Introduction

This paper reports a long-term study on secondary succession in an ecosystem consisting of three shrub species, one species of grass, a few forbs, and planted ponderosa pines. Because the study presents trends on the presence, density, and development of these species and their ascendance and decline, it has strong successional overtones. Because it demonstrates that even small amounts of an aggressive shrub species can significantly reduce pine seedling growth, it suggests at least one vegetation management principle. And because it creates an environment in which a less aggressive species excludes a more aggressive species, it suggests a biological means for manipulating unwanted vegetation.

Recent polls, newspaper articles, and proposed legislation seem to be emphasizing that the American people want the inherent productivity of the forest to be maintained, and that it provide a full range of amenities and commodities for future generations. Emphasis is being placed on ecosystems and especially on ecosystem components and processes. Sometimes, ecosystems need to be nudged a bit. Large burned areas that once were forest, for example, have no tree seed source and centuries can pass before a forest reoccupies the land. Here, ecosystem processes can be speeded up by manipulating a key component like plant species. Manipulation could be for a variety of reasons: to create a future forest, to provide an economic crop, to grow plants along with trees whose seeds would be critical to wildlife, or simply to provide a broad base of species and age classes and be in position to capitalize on values and commodities that will be needed in the future (McDonald and others 1994). In forestry, much knowledge has been generated on economic species (primarily conifer trees in the western United States), but little is available on the currently uneconomic hardwoods, shrubs, forbs, and grasses.

Stewart (1987) identified several major areas in forest vegetation management that needed research. One specific need was to evaluate "the effect of density and composition of the weed community on treatment response and degree of control." Only data from a long-term study can fully evaluate this need.

Abundant historical and scientific evidence shows that competing plants cause major losses in conifer seedling survival and subsequent growth (McHenry 1985). That competing vegetation must be controlled to provide site resources to conifer seedlings is almost universally agreed upon (Gjerstad and Glover 1992, McDonald and Fiddler 1989, Stewart and others 1984). In almost all plantations, even those with good site preparation, competing plant species either kill seedlings outright or reduce their growth below the potential of the site (McDonald and Fiddler 1986a).

This paper documents long-term (1962-1992) trends in shrub, grass, and ponderosa pine seedling development for four different initial shrub densities: no shrub, light, medium, and heavy shrubs. All were studied for 27 years. The fourfold objectives of this paper are both ecological and silvicultural: (1) to quantify density, foliar cover, height, and crown volume of shrubs and grass; diameter, foliar cover, height, and crown volume of ponderosa pine, (2) to denote growth dynamics of these species and trends in succession, (3) to relate shrub development to ponderosa pine survival and growth, and (4) to develop regression equations for each species in terms of the above variables, and to ascertain which shrub variable best quantifies competition to pine seedlings.

Methods

Location and Site Characteristics

The study site is located on the Mt. Shasta Ranger District of the USDA Forest Service's Shasta-Trinity National Forests, about 3 airline miles north of the city of

Mt. Shasta, and about an equal distance southwest of the mountain itself. The Township and Range survey notes of 1879 portray the vegetation in what is now the study area. The entire township was described as being "very heavily timbered" with five species of conifers and "some" oak. As close as can be determined, at least part of the study area supported this type of forest. Part of it also supported "dense chaparral undergrowth," which implies an overstory of trees. The recorded diameter of bearing trees (those marked to denote the location of section corners or quarter corners) varied between 4 and 60 inches at breast height. The largest breast-height diameter of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) was 50 inches, sugar pine (*Pinus lambertiana* Dougl.) 60 inches, and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) 38 inches. Trees of California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), incense-cedar (*Libocedrus decurrens* Torr.), and California black oak (*Quercus kelloggii* Newb.) were present but smaller.

In December 1886, the Central Pacific Railroad, which was extending its lines north from Redding, California and south from Medford, Oregon, met—forming an extensive West Coast rail network. The railroad was key to utilizing the vast timber resource in the area, and the logging and lumbering industries virtually exploded (Zanger 1992). By 1889, at least 10 sawmills were located near Sisson (renamed Mt. Shasta in 1923). Intense logging and lumbering, plus the inevitable spark lead to one fire after another. By 1898, a large area near Black Butte, which is very near the study area, was noted as being a brushfield (Barrett 1935).

By 1960, the brushfield consisted of a mass of vegetation 5 to 7 feet tall, that was virtually impenetrable to man or beast. Greenleaf manzanita (*Arctostaphylos patula* E. Greene), snowbrush (*Ceanothus velutinus* Hook.), and Sierra plum (*Prunus subcordata* Benth.) were the most abundant species. Conifer trees and seedlings were absent.

The 30-acre study area was cleared with a bulldozer in 1961 with shrubs being pushed into windrows (*fig. 1*) along with an estimated 4 to 6 inches of soil. Ponderosa pine seedlings, grown in the nursery for 2 years, were machine planted in April 1962 at an 8- by 10-foot spacing. The seed source was from zone

Figure 1—A ponderosa pine plantation similar to that in the study area. Notice the shrub development in the windrows. Mt. Shasta is in the background, circa 1970's.

"X," which was entitled "North Coast Pine," and included the Klamath Mountains Province (Fowells 1946).

A pioneering study by Jay Bentley began in 1961 when he and coworkers installed extensive trials for controlling shrub species that resprouted from root crowns and rootstocks, or arose from seeds buried in the soil. These trials involved dividing the area into many rectangular "bays," each of about 0.2 acres, sandwiched between windrows, and randomly applying various herbicides, dosages, application techniques, and timings of application (Bentley and others 1971). Some trials ended in 1962, some in 1964. Some were effective and some were not. The net effect was to leave a large area covered with a wide range of shrub densities (including no shrubs), ideal for a study whose aim was to quantify subsequent plant community-ponderosa pine relationships.

The study began in summer 1966. All bays were surveyed and the shrub density in each was recorded as no shrubs, light, medium, or heavy shrubs (*fig. 2*) based on Bentley's density data and relative visual differences. Values of about 5,000, 10,000, and 15,000 plants per acre separated the light, medium, and heavy designations. The number of bays in each shrub category ranged from 9 to 15. We then randomly chose four bays in each category as our sample. Each category was in effect a "treatment."

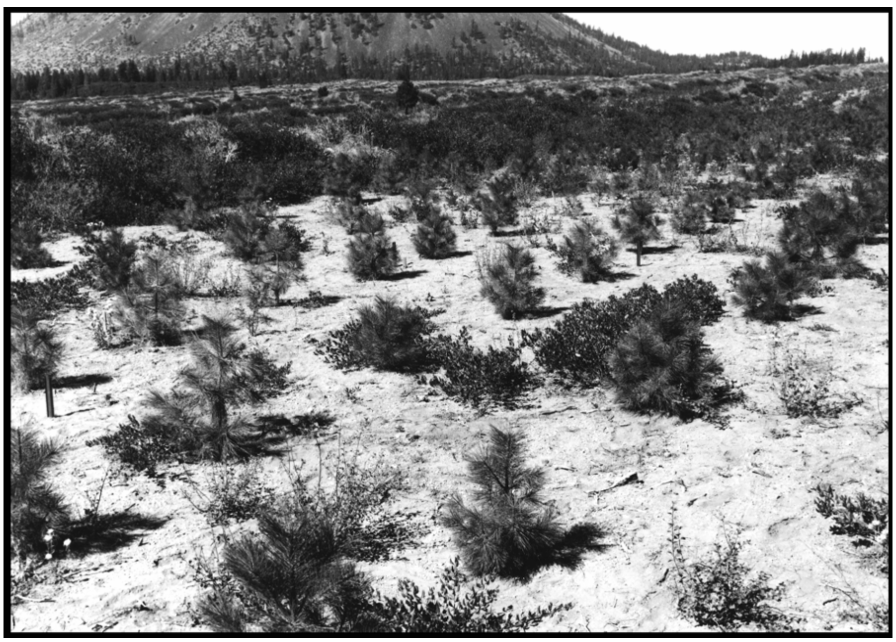
Site quality of the area is low (Conlin 1963) with dominant mixed conifers averaging 40 feet in height in 50 years (Biging and Wensel 1984). Fertility is rated as borderline for conifers (Conlin 1963). The slope of the study area is gentle (5 percent) with only minor dissection. The aspect is west and the elevation is about 4,100 feet. The soil is 42 to 54 inches deep, and of outwash material derived from andesitic rock. Soil texture grades from sandy loam near the surface to very gravelly sandy loam at the lowest horizon. The coarse soil tends to be well drained or excessively well drained. Mean annual precipitation is 38 inches with most falling in winter, about half as snow. The mean annual temperature is 49 °F and the growing season is about 130 days.

The plant community when we began the study consisted of the same shrub species noted earlier, the planted ponderosa pines, and a few other shrub and forb species. No grasses or natural conifer seedlings were present. Most vegetation was from seeds that were dormant in the soil or blew in on the wind. However, a few snowbrush plants sprouted from root crowns and all Sierra plum plants originated from roots and root crowns that had escaped the bulldozer.

Several species of insects besieged the plantation and affected the growth and form of the ponderosa pines. The principal species were the pine needle-sheath miner (*Zelleria haimbachi* Busch) (Stevens 1959) and the gouty pitch midge (*Cecidoymia piniinopis* Osten Sacken) (Bedard and others 1989). Because they were part of the ecology of the plantation and influenced the development of the pines, their damage was surveyed and extensive notes taken on their effect. Damage was recorded separately for death of the terminal shoot and death of lateral twigs.

Figure 2—Competing vegetation and ponderosa pine seedlings in (A) no-shrub, (B) light-shrub, (C) medium-shrub, and (D) heavy-shrub plots, Mt. Shasta brushfields, 1966.

A



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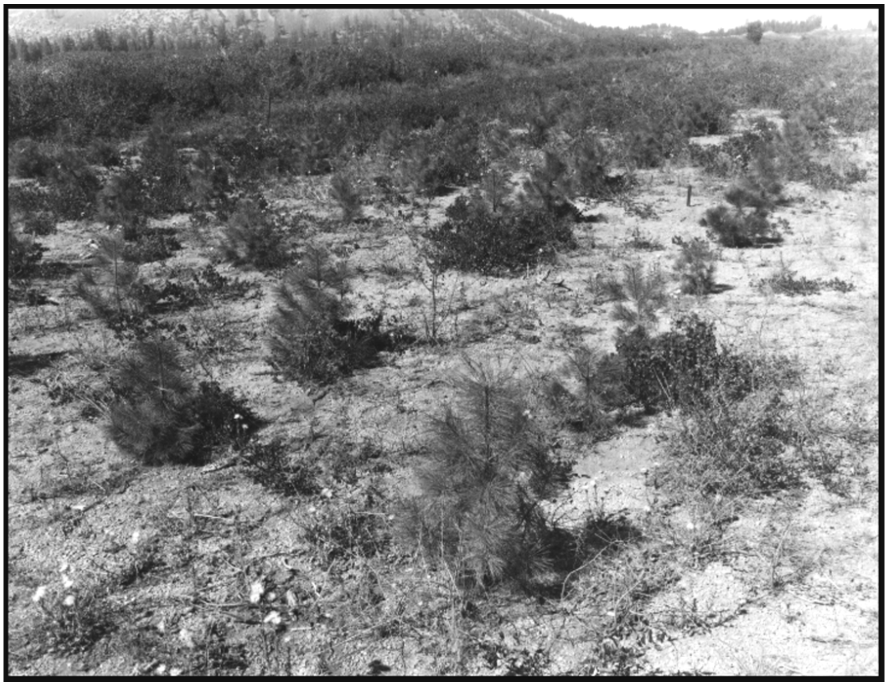

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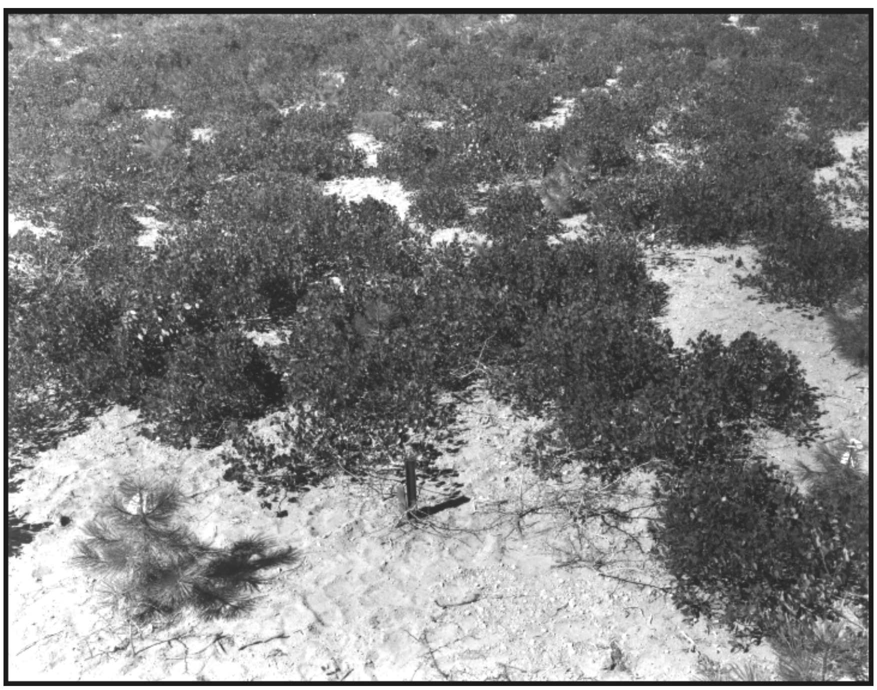


D

Study and Design

The experimental design was completely randomized with four treatment categories and four replications, each referred to as a "plot." Small manzanita and snowbrush seedlings were hand pulled in the no-shrub plots for the first two years. None appeared after that.

