intervals on half of each spacing treatment. Understory vegetation was allowed to naturally develop on the other half. The average crown cover for the understory was 21% in 1959 and 30% in 1994, respectively. Freezing temperatures can damage some shrubs, if winter snow does not cover the shrubs (Busse et al. 1996). However, shrubs will recover the following summer (personal observations).

Manual control and 2,4,5-T were used in the initial removal of understory vegetation. In the following two removals, vegetation was removed by hand or by spraying 2,4-D (2,4-dichlorophenoxy acetic acid). After that, only manual control was performed.

Trough Springs Ridge

The study was established in a plantation on the eastern slopes of the North Coast Range of California. The plantation was originally hand planted in 1960 with 2–0 and 2–1 seedlings at spacings varying from 1.2 m × 1.2 m to 1.8 m × 2.4 m. When the study was installed in 1970, trees averaged 2.8 cm in DBH and 1.8 m in height. Stand density varied from 1422 to 3047 trees per ha. The soil is a Dystric Lithic Xerochrept (Maymen series) derived from Pre-Cretaceous metasedimentary rocks. Depth to lithic contact varies from 20 to 33 cm. Hoary manzanita (*A. canescens* var. *candidissima* [Eastw.] Munz) formed a uniform understory.

The original stand was thinned from below to four square spacings of 2.1, 2.4, 3.0, and 4.3 m to achieve a density of 2200, 1680, 1076, and 549 TPH, respectively. Each spacing was assigned to three 0.10 ha plots in a randomized block design. All plots were surrounded by a buffer strip 6 m wide. Five years later, in fall 1975, when all trees and shrub measurements were repeated, average diameter increased only 2 cm, and vigor of the trees had visually deteriorated, probably because soil moisture and nutrients were limited by severe shrub competition. A shrub density treatment was superimposed on each stand density plot. Each 0.10 ha plot was divided into three equal subplots. All shrubs were manually removed from one-third, left untouched in one-third with 35% crown cover, and every other shrub from the final third with 15% crown cover. By 1990, the average crown cover became 90% in no-removal plots and 47% in the half-removal plots, respectively.

Measurements

Challenge

Height and diameter at breast height (if tree height reached 1.37 m) were measured every year from 1968 to 1975, every 2 years from 1975 to 1985, every 4 years from 1985 to 2002. Volumes were determined by computing the stem segments as truncated cones with a modified STX program (Grosenbaugh 1964) from groundline to tip for about 120 trees, 6 from each subplot. Then, volume, as a function of DBH squared and height, was computed for trees with both no shrub removal and full shrub removal plots. Individual-tree volume was estimated with these equations.

Pringle Falls

Height and DBH of all trees were measured every 4–5 years from 1959 to 1994. Volume was calculated with equations developed for ponderosa pine in central Oregon by Cochran et al. (1984).

Trough Springs Ridge

Tree height and DBH was measured every 5 years from 1970 to 1996, except for the last period, which was 6 years. DBH was measured on every tree within each plot, whereas height was measured for 20% of the trees systematically selected. Then, the regression equations between height and DBH were established for each measurement year, and heights of the other 80% trees were estimated. We used the same method to calculate stem volume for individual trees as was used in the Challenge study.

Mortality and climatic data

Tree condition and mortality were evaluated at each measurement period. Because these studies have lasted for at least three decades, climatic patterns during this period are very important for the data interpretation. Therefore, climatic data from the closest weather stations to study sites were summarized (Western Regional Climate Center, www.wrcc.dri.edu, 16 September 2005). Strawberry Valley (1160 m elevation), California, is about 16 km northeast of Challenge. Bend (1110 m elevation), Oregon, is about 48 km northeast of Pringle Falls. Stony Gorge Reservoir (240 m elevation), California, is about 32 km northeast of Trough Springs Ridge. These stations provide the most complete data for the respective sites during the last 50 years.

Statistical analysis

The primary focus of the analysis was stand-level volume for each measurement year and periodic annual increments (PAI) in volume. We focused on stem volume, because it is the major portion of aboveground total biomass accumulation. Therefore, stand volume or PAI volume were chosen as

Table 2. Summary of type 3 tests of fixed effects including source of variation, degrees of freedom for both numerator (num) and denominator (den), and probability values for cumulative volume (Vol.) and periodic annual increment (PAI) of volume after ponderosa pine density and shrub control studies were established on the Challenge Experimental Forest, Pringle Falls Experimental Forest, and on Trough Springs Ridge, Mendocino National Forest.

	Challenge Experimental Forest				Pringle Falls Experimental Forest				Trough Springs Ridge			
	Numerator df	Denominator df	Volume ($m^3 \cdot ha^{-1}$)	PAI volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	Numerator df	Denominator df	Volume ($m^3 \cdot ha^{-1}$)	PAI volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	Numerator df	Denominator df	Volume ($m^3 \cdot ha^{-1}$)	PAI volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$)
Block	1	4	0.142	0.130	2	8	0.302	0.508	2	6	0.005	0.015
Density (D)	4	4	0.109	0.126	4	8	<0.001	<0.001	3	6	0.018	0.442
Shrub (S)	1	5	0.006	0.019	1	10	<0.001	<0.001	2	16	<0.001	<0.001
$D \times S$	4	5	0.661	0.636	4	10	0.096	0.449	6	16	0.761	0.934
Year (Y)	14	140	<0.001		8	160	<0.001		5	120	<0.001	
$Y \times D$	56	140	0.001		32	160	<0.001		15	120	0.631	
$Y \times S$	14	140	<0.001		8	160	<0.001		10	120	<0.001	
$Y \times D \times S$	53	140	0.982		32	160	0.906		30	120	1.000	
Year	15	142		<0.001	7	140		<0.001	4	96		<0.001
$Y \times D$	60	142		<0.001	28	140		<0.001	12	96		0.295
$Y \times S$	15	142		<0.001	7	140		<0.001	8	96		<0.001
$Y \times D \times S$	57	142		0.999	28	140		0.714	24	96		1.000

the dependent variables for the mixed linear model with year of sampling, block, tree density, and shrub treatment as explanatory variables. Because each plot or subplot (the experimental unit) was remeasured many times, each experimental unit was assumed to be the subject of the repeated measurements (the random effects). SAS MIXED procedure was used to estimate the regression parameters (SAS Institute Inc. 2001). The statistical model follows:

$$\text{Response} = B + D + S + D \times S + Y + D \times Y + S \times Y + D \times S \times Y + \text{EU} + \text{residual}$$

where, for the fixed effects, B is block effect, D is density effect, S is shrub control effect, Y is year or period effect, and $D \times S$, $D \times Y$, $S \times Y$, $D \times S \times Y$ are the interactions between and among terms. EU, the experimental units (plot or subplot) are the random effects assumed normally distributed, independent from each other, and independent from the residual error. In addition, we used the general linear model over-dispersed Poisson regression with the Bonferroni approach to compare the mortality between shrub treatments and among densities.

Results

Challenge

Cumulative volume and periodic annual increment (PAI) in volume differed significantly between no shrub removal and full shrub removal ($P < 0.02$), but no difference was detected among stand densities ($P > 0.10$) (Table 2). There was no significant interaction between density and shrub treatment in both variables ($P > 0.63$). The period or measurement year effect and interactions between treatment and period or year were highly significant except for three-way (period × density × shrub) interaction.

Compared with the 1985 results reported previously (Oliver 1990), we found that rank of total stand volume had changed from 1329 > 2745 > 746 > 331 > 479 TPH in 1985 to 1329 > 746 > 331 > 479 > 2745 TPH in 2002 for the full shrub removal plots (Fig. 1). If shrubs were not removed, the rank was 2745 > 1329 > 746 > 331 > 479 TPH in 1985 and 1329 > 2745 > 746 > 331 > 479 TPH in 2002. Plots with full shrub removal grew more volume than plots with no shrub removal in general. However, the trend reversed in the highest density level of 2745 TPH at the last measurement in 2002.

For PAI volume, we found that treatments with full shrub removal had more increment than those with no shrub removal before 1985. Yet, after that, no shrub removal plots had more increment than full shrub removal plots; this reverse trend occurred gradually from the plots with higher densities to those with the lower densities (Fig. 1). Interestingly, PAI volume decreased regardless of stand density or shrub treatment during the last period.

Overall, trees in the full shrub removal plots tend to be larger in DBH than trees in the no shrub removal plots (Fig. 2). However, the largest trees within each stand density are not necessarily in the full shrub removal plots. DBH variation was much greater in the no shrub removal plots than in the full shrub removal plots.

Fig. 1. Periodic annual increment (PAI) of volume and total cumulative volume (mean ± 1 SD) for ponderosa pine planted under five density levels that were split into either no shrub removal or full shrub removal at the Challenge Experimental Forest in Northern California. For PAI volume panels, drop lines at the bottom of the *x*-axis are periods that are referenced with the end-of-period years at the top of the *x*-axis. Period 1 (1970), 2 (1971), 3 (1972), 4 (1973), 5 (1974), 6 (1975), 7 (1976–1977), 8 (1978–1979), 9 (1980–1981), 10 (1982–1983), 11 (1984–1985), 12 (1986–1989), 13 (1990–1993), 14 (1994–1997), 15 (1998–2002).