Each plot was rectangular and consisted of about 60 pine seedlings surrounded by at least two rows of buffer (seedlings receiving similar treatment). Forty healthy seedlings, identified as potential crop trees, then were chosen for treatment. No small, misshapen, or discolored seedlings that would have been removed in the first thinning were chosen. On each of the sample seedlings, stem height and stem diameter at breast height were measured. The seedlings also were checked for possible injury from wind, drought, or insects.

Sampling intensity of shrubs and other vegetation was five randomly selected subplots in each plot. Subplots were square and contained 1 milacre (0.001 acre). The most abundant species were measured for density, foliar cover (the sum of shadows that would be cast by leaves and stems of individual species expressed as a percentage of the land surface) (Daubenmire 1968), and average dominant height (average of the three tallest stems measured from mean groundline to top of plant). Less abundant species were not measured, but noted in a species list. Crown volume for shrubs and grass was calculated by multiplying foliar cover in square feet times height in feet. Crown volume for ponderosa pine, which was the space occupied by both crown and stem, was calculated using the formula of a cone ($1.047\ r^2h$). Volume in both instances was expressed on a per-acre basis.

Vegetation was measured in late summer or fall during various intervals, which were close together early in the study and widened at the study end. To test for treatment effects and significant differences among treatments, one-way analysis of variance of treatment means (fixed model, Steel and Torrie 1980) and Tukey tests were the analytical tools (SAS Institute 1988). Because natural resource managers may wish to express these species' development on similar sites, regression equations are presented for each species' density, foliar cover, height, and crown volume (SAS Institute 1988) on the basis of 1966-1992 data. One equation was fitted for each treatment and species. The general regression model was:

$$Y_{ij} = a + bx_{ij} + error_{ij}$$

where: Y = average response per plot;

a = intercept;

b = coefficient;

x = function of age (age^2, ln of age, or age);

i = 1,2,3,4; replication (number of plots/replication = 4);

j = 1,2, . . . y (y = number of yearly intervals).

The regression analyses ignore the fact that measurements were taken on permanent plots measured at yearly intervals and are not truly independent. This may underestimate the standard errors and possibly increase the significance of the estimated coefficients (intercept and slope).

And because we wished to determine which shrub variable explained the most variation in the various pine parameters, we regressed the pine parameters against the shrub variables. For this test, "shrub" was all shrub species in all categories. The general regression model was linear as before, where:

Y = average pine diameter, height, foliar cover per acre, or crown volume per acre response per plot,

a = intercept,

b = coefficient, and

x = shrub density, height, foliar cover per acre, or crown volume per acre at ages 10, 20, and 29. Three forms of each shrub variable (numerical value, value^2, and natural log of value) were tested.

Each pine parameter was regressed separately against each shrub variable, each treatment, each year, and each form.

Significance in all tests was at $\alpha = 0.05$. The α levels (type I errors) given for comparing means apply to each measurement time separately.

Results

Plant Diversity

The natural plant community on all plots at the beginning of the study (1966) consisted of 6 shrubs, 10 forbs, and one graminoid (*table 1*). One year later, a few plants of needlegrass (*Achnatherum nelsonii* [Scribner]) were noticed in the no-shrub and light-shrub plots. One other forb was found on study plots in 1975 and another in 1979. These were the only increases in species over the initial plant community. Two ephemeral forb species are noteworthy because of their contrasting habits. Baker's globe mallow (*Iliamna bakeri* [Jepson] Wiggins) is a relatively tall (2.5 feet) perennial that had invaded the study plots in 1966, peaked in 1971, and disappeared by 1979. It occupied only the most open places. American vetch (*Vicia americana* Willd. var. *americana*) is an annual that is both short (4 inches) and sprawling (up to 1.2 feet tall in deep shade). It invaded the study plots in 1975, peaked in 1979, and was gone in 1983. It tended to occupy the most dense plots although it was present in one light-shrub plot for some time.

Total number of species declined over time from the initial 17 members to 13 species in 1979, 11 species in 1983, and 8 species in 1992. By the study's end, the dominance of the shrubs and pines was nearly complete. Only two plants of one forb, three of another, and some short plants of needlegrass could be found.

Table 1—*Natural vegetation in study plots, Mt. Shasta brushfield, Shasta-Trinity National Forests, California, 1966-1992*

Species	1966	1977	1979	1983	1992
Shrubs					
Amelanchier pallida	X	X	X	X	-
Arctostaphylos patula	X	X	X	X	X
Ceanothus prostratus	X	X	X	X	X
Ceanothus velutinus	X	X	X	X	X
Chrysothamnus nauseosus	X	X	X	X	X
Prunus subcordata	X	X	X	X	X
Forbs					
Carduus nutans	X	-	-	-	-
Eriogonum spp.	X	X	X	X	X
Gayophytum spp.	X	-	X	-	-
Hypericum perforatum	X	-	-	-	-
Iliamna bakeri	X	X	-	-	-
Lilium spp.	X	X	X	X	-
Polygala cornuta	X	X	X	X	X
Stephanomeria paniculata	-	-	X	-	-
Tragopogon dubius	X	X	-	-	-
Vicia americana	-	X	X	X	-
Viola lobata	X	X	-	-	-
Unknown forb	X	X	-	-	-
Graminoids					
Carex spp.	X	-	-	-	-
Achnatherum nelsonii	-	X	X	X	X

Greenleaf Manzanita

Recorded observations of greenleaf manzanita during the study period showed a consistent trend of increasing development with virtually no damage from wind, frost, drought, or insects. The only damage noted was on July 26, 1977 (the second of 2 consecutive years of severe drought) when greenleaf manzanita was noted as having lost more than half of its leaves. No lasting effect from this leaf fall was recorded, however. One other botanically interesting event was that manzanita first began to layer in 1973—a process uncommon for this species. Layering is a process in which a stem, usually on an open-grown plant, touches the ground and develops roots at that point. Because layered plants remained attached to the parent, they were not considered as new plants and hence did not increase plant density.

In 1966, density of this evergreen shrub ranged from almost 1,500 plants per acre in the light-shrub category to almost 6,500 per acre in the heavy-shrub category—a statistically significant difference that continued through 1969, but not thereafter (*table 2*). From 1969 to 1992, manzanita density in the three shrub categories was relatively stable—gaining a little in the light-shrub category from new seedlings and decreasing a little from mortality in the medium- and heavy-shrub categories. At the end of the study, manzanita density ranged from 2,550 plants per acre to 4,750 plants per acre.

Table 2—*Average density, cover, height, and volume of greenleaf manzanita by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992*

Year	Category	Density	Cover	Height	Volume
		plants/acre	*ft^2/acre*	*ft*	*ft^3/acre*
1966	Light	1,499 a[1]	0 a	0.3 a	0 a
	Medium	4,246 ab	832 b	0.8 b	1,107 a
	Heavy	6,494 b	3,580 b	1.3 c	5,194 b
	Standard error	1,015	489	0.1	833
1969	Light	2,150 a	950 a	0.9 a	1,345 a
	Medium	4,900 ab	4,350 a	1.9 b	9,845 a
	Heavy	5,650 b	8,450 b	2.4 c	20,905 b
	Standard error	800	861	0.1	2,267
1971	Light	2,200 a	1,550 a	1.4 a	2,765 a
	Medium	4,800 a	5,300 a	2.6 b	15,110 b
	Heavy	5,350 a	11,250 b	2.9 b	33,290 c
	Standard error	649	1,034	0.2	2,691
1975	Light	2,450 a	2,750 a	1.9 a	6,665 a
	Medium	4,750 a	5,750 a	3.0 b	18,370 a
	Heavy	4,800 a	12,300 b	3.3 b	41,845 b
	Standard error	886	1,074	0.2	3,592
1979	Light	2,300 a	4,350 a	2.7 a	13,825 a
	Medium	4,700 a	7,650 a	3.8 b	30,325 b
	Heavy	4,750 a	15,200 b	4.0 b	61,355 c
	Standard error	836	1,060	0.2	4,107
1983	Light	2,400 a	6,950 a	3.4 a	27,445 a
	Medium	4,600 a	13,400 a	4.5 b	63,060 b
	Heavy	4,750 a	23,100 b	4.4 ab	102,780 c
	Standard error	811	1,835	0.3	7,525
1992	Light	2,550 a	9,150 a	4.4 a	47,445 a
	Medium	4,550 a	19,800 b	5.7 b	114,310 b
	Heavy	4,750 a	29,100 c	5.6 ab	163,355 c
	Standard error	783	2,215	0.3	11,513

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

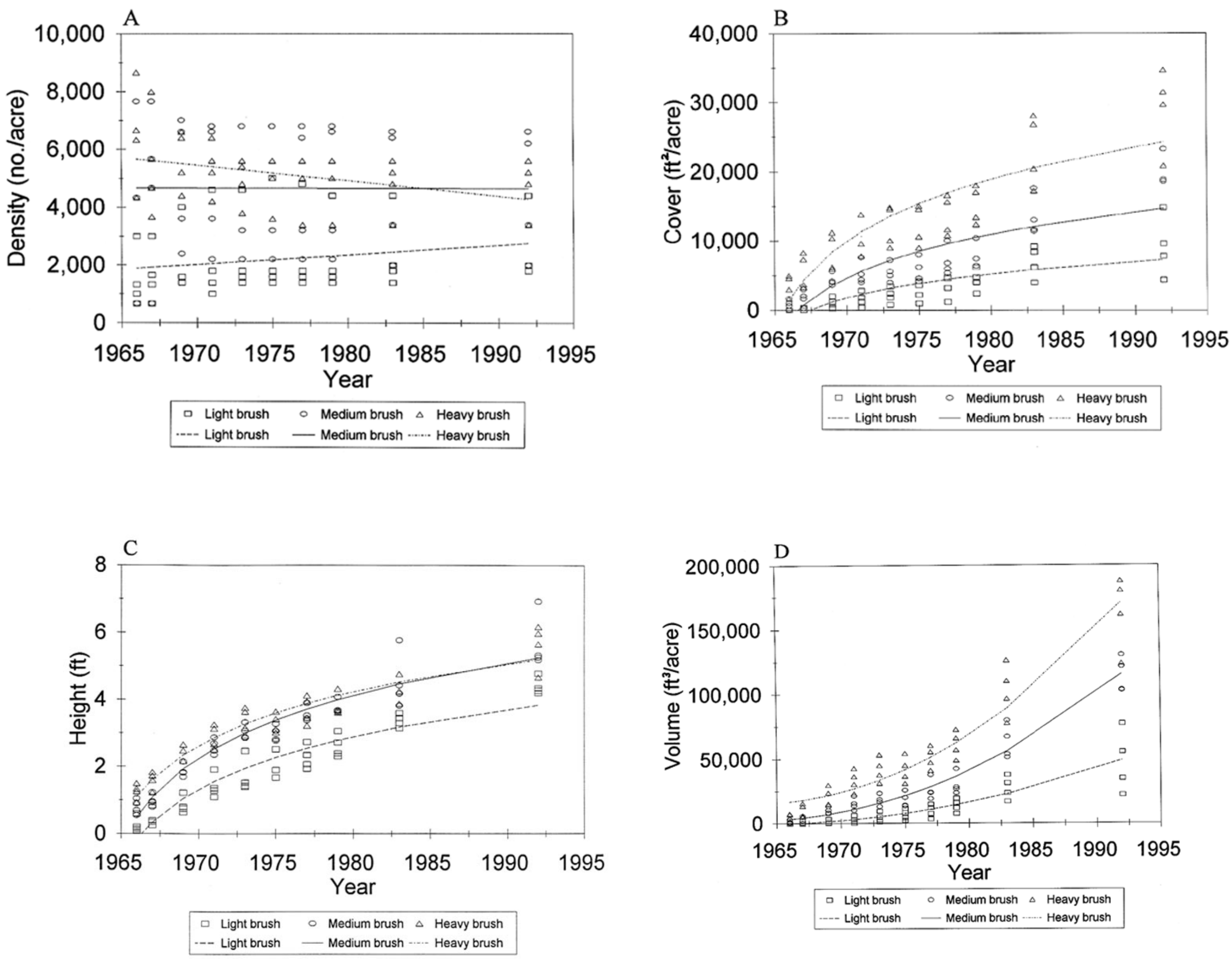
Foliar cover of greenleaf manzanita was dynamic. It increased in all shrub categories and differed statistically in various combinations among them for the entire study. By study end, foliar cover ranged from 9,150 ft^2 per acre in the light category to 29,100 ft^2 per acre in the heavy-shrub category.

Manzanita height followed much the same pattern of steady increase in all shrub categories with statistically shorter plants in the light-shrub category. By study end, plants averaged 4.4 to 5.7 feet tall (*table 2*).

Above-ground volume consistently increased in all shrub categories throughout the study period. By the end of the study, manzanita volume ranged from 47,445 ft^3 per acre in the light-shrub category to 163,355 ft^3 per acre in the heavy-shrub category (*table 2*). Crown volume per acre was always statistically larger in the heavy-shrub category relative to light shrubs and differences were statistically significant among all categories from 1979 through 1992.

The relationship of manzanita density, foliar cover, height, and volume over the 1966 through 1992 period are portrayed in *figure 3*. The regression equations are shown in the appendix.

Figure 3—Relationship of greenleaf manzanita to shrub density category for (A) density, (B) foliar cover, (C) height, and (D) crown volume, Mt. Shasta brushfields, 1962-1992.



Snowbrush

Development of snowbrush during the study period was characterized by rapid growth, periodic damage by abiotic agents, and finally by rapid senescence (*table 3*). One event in early October 1971 was notable because it did not happen. This was the year when one of the largest outbreaks of the California tortoiseshell (*Nymphalis californica* Boisduval) on record took place. On warm sunny days, tens of thousands of butterflies passed through the plantation in a given day. Their flight began about 12 p.m. and ended about 6 p.m. They flew just above the trees and shrubs in a southeast direction, generally quartering the gentle south wind. Although they defoliated several species of *Ceanothus* at mid elevations throughout much of northern and central California, they did not pause and consume snowbrush leaves in the study area.