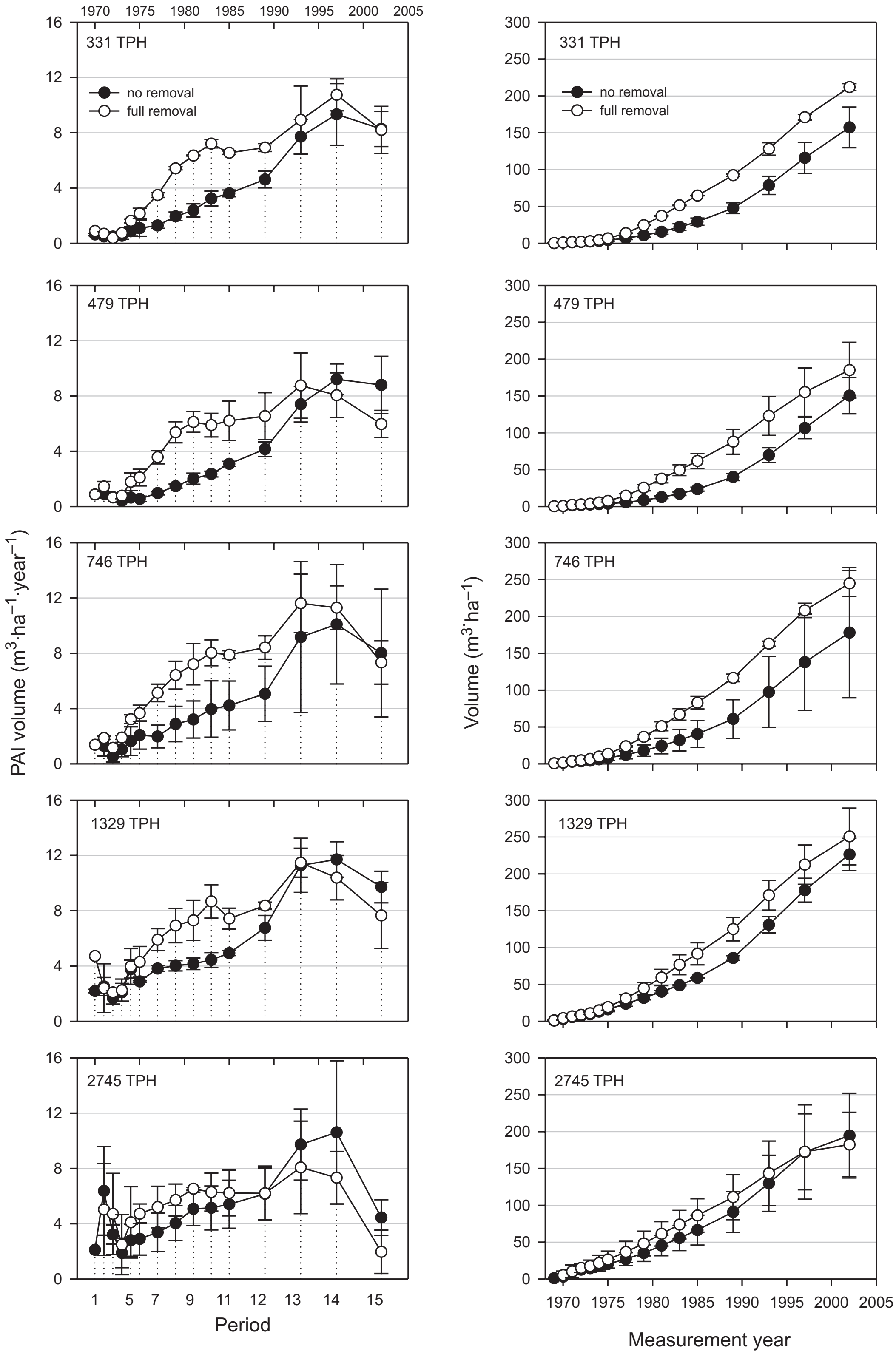
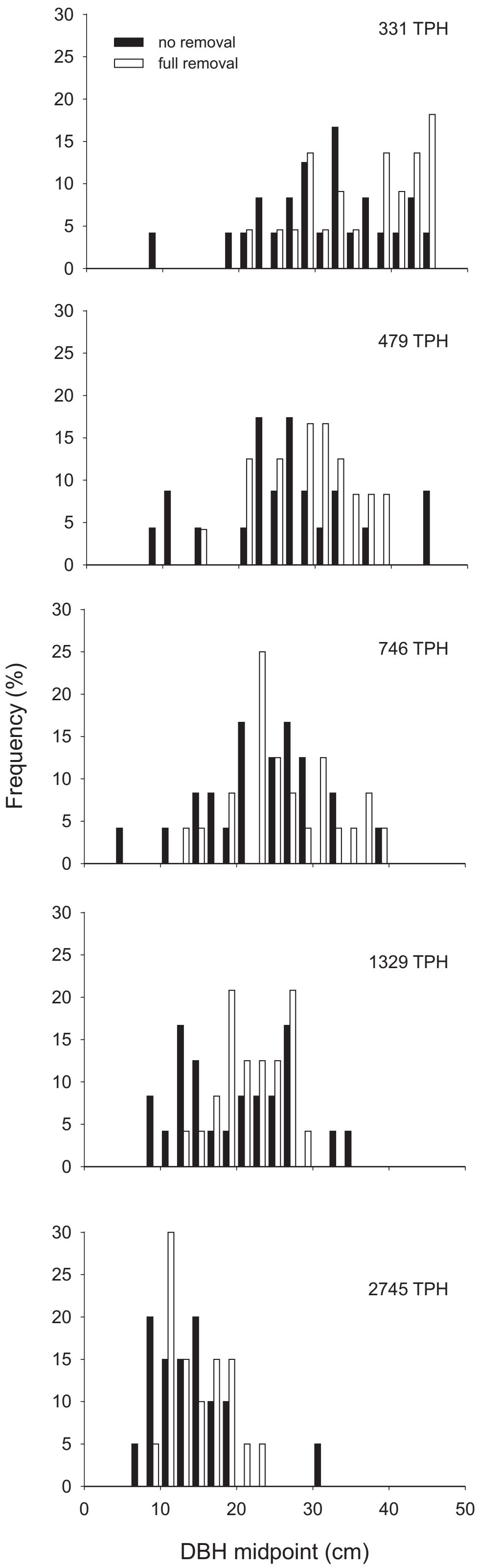


Fig. 2. Diameter-class frequency distributions for ponderosa pine grown with shrub present and absent at five density levels at the Challenge Experimental Forest in northern California. The latest data are presented.



Pringle Falls

Total cumulative volume and PAI volume differed significantly among densities and between full shrub removal and no shrub removal ($P < 0.01$), while the interaction of stand density and shrub treatment was not significant ($P > 0.09$) (Table 2). Similar to Challenge, the period or measurement year effect and retrospective interactions were highly significant except for the three-way (period × density × shrub) interaction.

Plots at higher stand densities produced more total volume and PAI volume than the lower density plots (Fig. 3). Plots with full shrub removal always had greater PAI volume than did those with no shrub removal, except for the final measurement period at the highest stand densities when PAIs were essentially equal. In addition, PAI volume declined considerably regardless of treatments in the last period (Fig. 3).

As expected, the lower density plots included trees of larger diameters than did higher density plots (Fig. 4). Trees in the full shrub removal plots tended to be larger in DBH than were trees in the no shrub removal plots. Yet, variation in DBH distribution tended to be the same between shrub treatments.

Trough Springs Ridge

Total volume and PAI volume differed significantly among shrub treatments ($P < 0.01$), and differences continued to widen between the extreme shrub control treatments. However, density effects were significant for total volume ($P < 0.02$), but not significant for PAI volume ($P > 0.44$). Density by shrub interaction was not significant for either variable ($P > 0.76$). The period or measurement year effect and retrospective interactions with shrub treatment were significant, but not with density nor with density and shrub interactions (Table 2).

As we expected, full shrub removal increased tree growth significantly when compared with other shrub treatments (Table 2; Fig. 5). Yet, there was no difference between no shrub removal and half shrub removal regardless of stand densities. PAI volume tended to slow during the fourth period (Fig. 5).

DBH distribution showed that trees in the full shrub removal plots tend to be larger than are trees in the half shrub removal plots, which in turn are larger than are trees in the no shrub removal plots (Fig. 6). Interestingly, unlike at Challenge and Pringle Falls, variation in volume and DBH was larger in the full shrub removal plots than in the no shrub removal plots (Figs. 5 and 6).

Mortality

After more than two decades since the studies were installed, differences in mortality were not significant between no shrub removal and full shrub removal at Challenge ($P >$ 0.77) and Pringle Falls ($P > 0.16$). As we expected, however, the densest plots showed significantly more mortality than the majority of the lower stand density plots ($\alpha = 0.05/10 = 0.005$ at Challenge: 2745 TPH vs. 331, 764, and 1329; 331 TPH vs. 764 and 1329 TPH. $\alpha = 0.05/6 = 0.017$ at Pringle Falls: 1235 TPH vs. 2469 TPH). The 154 and 309 TPH treatments were not included in the analysis, because no tree died in these plots (Table 3). In general, more trees died at both sites

Fig. 3. Periodic annual increment (PAI) of volume and total cumulative volume (mean ± 1 SD) for ponderosa pine suppressed saplings thinned into five density levels that were combined with two shrub treatments: no removal and full removal at the Pringle Falls Experimental Forest in Central Oregon. For PAI volume panels, drop lines at the bottom of the *x*-axis are periods that are referenced with the end-of-period years at the top of the *x*-axis. Period 1 (1960–1963), 2 (1964–1967), 3 (1968–1971), 4 (1972–1975), 5 (1976–1979), 6 (1980–1984), 7 (1985–1989), 8 (1990–1994).

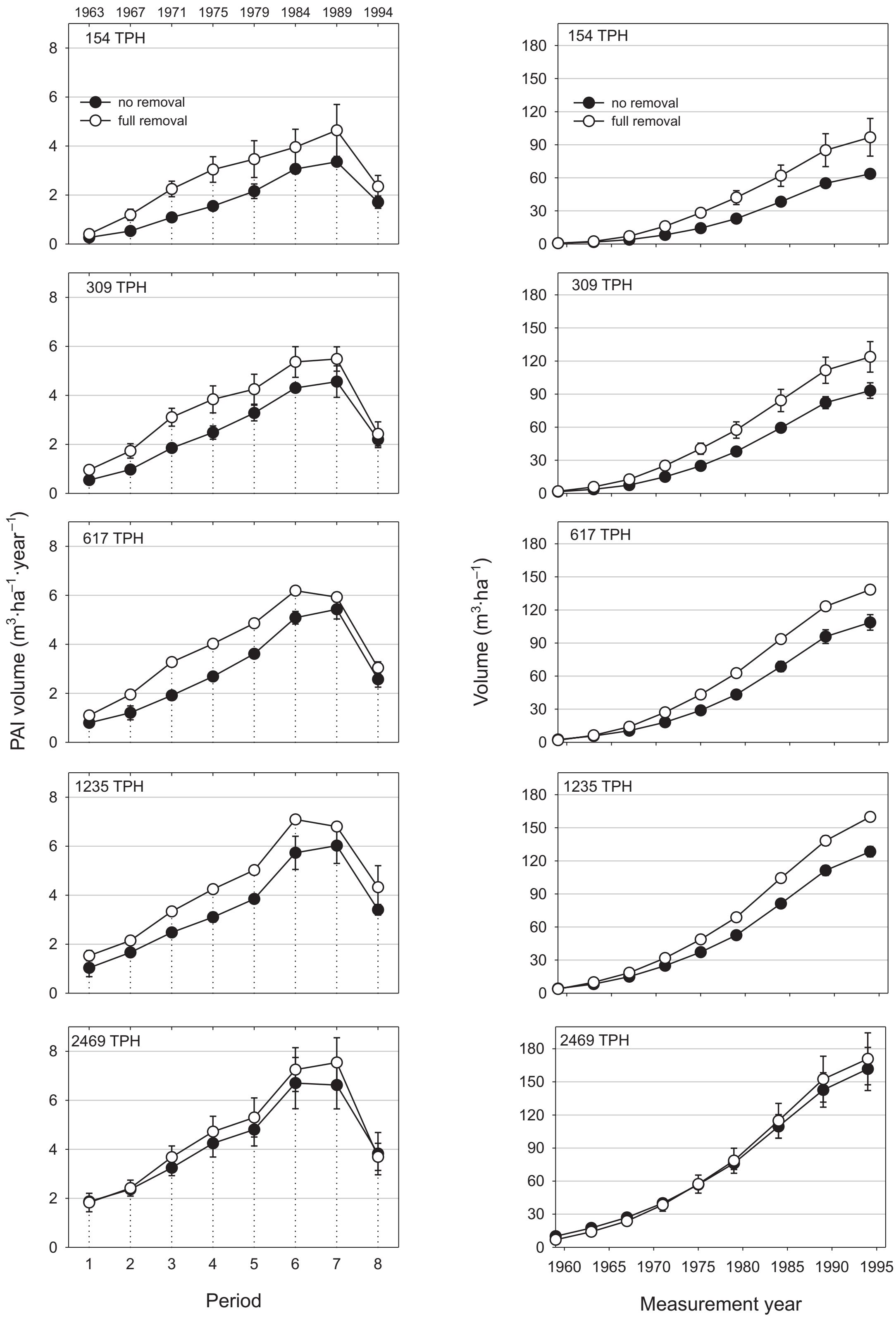
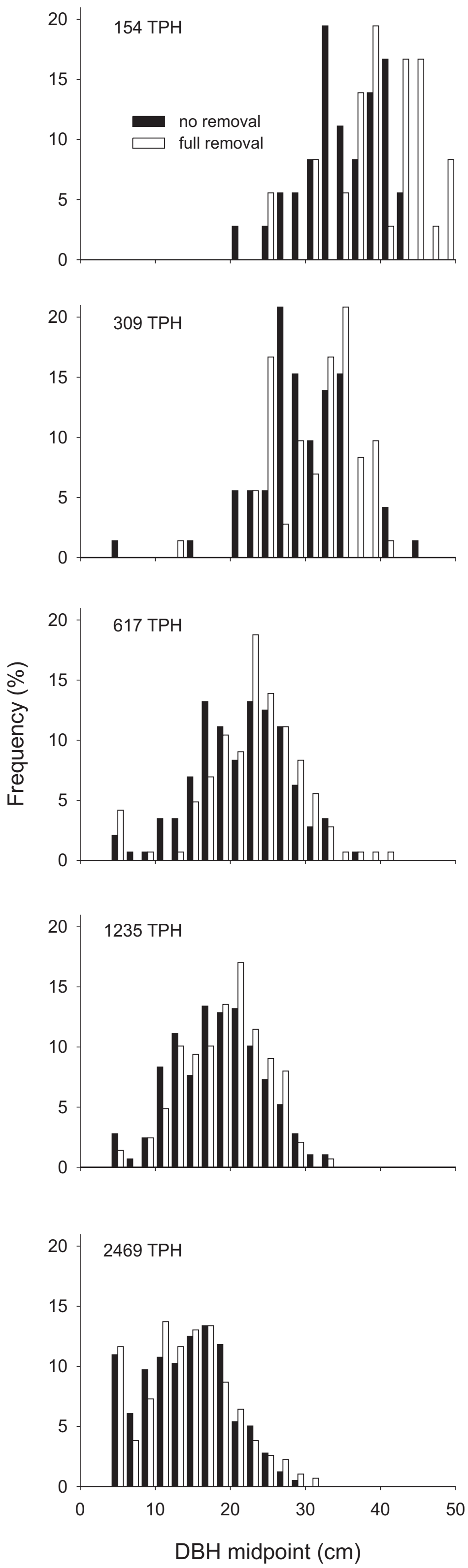