Based on recorded observations, the winter of 1972-1973 was severe and many upright stems of snowbrush froze and died back to the root crown. New sprouts were prolific, however, and regrowth was rapid through 1975. Like manzanita, the 1976-1977 drought caused early loss of snowbrush leaves. It also killed upright snowbrush stems, and foliar cover declined. The cold, windy, virtually snowless winter of 1978-1979 exacerbated the decline of snowbrush,

Table 3—***Average density, cover, height, and volume of snowbrush by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992***

Year	Category	Density	Cover	Height	Volume
		plants/acre	*ft²/acre*	*ft*	*ft³/acre*
1966	Light	1,082 a[1]	1,415 a	1.0 a	1,715 a
	Medium	1,249 a	1,665 a	1.2 ab	2,231 a
	Heavy	1,498 a	1,998 a	1.5 b	3,230 a
	Standard error	275	615	0.1	900
1969	Light	1,050 a	3,650 a	1.7 a	7,200 a
	Medium	1,400 a	5,450 a	2.3 a	13,410 a
	Heavy	1,650 a	4,300 a	2.1 a	9,535 a
	Standard error	298	830	0.2	2,616
1971	Light	1,100 a	5,350 a	2.6 a	16,505 a
	Medium	1,400 a	7,850 a	3.1 a	26,300 a
	Heavy	1,700 a	5,900 a	2.7 a	18,220 a
	Standard error	254	1,495	0.3	6,204
1975	Light	1,050 a	5,950 a	2.9 a	17,990 a
	Medium	1,450 a	8,500 a	3.0 a	27,340 a
	Heavy	1,500 a	5,950 a	2.8 a	18,695 a
	Standard error	267	1,634	0.3	6,313
1979	Light	900 a	4,450 a	3.5 a	16,985 a
	Medium	1,250 a	6,800 a	3.8 a	27,605 a
	Heavy	1,400 a	4,650 a	3.5 a	18,165 a
	Standard error	270	1,025	0.3	6,369
1983	Light	800 a	4,350 a	3.8 a	19,300 a
	Medium	1,050 a	8,300 a	4.1 a	39,275 a
	Heavy	1,200 a	5,000 a	4.1 a	22,815 a
	Standard error	278	2,077	0.4	11,560
1992	Light	400 a	2,600 a	5.8 a	15,485 a
	Medium	600 a	2,250 a	6.1 a	14,065 a
	Heavy	950 a	1,750 a	5.6 a	11,305 a
	Standard error	237	823	0.5	4,958

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

and mortality—not just of upright stems—but of entire plants, was noted in all shrub categories. In 1983, some new sprouting from the root crown was recorded, but entire plants continued to die. Individual stems died also, but this time, the lower (shaded) stems expired, rather than the exposed (upright) ones. The form of snowbrush plants also changed as remaining stems were forced to become more upright to stay in sunlight. By 1992, many plants and stems had died. Those left were generally tall and spindly.

Density of snowbrush in 1966 varied from more than 1,000 plants per acre in light-shrub plots to almost 1,500 plants per acre in heavy-shrub plots (*table 3*). For all shrub categories, mean density stayed relatively constant through 1971 and then decreased from 1975 through 1992. By the end of the study, density of snowbrush had decreased 65 percent to 400 plants per acre in light-shrub plots and by 44 percent to 950 plants per acre in heavy-shrub plots. At no time during the study were differences in snowbrush density among shrub categories statistically significant.

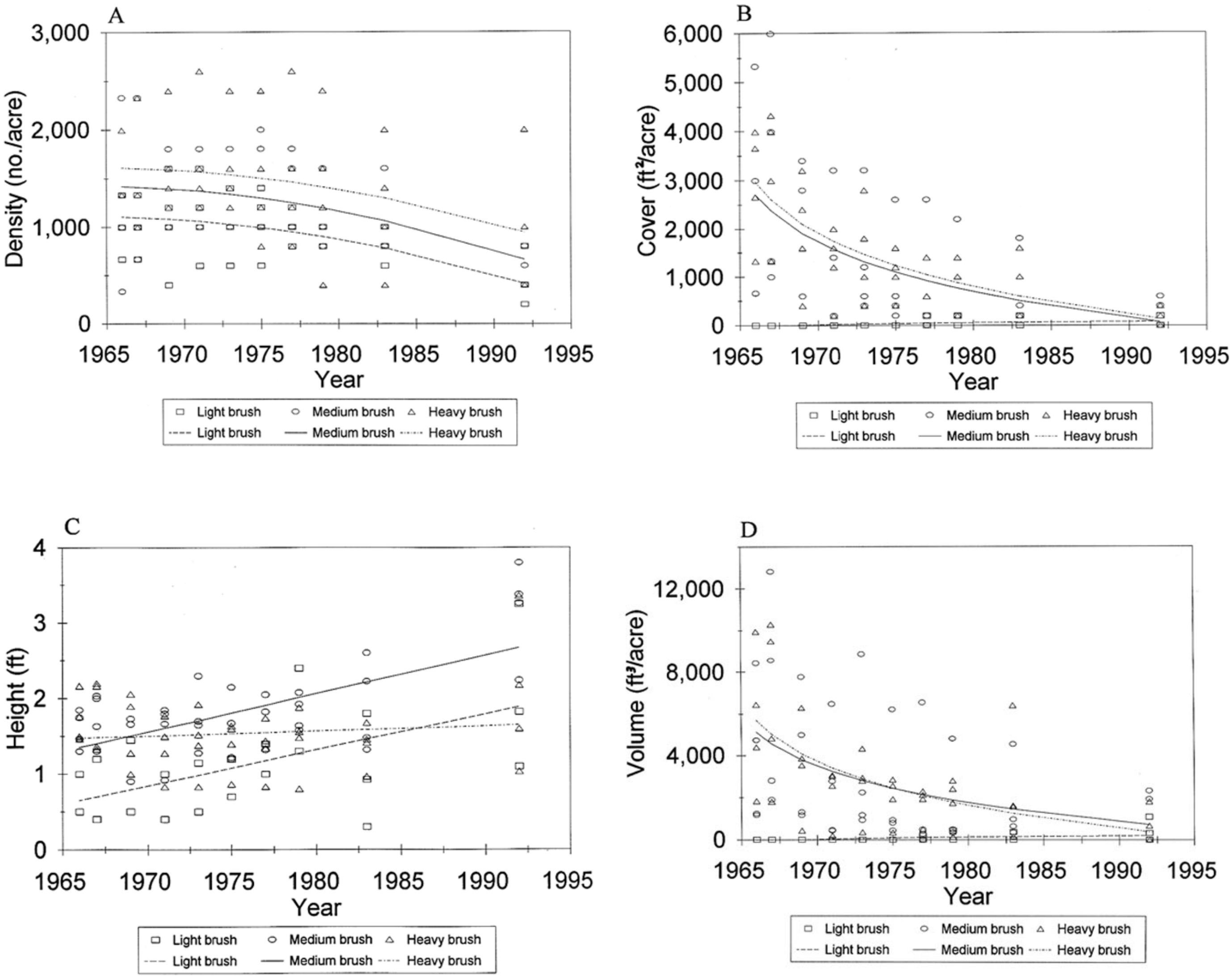
Foliar cover of snowbrush increased from 1966 through 1975 and then decreased through the end of the study. In 1975, average foliar cover peaked at 5,950 ft^2 per acre in the light-shrub category, at 8,500 ft^2 in the medium-shrub category, and at 5,950 ft^2 per acre in the heavy-shrub category (*table 3*). By the end of the study, foliar cover had decreased 56, 74, and 71 percent, respectively, for the light-, medium-, and heavy-shrub categories. Differences in foliar cover never were statistically significant among shrub categories during the study.

Average height of snowbrush generally increased with time in all shrub categories, reaching 5.6 to 6.1 feet in 1992. Other than in 1966, differences in average height were not statistically significant among categories (*table 3*). Some of the variation in foliar cover and height occurred when old stems died and new stems replaced them.

Average crown volume of snowbrush generally increased from 1966 through 1983, and then decreased markedly (*table 3*). At the study end in 1992, snowbrush volume by shrub category (decrease from 1983 in parentheses) was light, 15,485 ft^3 per acre (20 percent); medium, 14,065 ft^3 (64 percent); and heavy 11,305 ft^3 per acre (50 percent), respectively. No statistically significant differences in crown volume occurred at any measurement date during the study.

The relationship of snowbrush density, foliar cover, height, and volume over the 1966 through 1992 period are portrayed in *figure 4*. The regression equations are shown in the *appendix*.

Figure 4—Relationship of snowbrush to shrub density category for (A) density, (B) foliar cover, (C) height, and (D) crown volume, Mt. Shasta brushfields, 1966-1992.



Sierra Plum

This species was damaged by abiotic agents and suffered from suppression almost from the beginning of the study. In 1967, a 2- to 6-inch dieback of exposed shoots was noted in all shrub categories; wind and drought were the probable cause. In 1969, many stems were bent or broken, apparently from snow. Exposed shoots also died back. By 1969, most plants had become shorter than other shrub species. In 1973, a surge of new sprouts from horizontal roots was recorded, but from 1975 to the end of the study, Sierra plum generally was declining, especially in foliar cover. By 1992, most plants had died back several times and either had died outright or become shorter. Because a few plants put forth a tall vigorous shoot, especially where snowbrush plants had died, this shortening is not reflected in the height values for 1992, which actually increased over 1983 values in every shrub category (*table 4*).

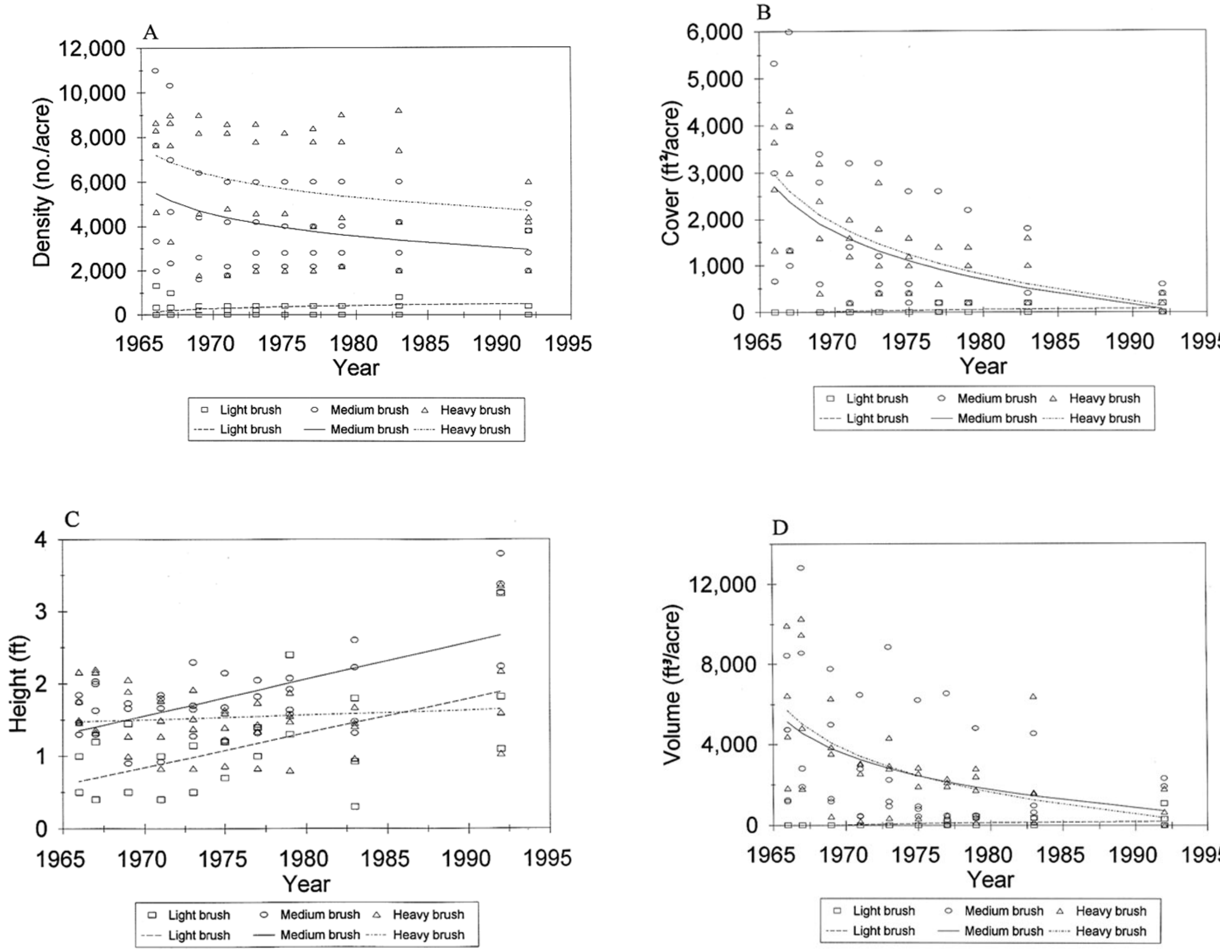
Although this plum produced many fruits and seeds, new *seedlings* were never found. After an initial decrease, mean density of Sierra plum in the light-shrub category increased from 150 plants per acre in 1969 to 1,150 plants per acre in 1992—all from roots or root crowns (*table 4*). In the medium-shrub category, density initially decreased and then remained relatively stable at 3,400 to 3,750 plants per acre. Density of Sierra plum in the heavy-shrub category also decreased initially, remained relatively

Table 4—*Average density, cover, height, and volume of Sierra plum by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992*