Fig. 4. Diameter-class frequency distributions for ponderosa pine grown with no shrub removal and full shrub removal within five density levels at the Pringle Falls Experimental Forest in central Oregon. The latest data from 2004 measurements are presented.



during the last measurement period. In contrast, mortality was negligible at Trough Springs Ridge and was unrelated to treatments or periods.

Climate

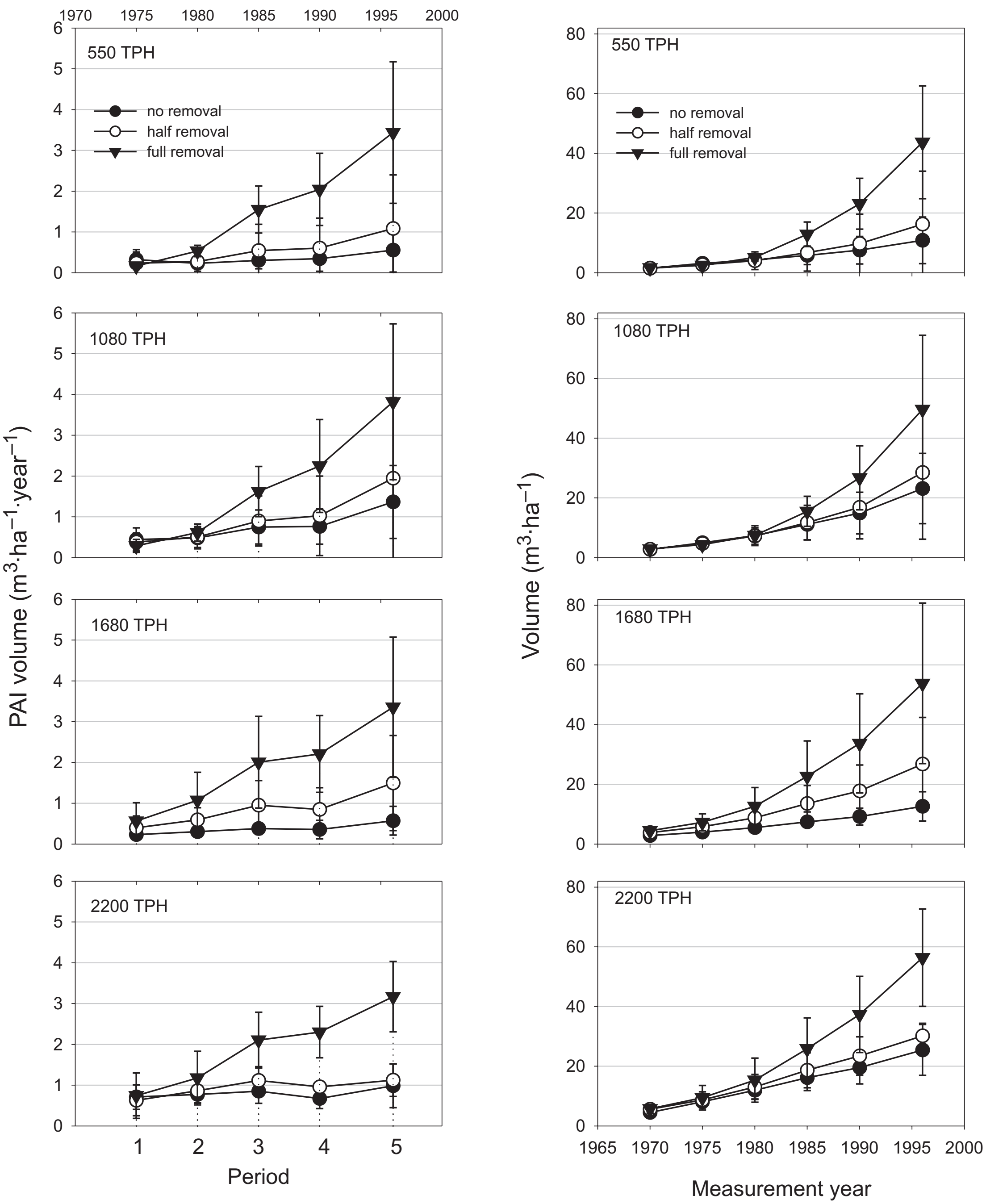
Weather patterns have been remarkably similar for northern California and central Oregon since 1985 (Fig. 7). For the last 20 years, precipitation was below average in most years except for 1986, 1993, 1995–1996, and 1998 in northern California and 1987, 1993, 1995–1996, and 1998 in central Oregon. Before 1985, the precipitation patterns varied slightly between the two regions, although a general trend was drier during the 1975–1980 period and wetter during the first half of the 1980s. There were two patterns for minimum air temperatures in the foothills of Sierra Nevada after the studies were initiated. From 1969 to 1983, annual air $T_{\min}$ was below the average about 4%, and since 1984 $T_{\min}$ was above the average about 4% except one year (Fig. 7). Similarly, two trends were also observed in central Oregon; colder from 1959 to 1977 and hotter from 1978 to 2004. Yet, there was lack of a clear trend for $T_{\min}$ in the North Coastal Range of California.