Year	Category	Density	Cover	Height	Volume
		plants/acre	*ft²/acre*	*ft*	*ft³/acre*
1966	Light	500 a[1]	0 a	0.7 a	0 a
	Medium	5,994 b	2,414 ab	1.6 b	3,888 ab
	Heavy	7,326 b	2,913 b	1.7 b	5,661 b
	Standard error	1,310	731	0.1	1,405
1969	Light	150 a	0 a	1.0 a	0 a
	Medium	3,750 ab	1,850 a	1.5 a	3,800 a
	Heavy	5,900 b	1,900 a	1.6 a	3,535 a
	Standard error	1,141	546	0.2	1,150
1971	Light	150 a	0 a	0.7 a	0 a
	Medium	3,550 ab	1,250 a	1.6 a	2,535 a
	Heavy	5,850 b	1,250 a	1.3 a	2,200 a
	Standard error	1,080	466	0.2	910
1975	Light	200 a	0 a	0.9 a	0 a
	Medium	3,750 ab	950 a	1.6 a	2,095 a
	Heavy	5,750 b	1,050 a	1.4 a	1,915 a
	Standard error	1,000	352	0.2	859
1979	Light	200 a	50 a	1.8 a	110 a
	Medium	3,750 ab	700 a	1.8 a	1,495 a
	Heavy	5,850 b	900 a	1.4 a	1,765 a
	Standard error	1,024	325	0.2	723
1983	Light	400 a	100 a	1.0 a	185 a
	Medium	3,750 ab	650 a	1.9 a	1,620 a
	Heavy	5,700 b	950 a	1.4 a	2,435 a
	Standard error	1,062	280	0.3	972
1992	Light	1,150 a	100 a	2.1 a	350 a
	Medium	3,400 a	250 a	3.2 a	1,060 a
	Heavy	4,150 a	150 a	2.0 a	615 a
	Standard error	793	108	0.5	457

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

Figure 5—Relationship of Sierra plum to shrub density category for (A) density, (B) foliar cover, (C) height, and (D) crown volume, Mt. Shasta brushfields, 1966-1992.



constant at about 5,800 plants per acre, and then decreased to 4,150 plants per acre at the end of the study. Statistically significant differences generally occurred between the fewer shrubs in the light-shrub category and the many more shrubs in the heavy-shrub category.

Although trends in mean foliar cover differed among shrub categories, no difference among categories was statistically significant at any measurement date. For the light-shrub category, cover began with zero and increased slightly to 100 ft^2 per acre at the end of the study (*table 4*). For the medium- and heavy-shrub categories, cover decreased consistently during the 27-year study to 250 and 150 ft^2 per acre, respectively. Overall decreases were 90 and 95 percent.

Mean height of Sierra plum varied inconsistently during the study, and other than initially, differences were never statistically significant among shrub density classes. At the end of the study, plum height ranged from 2 to 3 feet (*table 4*). Like snowbrush, the height of Sierra plum varied over the years from dieback and resprouting.

Crown volume of this shrub closely paralleled the trends in foliar cover and height noted above. In the light-shrub category, volume was absent through 1975 and then increased slightly throughout the study (*table 4*). Volume was larger in the other categories and generally decreased throughout the study period. The decrease was particularly sharp in 1992.

The relationship of Sierra plum density, foliar cover, height, and volume over the 1966 through 1992 period are portrayed in *figure 5*. The regression equations are shown in the *appendix*.

Combined Shrubs

Combined values for greenleaf manzanita, snowbrush, and Sierra plum reflect the contribution of the shrubs—a very important component of the total plant community in the Mt. Shasta brushfields. In 1966, density of combined shrubs ranged from 3,080 plants per acre in the light-shrub category to 15,318 plants per acre in the heavy-shrub category (*table 5*). Shrub density was significantly lower in the light-shrub category than in the medium- or heavy-shrub category, which did not significantly differ from each other throughout the study. Mean density of combined shrubs in the light-shrub category generally increased from the beginning of the study (3,080 plants per acre) to the end of the study (4,100 plants per acre). This contrasted with the trend of density in the other categories where it declined (11,488 shrubs per acre to 8,550 per acre in the medium-shrub category and 15,318 plants per acre to 9,850 per acre in the heavy-shrub category).

Mean foliar cover of combined shrubs generally increased throughout the study in all shrub density categories. From the beginning of the study to the end, the increases were: light shrubs 1,415 to 11,850 ft^2 per acre; medium shrubs 4,912 to 22,300 ft^2, and heavy shrubs 8,491 to 31,000 ft^2 per acre (*table 5*). Significantly

Table 5—*Average density, cover, height, and volume of combined shrubs by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992*

Year	Category	Density	Cover	Height	Volume
		plants/acre	*ft^2/acre*	*ft*	*ft^3/acre*
1966	Light	3,080 a[1]	1,415 a	0.7 a	1,324 a
	Medium	11,488 b	4,912 b	1.2 b	6,088 b
	Heavy	15,318 b	8,491 c	1.5 b	13,262 c
	Standard error	1,253	573	0.1	882
1969	Light	3,350 a	4,600 a	1.2 a	6,802 a
	Medium	10,050 b	11,650 b	1.9 b	23,321 b
	Heavy	13,200 b	14,650 b	2.1 b	30,618 b
	Standard error	1,420	926	0.2	2,758
1971	Light	3,450 a	6,900 a	2.1 a	14,979 a
	Medium	9,750 b	14,400 b	2.4 a	35,439 b
	Heavy	12,900 b	18,400 b	2.4 a	45,161 b
	Standard error	1,352	1,183	0.2	4,293
1975	Light	3,700 a	8,700 a	2.3 a	21,052 a
	Medium	9,950 b	15,200 b	2.5 a	38,500 b
	Heavy	12,050 b	19,300 b	2.6 a	50,419 b
	Standard error	1,333	1,227	0.2	4,126
1979	Light	3,400 a	8,850 a	3.0 a	28,700 a
	Medium	9,700 b	15,150 b	3.1 a	47,930 b
	Heavy	12,000 b	20,750 c	3.1 a	64,837 b
	Standard error	1,358	1,174	0.2	4,838
1983	Light	3,600 a	11,400 a	3.2 a	40,851 a
	Medium	9,400 b	22,350 b	3.4 a	79,437 b
	Heavy	11,650 b	29,050 b	3.4 a	100,928 b
	Standard error	1,256	1,803	0.2	8,989
1992	Light	4,100 a	11,850 a	4.3 a	60,152 a
	Medium	8,550 b	22,300 b	4.7 a	107,540 ab
	Heavy	9,850 b	31,000 b	4.5 a	140,442 b
	Standard error	1,009	2,490	0.3	12,982

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

more cover was present in the medium- and heavy-shrub categories than in the light-shrub category, although in 1966 and 1979 shrub cover differed significantly among all three categories.

Mean height also increased in all shrub categories during the study. By the end of the study, the height of combined shrubs ranged from 4.3 to 4.7 feet and did not differ statistically among categories (*table 5*).

To further understand the performance of these shrubs, periodic annual height increment (PAI), defined as the difference in height between succeeding years divided by the number of years in the period, was calculated for each shrub species and for combined shrubs. Individually, the PAI of manzanita was least variable and that of snowbrush most variable. When presented for combined shrubs, PAI, which was quite variable through 1980, became consistently small (less than 0.2 feet) in light-, medium-, and heavy-shrub categories in 1992 (*fig. 6*).

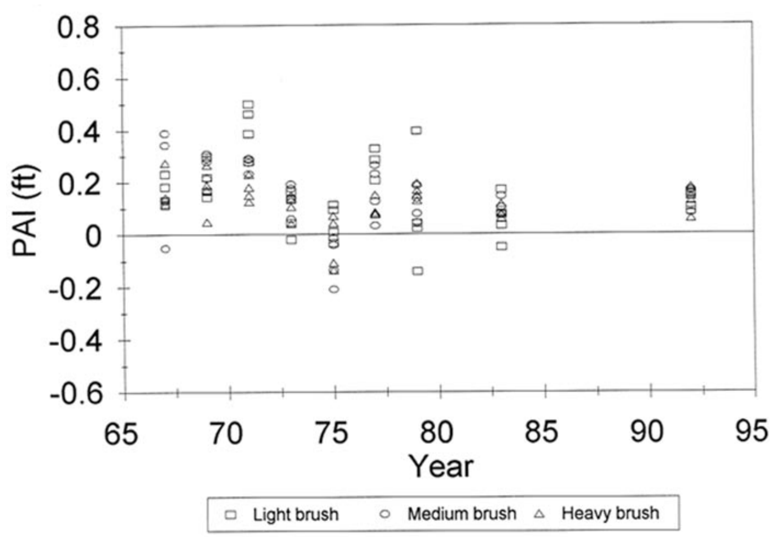
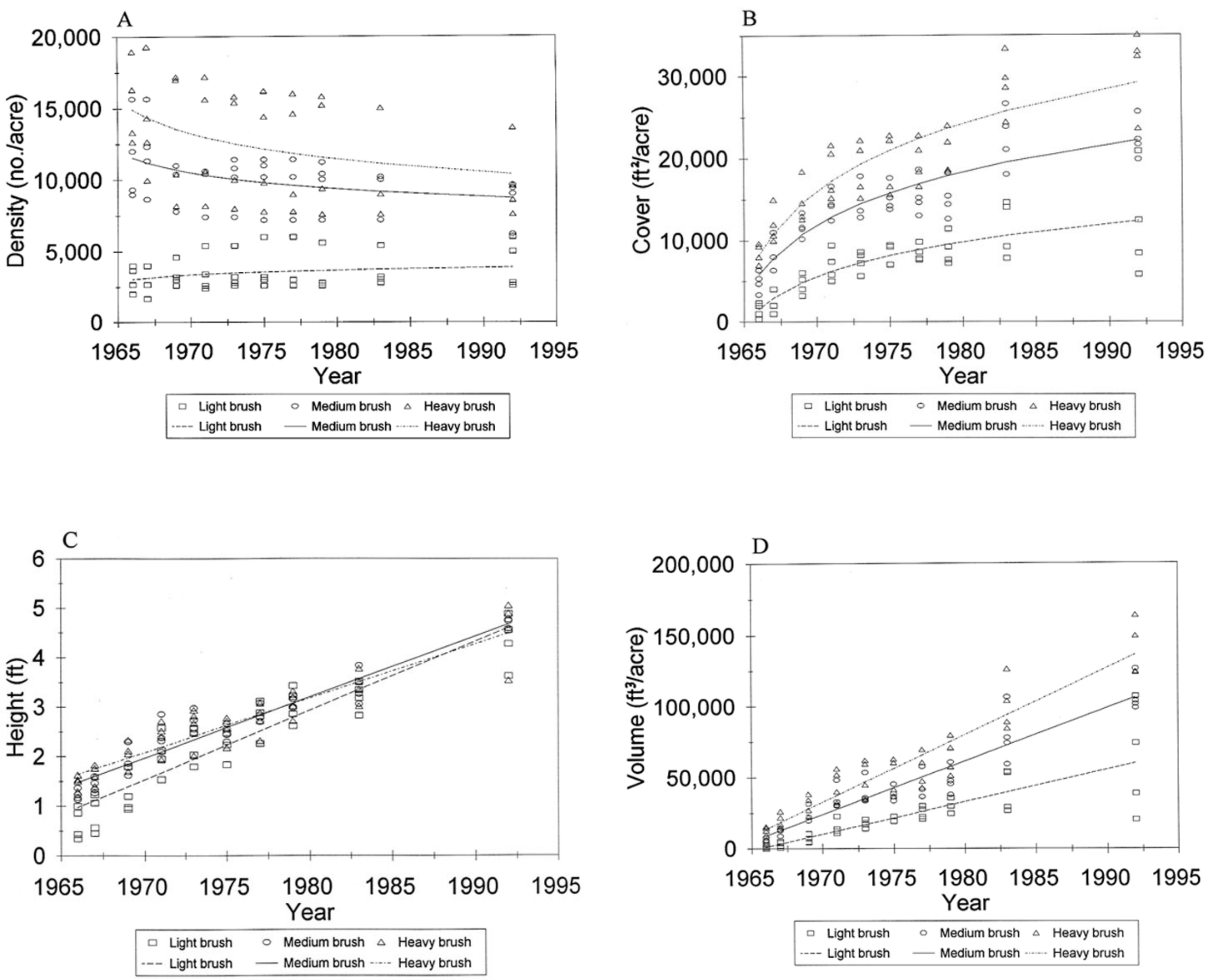


Figure 6—Periodic annual height increment (PAI) of combined shrubs, Mt. Shasta brushfields, 1966-1992.

The average crown volume of combined shrubs, which differed significantly among all shrub categories in 1966, significantly differed only between light shrubs and the other two categories from 1969 through 1983 (*table 5*). In 1992, volume differed significantly only between the light-shrub and heavy-shrub categories. Total combined shrub volume at the end of the study by category was: light, 60,152 ft^3 per acre; medium, 107,540 ft^3 per acre; and heavy, 140,442 ft^3 per acre.

The relationship of combined shrub density, foliar cover, height, and volume over the 1966 through 1992 period are portrayed in *figure 7*. The regression equations are shown in the appendix.

Figure 7—Relationship of combined shrubs to shrub density category for (A) density, (B) foliar cover, (C) height, and (D) crown volume, Mt. Shasta brushfields, 1966-1992.



Needlegrass

Formerly classified as *Stipa columbiana*, this grass now has been placed in the genera *Achnatherum* and given the specific epithet *nelsonii* (Hickman 1993). Beginning in 1967, needlegrass rapidly invaded the study area. This grass first colonized bare areas in no-shrub and light-shrub plots and by 1969 had moved into medium-shrub plots. It occurred in all plots in these categories and one heavy-shrub plot in 1971 (*table 6*). In 1979 and 1983, needlegrass had expanded to three of the four heavy-shrub plots. Where it was free of shrubs and not directly under pines, its developmental pattern over several years was from a few single stems per acre, to thousands of single stems, to a combination of well-defined clumps and many single stems (*fig. 8*). When the needlegrass population declined, it followed a last-in/first-out pattern. By 1992, it was present only in the no-shrub plots.