Discussion

The results of this study indicate that, in general, stand volume is increased by controlling competing shrubs, as the previous reports suggested (Oliver 1984, 1990; Cochran and Barrett 1999). This trend, however, may be converging as stands develop under high stand densities. The timing of this convergence, primarily of PAI volume, depends on stand density and site quality. A dense stand on a productive site, such as at Challenge, tends to develop quickly resulting in a convergence of the curves for stands with and without understory shrubs as early as 20 years for PAI volume and as early as 34 years for total volume (Fig. 1). At Pringle Falls on a site of intermediate productivity, the PAI volume curves converged in 36 years (Fig. 3). At Trough Springs Ridge on a site of low productivity, both volume increment and accumulation were significantly greater for full shrub removal plots than for no shrub removal plots throughout the 26 years of observation (Fig. 5). The heavy stands of manzanita continue to capture the limited supply of soil moisture and nutrients, suppressing tree growth (Shainsky and Radosevich 1986; Powers and Reynolds 1999; Powers et al. 2004).

The response of volume accumulation to full shrub removal varied between –33% and 326% across all densities and sites. The magnitude of response within a specific density and site is mainly dependent on the time of observation. Obviously, the lack of response in the earlier stage reflected the effect of thinning an existing stand as was done at both Pringle Falls and Trough Springs Ridge. Response was rapid at the Challenge site because this study started with seedlings. The maximum responses, 56%–199% at Challenge and 7%–97% at Pringle Falls, occurred between 13 and 20 years after the studies were installed (Figs. 1 and 3). The magnitude and time varied with the stand densities. In contrast, difference between full shrub removal and no shrub removal was about 115%–326% at 26 years after initiation of

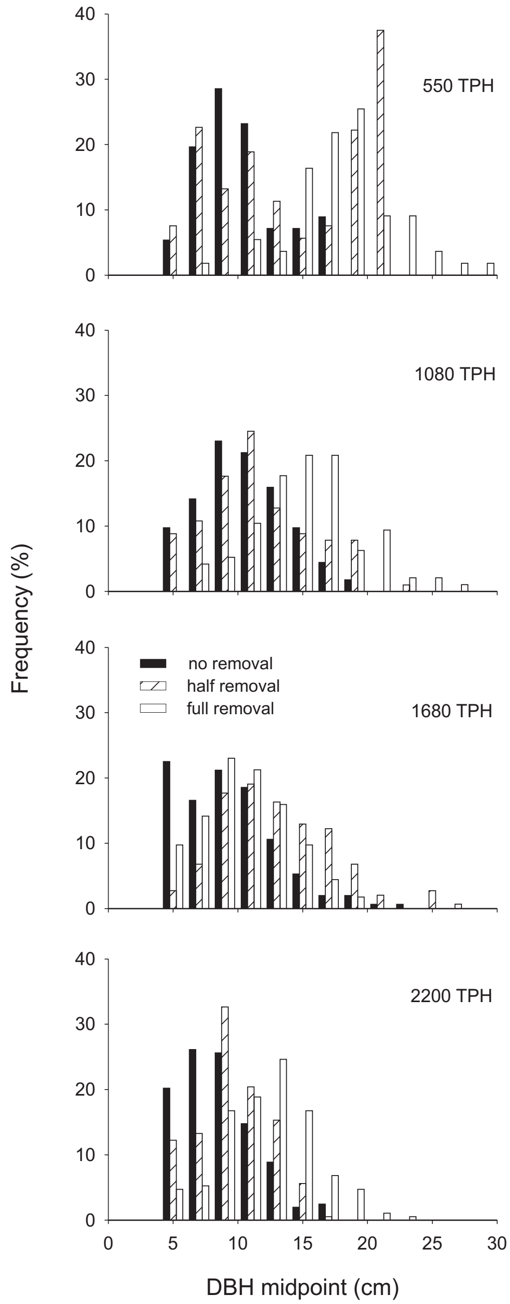
Fig. 5. Periodic annual increment (PAI) of volume and total cumulative volume (mean ± 1 SD) for ponderosa pine saplings thinned into four density levels that were split into three shrub controls: no removal, half removal, and full removal at Trough Springs Ridge, Mendocino National Forest in northern California. For PAI volume panels, drop lines at the bottom of the *x*-axis are periods that are referenced with the end-of-period years at the top of the *x*-axis. Period 1 (1970–1975), 2 (1976–1980), 3 (1981–1985), 4 (1986–1990), 5 (1991–1996).