In terms of density, 17,800 plants per acre were present in the no-shrub category in 1969 (*table 6*). Average number of plants in this category increased to 65,900 per acre in 1983, but decreased markedly to 12,850 per acre in 1992. Number of plants in the light-shrub category was about one-fourth this amount throughout this same timespan, but fell to zero in 1992. Density of needlegrass in

Table 6—***Average density, cover, height, and volume of needlegrass by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992***

Year	Category	Density	Cover	Height	Volume
		plants/acre	*ft²/acre*	*ft*	*ft³/acre*
1966	No shrubs	-	-	-	-
	Light	-	-	-	-
	Medium	-	-	-	-
	Heavy	-	-	-	-
	Standard error	-	-	-	-
1969	No shrubs	17,800 a[1]	1,950 a	1.7 a	3,725 a
	Light	4,300 ab	550 a	1.0 a	940 a
	Medium	2,550 b	50 a	1.6 a	55 a
	Heavy	0 b	0 a	-	0 a
	Standard error	3,563	497	0.2	924
1971	No shrubs	32,000 a	2,550 a	2.5 a	6,850 a
	Light	9,000 b	450 b	1.4 b	1,020 b
	Medium	6,850 b	150 b	1.5 ab	385 b
	Heavy	100 b	0 b	0.3 b	0 b
	Standard error	3,561	451	0.2	1,252
1975	No shrubs	44,950 a	4,300 a	2.4 a	10,240 a
	Light	13,050 b	600 b	1.4 b	1,080 b
	Medium	9,650 b	200 b	1.3 b	385 b
	Heavy	200 b	0 b	0.8 b	0 b
	Standard error	4,530	338	0.1	608
1979	No shrubs	50,000 a	4,450 a	2.5 a	11,360 a
	Light	17,650 b	600 b	2.0 ab	1,355 b
	Medium	8,200 bc	150 b	1.6 b	355 b
	Heavy	400 c	0 b	0.6 c	0 b
	Standard error	3,798	326	0.2	812
1983	No shrubs	65,900 a	4,750 a	2.9 a	14,175 a
	Light	16,800 b	700 b	1.9 b	1,575 b
	Medium	5,750 b	150 b	1.2 c	240 b
	Heavy	450 b	0 b	1.1 c	0
	Standard error	4,673	434	0.1	1,281
1992	No shrubs	12,850 a	400 a	0.7 a	540 a
	Light	0 a	0 a	- a	0 a
	Medium	0 a	0 a	- a	0 a
	Heavy	0 a	0 a	- a	0 a
	Standard error	6,027	200	0.3	270

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

Figure 8—Typical needlegrass density and development in the no-shrub category, Mt. Shasta brushfields, 1973.

the medium-shrub category increased from 1969 (2,550 plants per acre) through 1975 (9,650 plants per acre), declined from 1979 through 1983, and was zero in 1992. Needlegrass in the heavy-shrub category ranged from 100 plants per acre in 1971 to 450 plants per acre in 1983, to zero plants in 1992.

Average foliar cover of needlegrass, although never large, corresponded well to the trend in density. It was largest in the no-shrub category and decreased dramatically (*table 6*) as the amount of shrubs increased. In fact, needlegrass never developed well enough to have measurable cover in the heavy-shrub plots. In general, foliar cover in the no-shrub category differed significantly from all other categories.

Average height of needlegrass generally followed the same trends noted above. It tended to increase with time through 1983, reaching its maximum height of 2.9 feet in no-shrub plots in that year (*table 6*). Average crown volume also peaked in 1983, reaching 14,175 ft^3 per acre in no-shrub plots (*table 6*). It then decreased to 540 ft^3 per acre in these plots in 1992, and to zero in all others.

Because nearly all needlegrass plants had died by the end of the study. regression equations for density, foliar cover, height, and volume were not derived.

Ponderosa Pine

Because we did not begin this study until summer 1966, we quantified mortality well after its typical early-age peak. Consequently, during our study a few ponderosa pine seedlings died each year through 1975, with no single year having concentrated mortality. By 1979, survival of ponderosa pine saplings by treatment was:

No shrubs	99 percent
Light shrubs	98 percent
Medium shrubs	98 percent
Heavy shrubs	81 percent

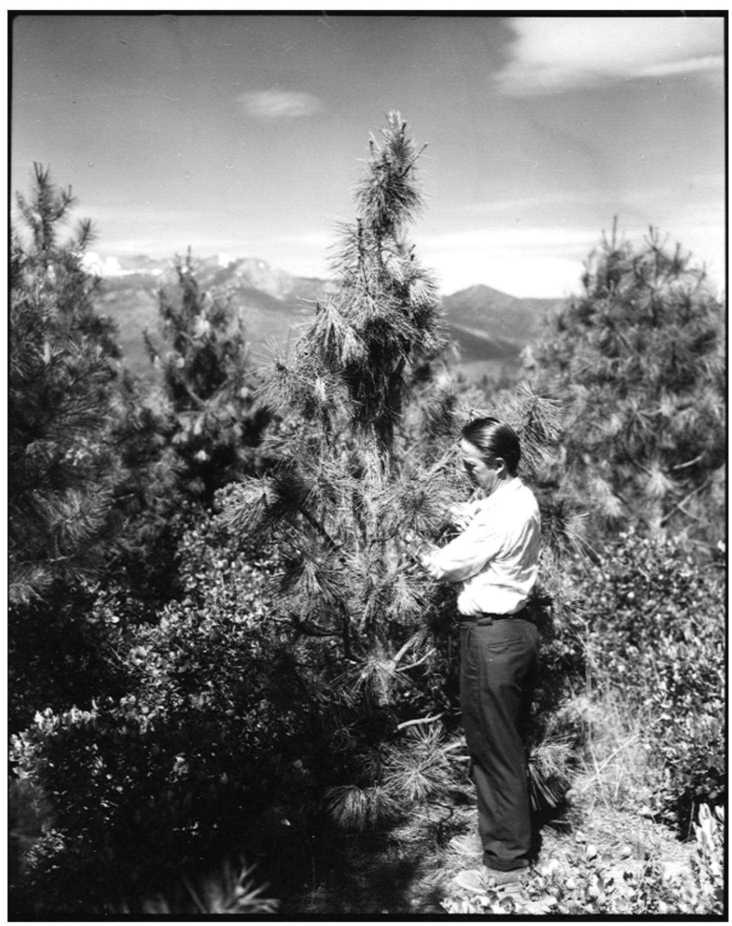
At the end of the study in 1992 only one additional pine had died, this being in a medium-shrub plot.

Damage to pine seedlings was almost entirely from winterburn and insects. Winterburn, as its name suggests, occurs when the ground is frozen and the wind pulls the moisture from the needles. This moisture cannot be replaced because the roots are inactive. This happened for several years, especially when the pines were younger. It caused many needles to turn brown and look unhealthy, but it did not kill any seedlings.

The gouty pitch midge and the pine needle-sheath miner did not kill any seedlings either, but their damage caused a loss of height growth on some seedlings and deformed others so badly that they will never become crop trees (*fig. 9*). Some pine trees were attacked repeatedly, others periodically, and still others only rarely. Insect damage was chronic. Rare was the year that at least a

Figure 9—(A) This 12-year-old ponderosa pine in heavy shrubs has at least four new terminals, (B) Although an extreme case, this 31-year-old pine shows the negative effects of heavy shrubs and repeated insect attacks.

A



few buds were not killed and also rare was the year that both of these insects were not present together in the plantation.

Insect damage was first recorded in 1968 but did not materially affect tree form until 1970. Death of terminal shoots was manifest primarily from 1970 through 1979 (*table 7*). By 1983, few trees were affected in this manner, although lateral shoots continued to be killed by these insects. Number of dead terminal shoots varied from year to year depending on the intensity of the insect attack. A general trend was that damage increased with increasing shrub density. The average number of pines with dead terminal shoots in each plot during the 1970-1979 period, for example, was 8 in no shrubs and 42 in heavy shrubs—or more than five times as many killed in the heavy-shrub category.

Table 7—*Average number of ponderosa pines with dead terminal shoots per plot in each shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1970-1979*

Category	Year						Total
	1970	1971	1973	1975	1977	1979	
No shrubs	0	1	1	3	3	0	8
Light shrubs	2	6	1	8	9	0	26
Medium shrubs	1	4	5	10	6	1	27
Heavy shrubs	5	7	11	8	9	2	42

B

Death of lateral shoots from insects also first showed up in 1970 but extended throughout the study period. After 1970 this form of damage worsened with 1971 through 1977 being a period of heavy attacks and much damage (*table 8*). For the 27-year period that we collected these data, 1975 was the worst. The statistics that follow quantify the effect of an epidemic by the pine needle-sheath miner and the gouty pitch midge. In 1975, the number of pines in the study, after mortality, totalled 613 trees. Of these, 598 or 98 percent had one or more dead lateral branches from insect damage. The average per tree was 22 dead laterals in the range of 2 to 200. One 14-foot-tall tree of good form was described as having 100 percent of its 200 lateral shoots infested; another 8.9-foot-tall pine had 80 laterals infested, which also was 100 percent. In spite of this, both trees were alive and growing well at the end of the study. In 7 of the 16 plots, 100 percent of the trees were infested to some degree. Even seedlings that were overtopped by shrubs were attacked. A general trend, which held from 1970 through 1979, was that in a given year, the average number of infested pines per plot was roughly similar regardless of shrub-density category. The average number of infested pines per plot in the heavy-shrub category is lower than that in other categories (*table 8*) from 1975 through 1979 because the average was influenced by mortality. About six trees per plot had died in this category, leaving fewer trees present to become infested. After 1979, the number of trees with dead lateral branches increased as shrub density increased.

Average breast-height diameter of ponderosa pine was measured from 1979 through 1992. During this period it increased from 5.08 inches to 7.85 inches in no-shrub plots, from 3.89 to 6.11 inches in light-shrub plots, from 2.91 to 4.56 inches in medium-shrub plots, and from 1.35 inches to 2.14 inches in heavy-shrub plots (*table 9*). Statistically, pine diameter differed among all shrub categories during this timespan.

Mean foliar cover of this pine increased in all shrub categories from 1966 through 1992. At the end of the study foliar cover was 24,050 ft^2 per acre in no-shrub plots, 12,400 ft^2 in light-shrub plots, 11,200 ft^2 in medium-shrub plots, and 4,150 ft^2 per acre in heavy-shrub plots (*table 9*). Statistically significant differences in general were consistent between the no-shrub and heavy-shrub categories and often between no-shrub and most of the other categories.

Mean ponderosa pine height differentiated rapidly among shrub categories after 1969. From 1975 through 1992 pine height at each measurement date was significantly different among all shrub categories (*table 9*). At the end of the study, pine height by shrub category was: no shrubs, 30.4 feet; light shrubs, 21.6 feet; medium shrubs, 15.2 feet, and heavy shrubs, 9.0 feet.

Average crown volume of ponderosa pine increased in all shrub categories during the study, and in general differed significantly between the no-shrub and all other categories (*table 9*). Average volume of pines ranged from 237,894 ft^3 per acre in the no-shrub category to 15,125 ft^3 per acre in the heavy-shrub category at the end of the study.

The relationship of ponderosa pine foliar cover, height, and crown volume over the 1966 through 1992 period are portrayed in *figure 10*. The regression equations are shown in the *appendix*.

To ascertain which shrub variable explained the most variation in a given ponderosa pine sapling parameter, we regressed four pine parameters against four shrub variables, three timespans, and three forms of numerical values. Of the 132 regressions that we examined, 81 showed a significant relationship among tested parameters at the 0.05 level. Here one should remember that although a relationship may be significant, it may not explain much of the variation in a given parameter.

Table 8—*Average number of infested ponderosa pines and number of dead lateral shoots per plot in each shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1970-1992*

Category	Year							
	1970		*1971*		*1973*		*1975*	
	S[1]	L	S	L	S	L	S	L
No shrubs	1	1	17	348	18	219	39	760
Light shrubs	1	5	20	387	17	200	39	1,160
Medium shrubs	1	2	21	302	23	258	39	894
Heavy shrubs	1	7	20	216	20	162	32	528
	1977		1979		1983		1992	
	S	L	S	L	S	L	S	L
No shrubs	29	254	18	103	7	62	3	43
Light shrubs	25	222	20	191	9	71	3	26
Medium shrubs	29	313	16	122	13	128	6	40
Heavy shrubs	22	225	15	81	14	100	8	34

[1]S = Number of infested pines; L = number of dead lateral shoots on them.