the study and was still widening at Trough Springs Ridge (Fig. 5).

Although the percentage of volume increment by shrub removal was the highest on Trough Springs Ridge, absolute volume increment was much smaller than at Challenge. If the plots had been harvested in 2002, 55 $m^3 \cdot ha^{-1}$, more wood volume would have been produced at the density of 331 TPH in the full shrub removal plots than in the no shrub removal plots at Challenge (Fig. 1). Similarly, 35, 67, 25, and –12 $m^3 \cdot ha^{-1}$ more wood volume would have been produced at 447, 746, 1329, and 2745 TPH, respectively. The negative value in the densest plots was mainly caused by the lower PAI volume in the full shrub removal plots than in the no shrub removal plots for the last 10 years (Fig. 1). At the Pringle Falls site, 30–33 $m^3 \cdot ha^{-1}$ more volume would have been produced by controlling shrubs at 154, 309, 617, and 1235 TPH (Fig. 3). Only 9 $m^3 \cdot ha^{-1}$ more wood was produced at the density of 2469 TPH. This difference was most

Fig. 6. Diameter-class frequency distributions for ponderosa pine grown with no shrub removal, half shrub removal, and full shrub removal within four density levels at Trough Springs Ridge, Mendocino National Forest in northern California. The 1996 data are presented.



likely explained by mortality caused by intense inter-tree competition in the plots without shrubs (Table 3). At Trough Springs Ridge, about 27–41 $m^3 \cdot ha^{-1}$ more wood was produced by controlling the shrubs (Fig. 5).

A combination of mortality, inter-tree competition, and drought was responsible for the PAI volume drop observed during the last two periods at Challenge and at Pringle Falls (Figs. 1 and 3). One or two dead trees on the small plot sizes used in these studies can reduce per hectare volumes significantly. As a result, the marked drop in PAI volume might be due primarily to mortality. However, we also observed that PAI volume decreased for those plots without mortality such as the 1329 TPH plots without shrubs and the 746 TPH plots with shrubs at Challenge (Fig. 1) and the 154 TPH and 309 TPH plots for both shrub treatments at Pringle Falls (Fig. 3). This general PAI volume decline suggests that the trees were also under some biotic or abiotic stress. At Pringle Falls, a pandora moth (*Coloradia Pandora* Blake) outbreak began in 1991 (Busse et al. 1996). Study trees were partially defoliated in 1992 and 1994. That PAI volume was reduced during the last period is not surprising (Cochran 1998). Furthermore, trees have been under severe water stress during the last two periods, in which precipitation deficit was as high as –50% and evapotranspiration increased because of higher-than-average minimum temperature from 1985 to 1994 (Fig. 7). The same climatic pattern occurred in northern California, and therefore PAI declines at Challenge can be partially explained by water stress. In addition, rapid stand development resulting in intense inter-tree competition for water and nutrients could also be the reason after stand canopy closure. For the last period at Trough Spring Ridge between 1991 and 1996, we did not observe similar PAI volume decline (Fig. 5). Reasons might be (*i*) these trees were at a "young" developmental stage and (*ii*) the trees were not under water stress because precipitation was above and temperature was considerably below average (Fig. 7). The evidence of a slowdown (Fig. 5) during the fourth period (1986–1990) when precipitation was deficient (Fig. 7) supports our second hypothesis.