Table 9—*Average breast-height diameter, cover, height, and volume of ponderosa pine by shrub category, Mt. Shasta brushfield, Shasta-Trinity National Forests, 1966-1992*

Year	Category	Diameter	Cover	Height	Volume
		inches	*ft²/acre*	*ft*	*ft³/acre*
1966	No shrubs	-	-	2.9 a	-
	Light	-	916 a[1]	2.9 a	761 a
	Medium	-	1,415 a	2.8 a	1,393 a
	Heavy	-	500 a	2.4 a	430 a
	Standard error	-	326	0.2	299
1969	No shrubs	-	5,750 a	6.8 a	12,856 a
	Light	-	3,250 ab	6.2 ab	5,370 b
	Medium	-	3,650 ab	5.5 b	6,804 b
	Heavy	-	1,450 b	3.9 c	2,027 b
	Standard error	-	628	0.3	1,318
1971	No shrubs	-	9,400 a	9.3 a	28,442 a
	Light	-	5,100 b	7.8 b	11,855 b
	Medium	-	5,150 b	6.8 b	11,844 b
	Heavy	-	2,000 b	4.5 c	3,411 b
	Standard error	-	774	0.3	2,315
1975	No shrubs	-	14,000 a	13.9 a	65,497 a
	Light	-	7,800 b	10.6 b	24,013 b
	Medium	-	6,450 bc	8.7 c	18,883 b
	Heavy	-	2,400 c	5.3 d	5,147 b
	Standard error	-	1,144	0.4	5,072
1979	No shrubs	5.08 a	20,050 a	16.5 a	113,128 a
	Light	3.89 b	12,600 ab	12.0 b	46,343 b
	Medium	2.91 c	9,800 bc	9.3 c	31,820 bc
	Heavy	1.35 d	3,400 c	5.8 d	8,554 c
	Standard error	0.15	1,775	0.4	8,785
1983	No shrubs	5.93 a	21,700 a	20.9 a	157,273 a
	Light	4.54 b	12,750 ab	14.9 b	59,856 b
	Medium	2.96 c	10,200 ab	10.8 c	39,501 b
	Heavy	1.30 d	4,200 b	6.4 d	12,664 b
	Standard error	0.24	3,162	0.6	19,789
1992	No shrubs	7.85 a	24,050 a	30.4 a	237,894 a
	Light	6.11 b	12,400 ab	21.6 b	82,325 b
	Medium	4.56 c	11,200 b	15.2 c	57,225 b
	Heavy	2.14 d	4,150 b	9.0 d	15,125 b
	Standard error	0.31	2,950	0.9	28,694

[1]For each year, treatment means in each column followed by the same letter do not differ significantly according to a Tukey test ($\alpha = 0.05$).

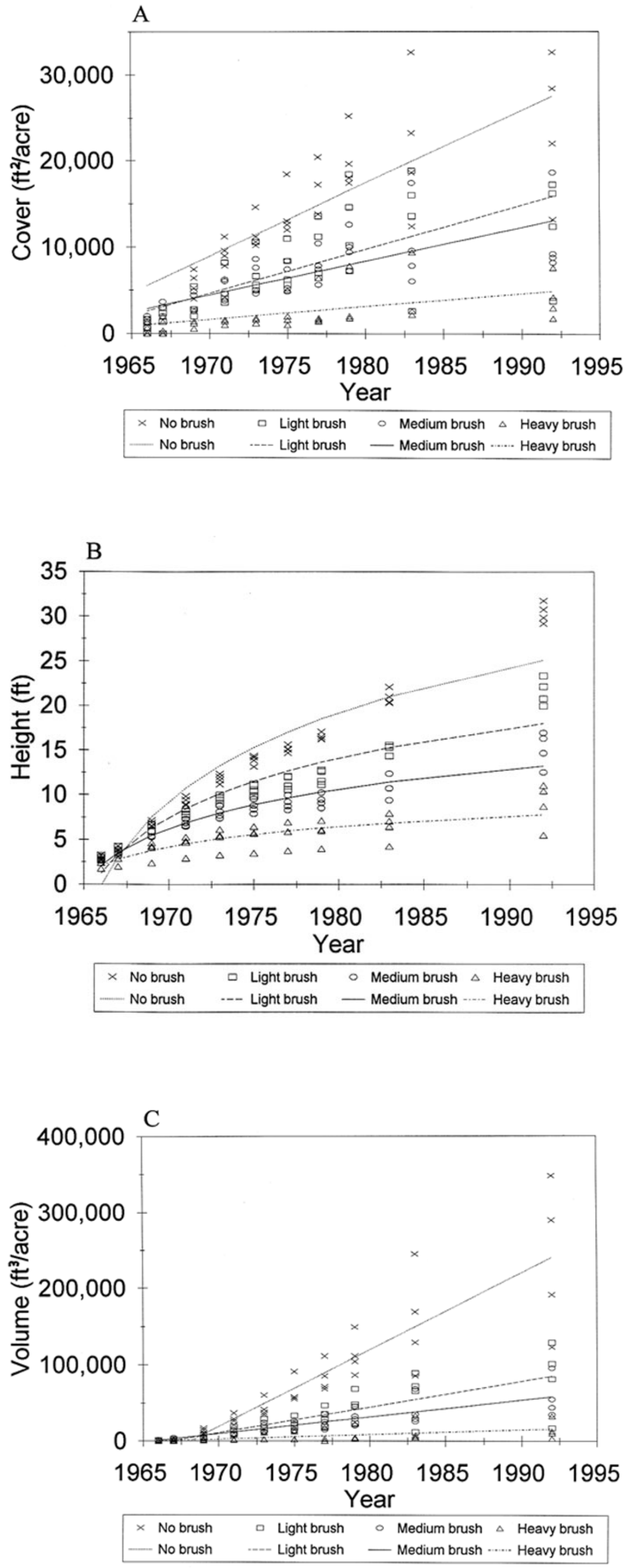


Figure 10—Relationship of ponderosa pine to shrub density category for (A) foliar cover, (B) height, and (C) crown volume, Mt. Shasta brushfields, 1966-1992.

The following shrub variables explained the most variation in ponderosa pine parameters on the basis of highest adjusted coefficients of determination (R^2) and P values:

Ponderosa pine *parameter*	**Combined shrubs** *variable*	*age*	**P**	**R^2**
Foliar cover	Foliar cover	29	0.0008	0.66
	Volume/acre	29	0.0028	0.57
Volume/acre	Foliar cover	29	0.0001	0.76
	Volume/acre	29	0.0004	0.70
Height	Ln density	20	0.0046	0.52
	Foliar cover	29	0.0001	0.79
	Volume/acre	20	0.0017	0.61
Diameter at	Ln density	20	0.0060	0.50
breast height	$(\text{Foliar cover})^2$	29	0.0001	0.76
	Volume/acre	20	0.0023	0.58

In general, mean shrub height was never significant, mean shrub density was relatively insignificant, numerical values were better than squared values or natural logarithms, and 29-year-old shrub data were best. Overall, foliar cover and crown volume per acre of combined shrubs explained the most variation in most pine parameters. These shrub variables are the ones that the vegetation manager may want to evaluate when determining competition in ponderosa pine plantations. And because foliar cover is much easier to estimate and relate to, it may be the most useful variable from a practical standpoint.

Discussion and Conclusions

Ecology

Before this study and its predecessor (Bentley and others 1971) began, the mature brushfield had little plant diversity. After site preparation, the area gained in diversity, and at study end it had lost what it had gained. However, an important native tree component—ponderosa pine—had been restored to the landscape. And in the no-shrub plots, the odds are that these pine trees will continue to grow well and reach maturity. By forming a forest, they bring to the landscape an increased opportunity for higher plant diversity in the future.

Cooper (1922) classified the *Arctostaphylos patula-Ceanothus velutinus* community as subclimax in successional state, but Frenkel (1974) noted that "the present chaparral type on Mount Shasta shows great stability, which possibly reflects changes in the soil brought on by severe fire." Thus, planted pines in the no-shrub environment not only have high potential to form a future forest, but they also bring this potential to the landscape much sooner than would have occurred naturally.

The long-term trend in density and development data developed for each species in this paper also has successional implications. Greenleaf manzanita, by virtue of its relatively high density, strong development, and lack of damage, has high potential to be a major component of this plant community for many more years. In contrast, the declining density, foliar cover, and volume of snowbrush indicate that it has low potential of being a major component of the future community. Its susceptibility to frost, drought, and wind reinforce the likelihood of this potential. Snowbrush will probably be a minor component overall, but perhaps strong in local areas where competition from trees and manzanita is less. The future role of Sierra plum in the plant community is not yet certain. This species has two attributes that the other shrubs did not have—capability to exist in the shade and ability to sprout in the shade, albeit with a single stem and little foliar cover. Its ability to develop vegetatively from roots and root crowns allowed it to produce new shoots that kept many plants alive. Although damaged by many abiotic agents, Sierra plum was able to recover from most of them and to actually gain in density in areas having a light amount of shrubs. Overall, this species seems likely to maintain a strong presence in the understory and to sprout when opportunities arise.

Needlegrass, like the various forbs, was an ephemeral species. Its role in succession, however, is interesting both from the standpoint of where it happened and what it caused not to happen. It first invaded bare areas, became most dense, developed best, and absented last from these areas. Its entire record in this study strongly portrays its strong presence and dynamic nature in habitats free of shrubs, and its much reduced presence and development in areas where shrubs were present. For example, if even a light amount of shrubs had existed, needlegrass density would have decreased by about 70 percent and foliar cover by about 80 percent from values in no-shrub plots.

Because of the ascending and descending trends in the various components of the vegetative community in the study plots, we surmised that after 31 years, a similar biological sum or carrying capacity (Ford-Robertson 1971) might be reached in all shrub categories. But which of our measured variables would best show this? Density was dominated by the huge number of needlegrass plants. Crown volume and height reflected mostly pine characteristics. Consequently, foliar cover seemed the only plausible descriptor of total vegetative development.

When foliar cover of grass, shrubs, and ponderosa pines in each shrub category was totaled (*table 10*), some major differences were evident. Foliar cover in all categories, except medium-shrub, reached its maximum after 22 years. This maximum ranged from 57 to 90 percent of that possible (43,560 ft^2—the area of an acre). Nine years later, or 31 years after planting, foliar cover actually decreased: by 8 percent in no-shrub plots; by 3 percent in light-shrub plots, and by 10 percent in heavy-shrub plots. As noted in *table 1*, no new plant species took advantage of this space. But as noted in *tables 2* and *4*, the density of greenleaf manzanita and Sierra plum increased in the light-shrub category.

Table 10—*Total foliar cover of all vegetation by shrub categories, Mt. Shasta brushfield, Shasta-Trinity National Forests, 5-31 years after planting, 1966-1992*

No. of years	No shrubs	Light shrubs	Medium shrubs	Heavy shrubs
	ft^2/acre			
5	-	2,331	6,328	8,991
14	8,300	17,100	21,850	21,700
22	26,450	24,850	32,700	39,250
31	24,400	24,200	33,500	35,150

That large differences in total foliar cover in the various shrub density categories exist after 31 years is puzzling. Perhaps foliar cover is not a good estimator of carrying capacity. Certainly it does not reflect growth in the third dimension—height. Even more important is that carrying capacity probably is not governed by density and development of vegetation above ground. Belowground is where the real quantifier of carrying capacity probably resides. Because soil moisture is the limiting environmental variable in summer-dry California, it follows that a moisture-related value, like root volume, would be a better quantifier of carrying capacity. Research on the belowground ecosystem is needed.

Belowground research also is needed to better define the competitive relationships of grasses, and needlegrass in particular. For grasses in North American grasslands, 85 percent of the total standing crop of live plants is below ground (Trappe 1981). The cumulative length of roots on grass plants can be huge. A single wild oat plant excavated after 80 days of growth had developed a total root system that measured more than 50 miles (Radosevich and Holt 1984). Logically, the impact of competition is below ground, and the agent of competition is the roots. Aboveground values of grass density, and especially of foliar cover and height, may or may not, but probably do not, reflect the true competitive ability of this grass.

Biological Control

Biological control of weeds is defined as the use of living organisms to lower plant pest populations to the point where the pests are no longer economic problems. Besides animals and microorganisms, biological control agents can be other plants that are either parasitic, competitive, or allelopathic (Rosenthal and others 1985).

The windrows surrounding the plots in this study were covered with tall vigorous shrubs that produced many seed crops. Seedlings from these crops plus those from seedbanks in the soil should have resulted in many young manzanita and snowbrush plants, especially on the bare ground of the no-shrub and light-shrub areas. Indeed, young plants of these species were present in no-shrub plots and were physically removed before needlegrass became established. Tiny manzanita plants were present after the grass became established as well. They were noticed early in the spring, but had disappeared by late summer. Physical or chemical interference by the grass kept them away.

That grasses can control woody shrubs by excluding new plants has been documented in California (Griffin 1982, Schimke and others 1970, Schultz and others 1955) and in Oregon (Klingler 1982). However, in these studies, the grass was seeded by hand or machines. Reports of control by naturally occurring species are scarce.

Biological control of aggressive competing species by a less aggressive species has special appeal to forest vegetation managers. Long-term costs may be lower, especially if additional release treatments are not needed. And in sensitive areas, biological control may be the only method available.

Grass can be a formidable agent in young plantations and many have failed because of it (Rietveld 1975, Roy 1953). However, if the pines become established before the grass, the pines usually dominate. And if the soil is deep, and the pines become established first, the grass roots do not grow as deep and the pine roots have a competition-free zone deep in the soil. We observed this in a pit dug in a no-shrub plot. In this study, the needlegrass did not invade until 1967 or about 5 years after planting and the soil was deep. Consequently, naturally occurring needlegrass excluded the deeper-rooted shrubs and in so doing indirectly aided pine growth (McDonald 1986). Of course, it also used site resources and cost the pines some growth. The tradeoff is unknown, but that there is a tradeoff, not just a cost, is now recognized.

Vegetation Management

Early control of competing vegetation is fundamental to rapid and continuing growth by ponderosa pines. Increasing evidence suggests that seedling growth is closely related to amount of resources, especially to available soil moisture. Any moisture used by competing vegetation is that much less available for conifer growth. Consequently, the advantage lies with those plants or species that are present first. Their roots are unimpeded by competitors' roots or toxins or mycorrhizae, and they are free to expand into surrounding soil. In turn, shoot growth also benefits. Thus it is important to accomplish complete or near-complete control of competing vegetation during the first growing season or within the first three seasons (McDonald and Fiddler 1986b, 1989, 1990).

Comparing the average diameter and height of ponderosa pine in the various shrub categories demonstrates the relationship of increasing shrubs and decreasing pine development (*table 11*). Even a light amount of shrubs costs the pines some growth. Medium and heavy amounts of shrubs cost progressively more. Are the differences made up? Periodic annual height increment (1983-1992) for pines in the no-shrub category was 1.1 feet per year; light shrub, 0.7; medium shrub, 0.5; and heavy shrub, 0.3 feet per year. These values plus the slope coefficients from the regression equations show that differences in pine height after 31 years are still widening.

Table 11—***Relationship between diameter and height of ponderosa pine and shrub category, 1992***

Shrub category	Average diameter	Loss in diameter[1]	Average height	Loss in height[1]
	inches		*feet*	
No shrubs	7.85	0	30.4	0
Light shrubs	6.11	1.74	21.6	8.8
Medium shrubs	4.56	3.29	15.2	15.2
Heavy shrubs	2.14	5.71	9.0	21.4

[1]Relative to no-shrub category.

How much loss of pine growth is too much? Fiske (1986) developed minimum size standards for average potential crop trees needed to meet future goals. Ponderosa pines, at age 30, on a site like that of the study should average 6 inches in breast-height diameter and be 20 feet tall. Thus, pines in the medium- and heavy-shrub categories in this study do not meet the standard, and treatment to control the shrubs or start the plantation over needs to be considered.

Visual observations plus the developmental trends presented in this study give insight to the health and future of the pine stand in the four shrub categories. In the no-shrub category, most pines are tall, full crowned, and growing well (*fig. 11*). Virtually none have been deformed by insects. In the light-shrub category, some variation in pine size and growth rate is apparent. Several pines are permanently deformed. In the medium-shrub category, much more variation in size and growth rate is present. Some pines are tall, others are short. Some are deformed. Many trees look stressed and support only current-year needles. Although almost all trees are taller than the shrubs, most are growing slowly. In the heavy-shrub category, the majority of surviving pines are above the shrubs but extend only a few inches in height each year. Many are deformed.

Although mortality of ponderosa pines virtually ceased after 1979, it is a tribute to the tenacity for life that additional trees have not died. In the heavy-shrub plots, several overtopped pines with a few living needles have survived for years beneath manzanita crowns. Another pine seedling has consisted of one

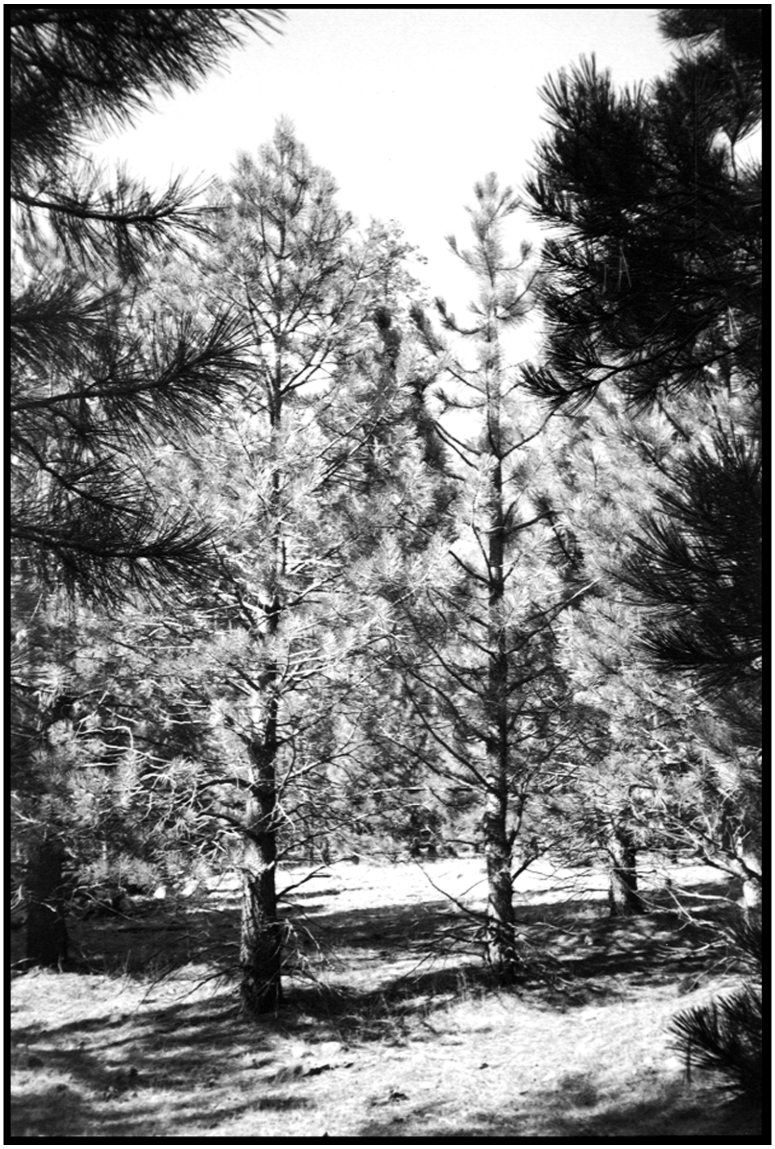


Figure 11—Tall, full crowned, and growing well, ponderosa pines in the no-shrub category have a good chance of becoming a future forest.

living lateral branch for many years. This branch “snakes” through manzanita stems into a small opening among the shrubs. In both instances the pines receive just enough light and water to stay alive.

Entomology

The timing and pattern of pine needle sheath miner and gouty pitch midge damage give clues to the environment preferred by these insects and have vegetation management implications. Insect damage did not begin to be serious until the pine seedlings were about 8 years old. Death of terminal shoots then became a major factor affecting growth for the next 10 years. More than five times more terminal shoots were killed on pines in heavy shrubs than in light shrubs during this timespan. The general trend was an increasing number of dead terminals with increasing shrub density. Apparently the shrub environment, or perhaps the weaker trees in the shrub environment, is favorable to the insects. After the trees reached a height of 12 feet, damage to terminals lessened appreciably.

Mortality of lateral pine shoots followed a similar trend. Damage to lateral branches began 1 year after the terminals were infested and ended about 3 years after damage to terminals declined. 1975 also was the year in which peak damage was observed. After the trees reached a height of about 12 feet, damage above this height lessened but continued in the middle and lower portions of the crown in larger trees. Number of trees damaged seemed to be independent of shrub category through 1979. After 1979, the number of trees damaged became disproportionally higher for trees in the medium- and heavy-shrub categories.

The shrub density/ponderosa pine/insect interaction became a negative synergism. By slowing pine growth, the shrubs hold the trees below a certain height. The insects then attack the trees, deform them, and together with the shrubs continue to hold the trees to a certain size where they are attacked repeatedly. The insects and the shrubs together do more damage to the pines than each alone.

Application

The material in this paper should have appeal to a broad range of specialists. Ecologists could find the developmental and successional relationships worthwhile. Wildlife biologists might be interested in the amount of browse and potential for nutritious berries and seeds. Fire and fuel specialists could use the height and volume relationships to calculate potential flame lengths and rates of spread. And landscape architects might note the time it took for the vegetation to limit the roadside view.

Similarly, the finding that the variation in most pine parameters was best explained by shrub foliar cover and crown volume per acre will be useful to forest managers when planning vegetation manipulation activities in plantations on similar sites.

In the introduction to their book on weed ecology, Radosevich and Holt (1984) noted: "By analyzing the way crops, weeds, and environment interact, perhaps it will be possible to grow more food in our fields and trees in our forests." This paper, which provides some long-term developmental relationships among shrubs, grass, and planted ponderosa pines, does not illustrate how to grow more trees, but it does show how to maximize growth on the young trees that are present, and the negative consequences of leaving various amounts of competition. Ultimately, this knowledge may be useful as well.

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Appendix

The fitted regression equations, which allow forest vegetation managers to model various parameters of greenleaf manzanita, snowbrush, Sierra plum, combined shrubs, and ponderosa pine on similar sites, should be useful to a broad audience. However, they should be used with caution. In some instances, the fit was good; in others, poor. Also, users should remember that individual species were influenced by varying amounts of competition from other species in the plant community, and this influence may differ from that elsewhere.

Greenleaf Manzanita

Density

Light shrubs: Y = 1,793.3 + 33.0 * age
Medium shrubs: Y = 4,675.2 - 1.2 * age
Heavy shrubs: Y = 5,819.3 - 53.3 * age

Standard errors for the intercept and slope coefficients were 474.3 plants per acre and 33.0; the squared multiple correlation coefficient (R^2) was 0.40; the standard error of the estimate ($S_{y.x}$) was 1,582 plants per acre; F = 16.88; and P value < 0.0001.

Foliar cover

Light shrubs: Y = - 5,721.4 + 3,863.6 * ln age
Medium shrubs: Y = - 8,951.2 + 7,018.1 * ln age
Heavy shrubs: Y = - 9,627.0 + 10,064.0 * ln age

Standard errors for the intercept and slope coefficients were 1,745.5 ft^2 per acre and 730.4; the squared multiple correlation coefficient (R^2) was 0.82; the standard error of the estimate ($S_{y.x}$) was 3,126.4 ft^2 per acre; F = 106.22; and P value < 0.0001.

Height

Light shrubs: Y = - 2.1 + 1.8 * ln age
Medium shrubs: Y = - 1.8 + 2.1 * ln age
Heavy shrubs: Y = - 0.9 + 1.8 * ln age

Standard errors for the intercept and slope coefficients were 0.2 foot and 0.1; the squared multiple correlation coefficient (R^2) was 0.92; the standard error of the estimate ($S_{y.x}$) was 0.42 foot; F = 263.31; and P value < 0.0001.

Volume

Light shrubs: Y = - 830.7 + 59.2 * age^2
Medium shrubs: Y = 2,106.4 + 134.7 * age^2
Heavy shrubs: Y = 15,001.0 + 185.2 * age^2

Standard errors for the intercept and slope coefficients were 2,154.5 ft^3 per acre and 6.8; the squared multiple correlation coefficient (R^2) was 0.93; the standard error of the estimate ($S_{y.x}$) was 10,359.9 ft^3 per acre; F = 308.30; and P value < 0.0001.

Snowbrush

Density

Light shrubs: $Y = 1{,}112.0 - 0.8 * age^2$
Medium shrubs: $Y = 1{,}426.3 - 0.9 * age^2$
Heavy shrubs: $Y = 1{,}616.4 - 0.8 * age^2$

Standard errors for the intercept and slope coefficients were 96.5 plants per acre and 0.3; the squared multiple correlation coefficient (R^2) was 0.26; the standard error of the estimate ($S_{y.x}$) was 464 plants per acre; F = 9.52; and P value < 0.0001.

Foliar cover

Light shrubs: $Y = 2{,}136.6 + 842.7 * \ln age$
Medium shrubs: $Y = 2{,}764.3 + 1{,}381.8 * \ln age$
Heavy shrubs: $Y = 3{,}272.9 + 440.6 * \ln age$

Standard errors for the intercept and slope coefficients were 1,682.3 ft^2 per acre and 704; the squared multiple correlation coefficient (R^2) was 0.08; the standard error of the estimate ($S_{y.x}$) was 3,013.2 ft^2 per acre; F = 2.97; and P value < 0.0148.

Height

Light shrubs: $Y = 0.7 + 0.2 * age$
Medium shrubs: $Y = 1.1 + 0.2 * age$
Heavy shrubs: $Y = 1.1 + 0.2 * age$

Standard errors for the intercept and slope coefficients were 0.2 foot and 0.01; the squared multiple correlation coefficient (R^2) was 0.8; the standard error of the estimate ($S_{y.x}$) was 0.63 foot; F = 96.56; and P value < 0.0001.

Volume

Light shrubs: $Y = -4{,}558.7 + 7{,}866.9 * \ln age$
Medium shrubs: $Y = -4{,}542.0 + 11{,}158.0 * \ln age$
Heavy shrubs: $Y = -335.4 + 6{,}299.3 * \ln age$

Standard errors for the intercept and slope coefficients were 6,832.7 ft^3 per acre and 2,859.3; the squared multiple correlation coefficient (R^2) was 0.21; the standard error of the estimate ($S_{y.x}$) was 12,238.4 ft^3 per acre; F = 7.41; and P value < 0.0001.

Sierra Plum

Density

Light shrubs: $Y = -16.9 + 157.1 * \ln age$
Medium shrubs: $Y = 6{,}718.3 - 1{,}117.5 * \ln age$
Heavy shrubs: $Y = 8{,}415.7 - 1{,}098.3 * \ln age$

Standard errors for the intercept and slope coefficients were 1,094.7 plants per acre and 458.1; the squared multiple correlation coefficient (R^2) was 0.60;

the standard error of the estimate ($S_{y.x}$) was 1,960.8 plants per acre; F = 35.96; and P value < 0.0001.

Foliar cover

Light shrubs: Y = - 79.8 + 47.9 * ln age
Medium shrubs: Y = 3,996.1 - 1,165.7 * ln age
Heavy shrubs: Y = 4,344.0 - 1,250.7 * ln age

Standard errors for the intercept and slope coefficients were 499 ft^2 per acre and 208.8; the squared multiple correlation coefficient (R^2) was 0.51; the standard error of the estimate ($S_{y.x}$) was 893.8 ft^2 per acre; F = 26.09; and P value < 0.0001.

Height

Light shrubs: Y = 0.5 + 0.05 * age
Medium shrubs: Y = 1.2 + 0.05 * age
Heavy shrubs: Y = 1.5 + 0.01 * age

Standard errors for the intercept and slope coefficients were 0.1 foot and 0.01; the squared multiple correlation coefficient (R^2) was 0.37; the standard error of the estimate ($S_{y.x}$) was 0.5 foot; F = 12.94; and P value < 0.0001.