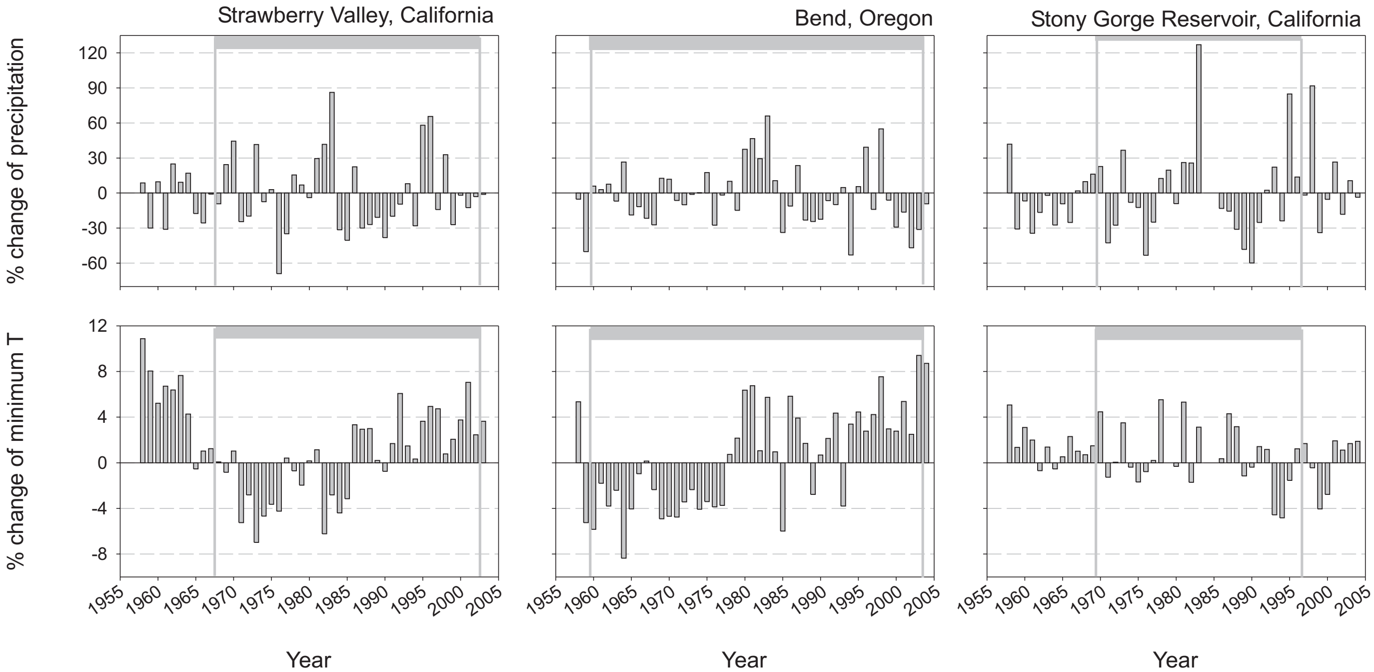
An unanswered question is why PAI volume in the no shrub removal plots converged or surpassed that in the full shrub removal plots at Pringle Falls and Challenge. One possible explanation is that the shrubs were shaded out and gradually died after canopy closure releasing water and nutrients to the trees during their "young" developmental stage. In addition, trees in the no shrub removal plots did not carry as much leaf area as did trees in the full shrub removal plots (personal observations). Soil water availability was higher in the no shrub removal plots than in the full shrub removal plots at the later stage (W.R. Horwath and R.F. Powers, unpublished data). Also, additional nutrients would be available through decomposition of the shrubs. If so, denser plots would close their canopies earlier, and PAI volume in the plots with shrubs would exceed PAI volume of plots without shrubs earlier than in the lower density plots. This is the case observed at Challenge (Fig. 1). Another possibility is that the no shrub removal plots showed greater soil carbon, nitrogen, and microbial biomass C, all indices of soil quality, than did the full removal plots (Busse et al. 1996). A more fertile soil would increase volume growth until it is constrained by inter-tree competition.

Objectives for managing young stands, whether they are for wood production, wildlife, aesthetics, or recreation, aim to enhance stand development with their attendant large tree component (Oliver 2000). Tree spacing and competing shrubs are integral factors affecting stand development. From these long-term studies, it appears that the diameter distribution at the end of the measurement period was more influenced by stand density than by shrub control at both Challenge and Pringle Falls (Figs. 2 and 4). However, the distribution was equally or more related to shrub control

Table 3. Mortality rate (%) of two shrub treatments across various densities (TPH, trees per hectare) in the measurement years when mortality changed for the studies at the Challenge Experimental Forest and the Pringle Falls Experimental Forest.

	Challenge Experimental Forest									
	No shrub removal					Full shrub removal				
Year	331 TPH	479 TPH	746 TPH	1329 TPH	2745 TPH	331 TPH	479 TPH	746 TPH	1329 TPH	2745 TPH
1970	0	0	0	0	0	0	0	0	0	0
1971	0	0	0	0	0	0	0	0	0	5
1974	0	4	0	0	0	0	0	0	0	5
1993	0	4	0	0	0	4	0	0	0	5
1997	0	4	0	0	9	8	0	0	0	9
2002	4	4	0	4	27	12	4	4	0	23
	Pringle Falls Experimental Forest									
	No shrub removal					Full shrub removal				
	154 TPH	309 TPH	617 TPH	1235 TPH	2469 TPH	154 TPH	309 TPH	617 TPH	1235 TPH	2469 TPH
1959	0	0	0	0	0	0	0	0	0	0
1967	0	0	1	0	1	0	0	1	0	0
1971	0	0	1	1	2	0	0	3	0	1
1975	0	0	1	1	3	0	0	3	0	2
1984	0	0	1	1	3	0	0	3	0	3
1989	0	0	1	1	5	0	0	3	0	3
1994	0	0	1	1	5	0	0	3	0	4
2004	0	0	3	3	9	0	0	5	1	8

Fig. 7. Percentage changes of annual precipitation and minimum temperature at Strawberry Valley, California from 1958 to 2003, Bend, Oregon from 1958 to 2004, and Stony Gorge Reservoir, California from 1958 to 2004 (missing 1984–1985) relative to average value, since weather data were recorded at Strawberry Valley (1948–2005), at Bend (1928–2005), and at Stony Gorge Reservoir (1948–2005), respectively. The horizontal bar on each panel indicates the years covered in this report.



than stand density at Trough Springs Ridge (Fig. 6). It is clearly evident that stand development can be arrested without shrub control on such low-quality sites.

The reduction in hazardous fuels can be another major advantage of controlling shrubs. Fire exclusion and minimal forest management over the last half century or more have created ponderosa pine forests at a high risk of stand-replacing wildfires. Early shrub removal and tree density control are the most effective and efficient ways to reduce this threat. When shrubs are controlled, trees can be planted at a wide spacing to maximize tree size and accelerate stand development. Precommercial thinning should be performed as soon as intensive intraspecific competition develops. At narrower spacings, potentially dominant trees can be identified as soon as the trees reach breast height (Oliver and Powers 1971).

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