Volume

Light shrubs: Y = - 219.2 + 125.9 ln age
Medium shrubs: Y = 7,270.3 - 1,944.8 ln age
Heavy shrubs: Y = 8,284.0 - 2,348.0 ln age

Standard errors for the intercept and slope coefficients were 1,164.6 ft^3 per acre and 487.4; the squared multiple correlation coefficient (R^2) was 0.41; the standard error of the estimate ($S_{y.x}$) was 2,086 ft^3 per acre; F = 17.38; and P value < 0.0001.

Combined Shrubs

Density

Light shrubs: Y = 2,635.3 + 369.0 * ln age
Medium shrubs: Y = 12,945.0 - 1,260.1 * ln age
Heavy shrubs: Y = 17,133.0 - 2,013.5 * ln age

Standard errors for the intercept and slope coefficients were 1,315.2 plants per acre and 550.4; the squared multiple correlation coefficient (R^2) was 0.73; the standard error of the estimate ($S_{y.x}$) was 2,355.7 plants per acre; F = 66.76; and P value < 0.0001.

Foliar cover

Light shrubs: Y = - 3,664.5 + 4,754.2 * ln age
Medium shrubs: Y = - 2,190.7 + 7,234.1 * ln age
Heavy shrubs: Y = - 2,009.7 + 9,254.3 * ln age

Standard errors for the intercept and slope coefficients were 1,580.3 ft^2 per acre and 661.3; the squared multiple correlation coefficient (R^2) was 0.86; the standard error of the estimate ($S_{y.x}$) was 2,830.5 ft^2 per acre; F = 145.87; and P value < 0.0001.

Height

Light shrubs: Y = 0.6 + 0.1 * age
Medium shrubs: Y = 1.1 + 0.1 * age

Heavy shrubs: Y = 1.3 + 0.1 * age

Standard errors for the intercept and slope coefficients were 0.1 foot and 0.01; the squared multiple correlation coefficient (R^2) was 0.88; the standard error of the estimate ($S_{y.x}$) was 0.3 foot; F = 180.55; and P value < 0.0001.

Volume

Light shrubs: Y = - 5,652.6 + 2,264.3 * age
Medium shrubs: Y = - 2,191.8 + 3,738.4 * age
Heavy shrubs: Y = - 361.4 + 4,713.6 * age

Standard errors for the intercept and slope coefficients were 3,534.3 ft^3 per acre and 246.1; the squared multiple correlation coefficient (R^2) was 0.88; the standard error of the estimate ($S_{y.x}$) was 11,789.4 ft^3 per acre; F = 172.59; and P value < 0.0001.

Ponderosa Pine

Foliar cover

No shrubs: Y = 3,009.7 + 845.4 * age
Light shrubs: Y = 1,080.2 + 509.7 * age
Medium shrubs: Y = 1,705.2 + 391.2 * age
Heavy shrubs: Y = 609.7 + 148.5 * age

Standard errors for the intercept and slope coefficients were 1,023.9 saplings per acre and 71.3; the squared multiple correlation coefficient (R^2) was 0.74; the standard error of the estimate ($S_{y.x}$) was 3,415.4 saplings per acre; F = 61.85; and P value < 0.0001.

Height

No shrubs: Y = - 12.4 + 11.2 * ln age
Light shrubs: Y = - 6.9 + 7.4 * ln age
Medium shrubs: Y = - 3.3 + 4.9 * ln age
Heavy shrubs: Y = - 0.7 + 2.5 * ln age

Standard errors for the intercept and slope coefficients were 0.9 foot and 0.4; the squared multiple correlation coefficient (R^2) was 0.92; the standard error of the estimate ($S_{y.x}$) was 1.7 feet; F = 264.89; and P value < 0.0001.

Volume

No shrubs: Y = - 51,079.0 + 10,037.0 * age
Light shrubs: Y = - 12,671.0 + 3,369.1 * age
Medium shrubs: Y = - 5,571.3 + 2,197.2 * age
Heavy shrubs: Y = - 1,474.9 + 601.6 * age

Standard errors for the intercept and slope coefficients were 6,472.1 ft^3 per acre and 450.7; the squared multiple correlation coefficient (R^2) was 0.83; the standard error of the estimate ($S_{y.x}$) was 21,589.3 ft^3 per acre; F = 106.11; and P value < 0.0001.

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Abstract

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On a poor site in northern California, a brushfield community was treated in various ways which left initial densities of no shrubs, light, medium, and heavy shrubs. Density and development (height, foliar cover, crown volume) for three shrub species (alone and combined), one grass, and planted ponderosa pine in these categories were quantified from 1966 to 1992. Successional trends (ascendance and decline) are presented for these species and for forbs from 1962 (the date pines were planted) through 1992. Regression equations that model density and development are presented for the shrubs and pine. In general, greenleaf manzanita prospered during the study; snowbrush initially developed well, but then declined; Sierra plum endured, but was relegated to the understory; needlegrass invaded rapidly, peaked early, and was mostly gone by the end of the study. Only a trace of forb species remained by study end. Needlegrass displayed strong environmental preference, becoming dense and developing well in shrub-free areas, but was scarcely present in heavy shrubs. Ponderosa pine grew well in no-shrub plots, fairly well in light-shrub plots, and poorly in medium- and heavy-shrub plots. Extensive testing showed that shrub foliar cover and crown volume per acre explained more variation in several pine parameters than shrub height or density.

Retrieval Terms: density, development, grasses, plant succession, ponderosa pine, shrubs

The Authors

Philip M. McDonald and **Celeste S. Abbott** are research forester and forester, respectively, assigned to the Vegetation Management Research Unit, located at the Station's Silviculture Laboratory, 2400 Washington Avenue, Redding, CA 96001.

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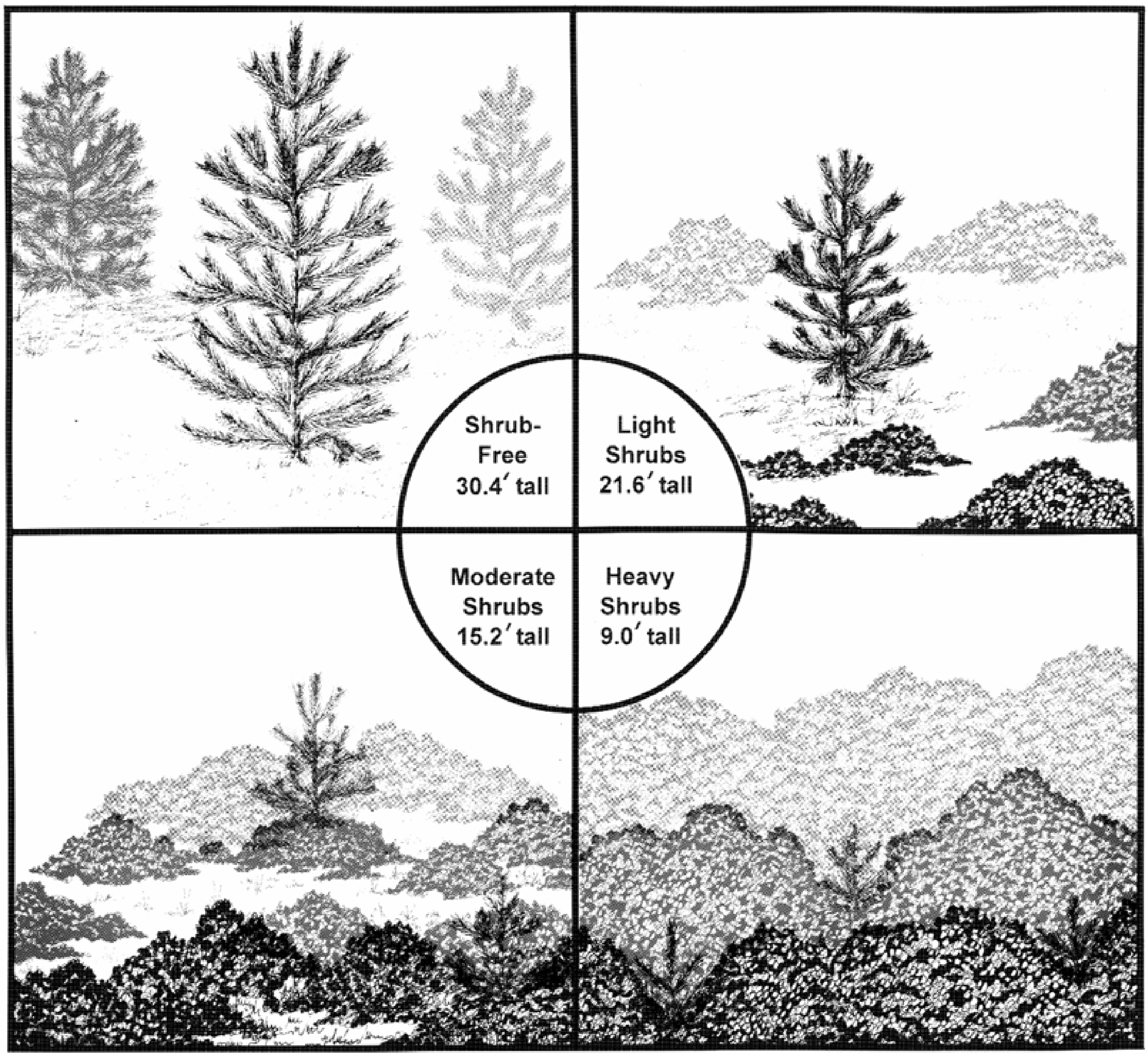
Vegetation Trends in a 31-Year-Old Ponderosa Pine Plantation: Effect of Different Shrub Densities

Philip M. McDonald   Celeste S. Abbott



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New conifer plantations characteristically are located in areas that have been severely disturbed by wildfire or timber harvest, or where the plant community consists of woody or herbaceous species with no economic value. If the area is a brushfield, the goal often is to restore tree species that traditionally were present there. In the area of this study, a mixed conifer forest had been present in the past. But after at least a decade of logging and fire (1887-1897), all the trees had disappeared and a large area had become clothed with a dense mass of vigorous shrubs. In the next 60 years or so, these shrubs undoubtedly produced many seed crops, each of which contributed to the seedbank in the soil. It is likely that subsequent fires burned the brushfield, as well, with each slightly modifying the soil and its nutrient- and water-conducting capability. Because the study area was part of a much larger area, no seed trees remained. The shrubs fully occupied the site and virtually no chance for the natural establishment of a forest existed.

In 1962, when the study area was cleared and planted, conversion from brush to trees was the land management objective. But because the growth potential of the site was low and the odds for success of a mixed conifer plantation also were low, only ponderosa pine was planted. This pine survives and grows well in hot, dry conditions on poor sites. Foresters recognized that conversion to the original mixed conifer forest involved two steps: (1) getting the forest started and creating a forest environment, and (2) in the less harsh forest environment, planting shade-tolerant trees characteristic of the mixed conifer type.

Revegetation on the bare soil of recently disturbed areas usually is rapid and highly variable. In this study, greenleaf manzanita and snowbrush originated from seeds in the soil, Sierra plum sprouted from roots and root crowns, and several species of forbs appeared from windblown seeds. In 1966, the natural vegetation consisted of 6 species of shrubs, 10 forbs, and one graminoid. In 1967, a native needlegrass became an important component of the plant community.

Previous herbicide trials had left the study area with various amounts of shrubs. In 1966, these were segregated into no-, light-, medium-, and heavy-shrub categories, and these became the "treatments" in this study. Many developmental characteristics (height, foliar cover, volume) of shrubs (alone and together), grass, and ponderosa pine were quantified in each category through 1992. Plant density also was quantified for shrubs and grass, and diameter at breast height was measured for pine.

The ascendance and decline of the various plant species portray successional trends in the study area. In general, greenleaf manzanita prospered in the plantation. It retained a relatively high density level and developed well in foliar cover and height. It was virtually undamaged by abiotic agents. Snowbrush was much less dense to begin with, developed well for the first 15 years, declined for the next 15 years, and clearly was fading from the plant community at the end of the study. Frost, drought, and wind contributed to its decline. Sierra plum, which developed only from vegetative propagules, will be a part of the future plant community, but mostly in the understory. It existed in the shade and sprouted in the shade—something the other shrub species did not do.

Needlegrass proved to be an ephemeral species that invaded the study area late and departed early. Its density and development keyed inversely to shrub density: the fewer the shrubs, the greater the needlegrass density and height. In 1983, for example, needlegrass density was 65,900 plants per acre in no-shrub plots and 450 per acre in heavy-shrub plots. About 540 plants per acre resided in no-shrub plots at the end of the study; none at all in other shrub categories. Because needlegrass invaded after the ponderosa pines had become established, its competitive effect was not as great as if it had been present earlier. Furthermore, its roots were not as deep as those of shrubs, and hence it was less competitive than them.

Ponderosa pine height and diameter, in general, differed statistically among all shrub categories during most of the study. Pines in the shrub-free category averaged 30.4 feet tall at study end, 21.6 feet tall in light shrubs, 15.2 feet tall in medium shrubs, and 9.0 feet tall in heavy shrubs. Furthermore, the pines were growing at an average rate of 1.1, 0.7, 0.5, and 0.3 feet per year in the no-, light-, medium-, and heavy-shrub categories, respectively. Plainly, even a small amount of shrubs cost the pines an appreciable amount of growth. Similar trends were present for diameter as well. After 31 years, ponderosa pines with any amount of shrubs are falling farther behind those with no shrub competition.

Because natural resource managers may want to mathematically express the long-term development of the shrubs, grass, and pine, regression equations are presented that model each species' density, foliar cover, height, and crown volume. In addition, several pine parameters were regressed against many shrub variables. Shrub foliar cover and volume per acre explained the most variation in most pine parameters. Consequently, shrub foliar cover is probably the most practical shrub variable to measure.

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The Forest Service, U.S. Department of Agriculture, is responsible for Federal Leadership in forestry.

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