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Development of a Mixed-Shrub–Planted Ponderosa Pine Community on a Poor Site After Site Preparation and Release

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Abstract

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On a poor site in northern California, a mature brushfield was treated in various ways that left initial density categories of light, medium, and heavy shrubs. Density, foliar cover, and height of seven shrub species (alone and combined) and ponderosa pine seedlings in these categories were quantified from 1967 through 1978. Heretofore, density and development data for five of the seven shrub species were unavailable. From the beginning to the end of the study, vegetation in the plantation was subjected to damage from insects, disease, snow, wind cupping, winterburn, a parasitic vine (dodder), and application of an herbicide. In general, greenleaf manzanita, which was the most abundant shrub species in the study area, prospered, as did bitter cherry, choke-cherry, and Fremont silk tassel; huckleberry oak endured; and bush chinquapin and mountain whitethorn declined. Among shrub categories at the end of the study in 1978, the density of combined shrubs ranged from 19,800 to 8,300 plants per acre; foliar cover from 14,000 ft^2 to 8,900 ft^2 per acre, and height from 2.8 to 2.5 feet. Ponderosa pine seedlings began to recover from damage in 1974, and because upturned branches had replaced dead and damaged tops, seedling form improved. Pine seedlings growing with a low amount of competition were significantly taller and had more foliar cover than counterparts with heavy competition in 1974, a finding that continued for foliar cover through 1978.

Retrieval terms: competition, northern California, plant community development, ponderosa pine seedlings, poor site, silviculture

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Ideally, each land type or segment of commercial forest land in California will provide valuable amenities and commodities, and serve as a needed species/structure/age component of an ecosystem. But for the land manager to obtain the desired amenities and commodities, knowledge is needed on what plant species are present, how they develop, which ones dominate, and what effect currently undesirable species have on desired species. When such knowledge is available for all, or at least most of the segments, ecosystem management will become both easier and sustainable. Silviculture research can provide some of this knowledge. Natural revegetation of a treated brushfield on a poor-quality, ridge-top site in northern California, and planted ponderosa pine seedlings serve as the setting for this study, and provide answers to some of the above questions. The answers pertain only to this particular segment of forest land and to others having a similar environment.

The objectives for this 12-year (1967-1978) study were threefold: (1) to identify the plant species on study plots and denote changes in species richness during the study period; (2) to quantify density, foliar cover, and height of principal shrubs, and density and height of abundant forbs, ferns, and grasses; (3) to quantify foliar cover and height of ponderosa pine seedlings, denote their recovery from several forms of damage, and determine their interaction with shrubs in three initial density categories of light, medium, and heavy shrubs.

For the first objective, species richness decreased from 29 to 26 species. At the end of the study in 1978, the natural plant community consisted of 1 conifer, 1 hardwood, 10 shrubs, 12 forbs, 1 grass, and 1 fern. For the second objective, greenleaf manzanita was the most abundant species and had the highest density and foliar cover of the seven shrub species that were quantified. Greenleaf manzanita and bitter cherry, choke-cherry, and Fremont silk tassel generally increased in density, cover, and height in all three of the initial density categories, and will be present in the plant community of the near future. The status of huckleberry oak in the future plant community is unclear. Average density and foliar cover values suggest that this oak is maintaining its position in the community, but its low average height makes it vulnerable to taller shrubs and pines. Mountain whitethorn and bush chinquapin had generally declining values in most density categories and probably will have only a minor presence in the plant community of the future. Because these seven shrub species dominate both vertically and horizontally, other species of shrubs, forbs, ferns, and grasses probably will be sparse and poorly distributed in the near future.

For objective three, only 12 percent of ponderosa pine seedlings perished during the study in spite of the harsh ridge-top environment. Pine foliar cover and stem height increased steadily throughout the study in all three initial shrub density categories. By the end of the study, mean pine foliar cover ranged from 12,550 ft^2 per acre in the low shrub category to more than 5,900 ft^2 per acre in the high shrub category. Values for average height in similar categories were 8.1 to 5.8 feet. From the beginning to the end of the study, ponderosa pine seedlings were beset by damage from snow, wind cupping, winterburn, insects, disease, a parasitic vine (dodder), and application of an herbicide that was applied in October 1967 to release the plantation from competition. Rare was the year that at least some damage did not occur. The resiliency of the pine seedlings was remarkable, and after upturned branches replaced dead and deformed tops, it was difficult to tell that damage had occurred on many of the seedlings. By the end of the 1974 growing season, the relationship of the pines to the competing shrubs was becoming clear. Where competition was low, the pines had significantly more foliar cover and height than pines in the high shrub density category; where competition was intermediate, as in the medium shrub category, the pines also had significantly more foliar cover than counterparts in the high shrub category. Graphs of pine cover and height showed a clear trend of increasing growth with decreasing amounts of shrubs.

Silviculturists have many techniques to manipulate unwanted vegetation, and to nudge an area with low plant diversity and little vertical structure toward one with a more natural species composition and a more variable structure. Site preparation, which tends to lessen the number and size of mature competing plants, and plantation release, which often lessens the effect of new or reestablished competing plants, aid in the establishment of a desired species by increasing the amount of available site resources. An arborescent species, ponderosa pine, which historically had been part of the plant community, was not present in the mature brushfield when this study was installed. Now it is present and growing well, at least where the competing shrubs are of low and medium density. As a young pine stand with 26 other species of vegetation, it forms a specific vegetative assemblage about which some information is now available and whose developmental trajectory can be postulated. Because the pines provide contrast to the mature stand of trees nearby, they have amenity value. Because they could eventually become a crop of timber and wood products, they have commodity value as well.

Introduction

The practice of silviculture in the era of ecosystem management needs not only to employ its traditional emphasis on trees, but also to concentrate on lesser vegetation, particularly on land disturbed both naturally and by humans. Manipulating lesser vegetation could be for a variety of reasons: to help create a future forest, to enhance stream flow, to provide an economic crop, to grow plants whose seeds or browse would be critical to wildlife, or simply to have present a broad base of species and age classes, and thus be able to provide amenities and commodities that will be needed in the future.

Broadening the art of vegetation management to include detailed information on lesser vegetation is increasingly recognized. Gordon (1979) recommended that foresters begin to build a database for vegetation that is expected in specific areas. Hungerford (1986) stated, "research is needed on seed dissemination and establishment requirements for many species." Wagner and Zasada (1991) noted that forest managers across North America need to consider the potential effect of noncrop vegetation on nearly every acre of newly forested land. Rietveld (1992) advocated an increased demand for diverse tree and shrub nursery stock, especially for species that provide food and shelter for wildlife. Aune and others (1993) suggested that greater within-stand species variation will be desired in the future and "the growing and planting of high quality seedlings of hardwood trees, shrubs, and other flowering plants is now expanding to meet multi-resource objectives." O'Hara and others (1994) stated that future forestry must embrace "a mix of commercially valuable and nonvaluable species." McDonald and others (1996) noted a weakness and a need when beginning ecosystem management in areas that had or should have a forest on them. The weakness is that "very little is known about the shrub, forbs, and grasses in the community." The need is for "knowledge on silvicultural treatments that will provide desired plant communities at specific times in the future."

Ecosystem managers of the future are going to need a tremendous amount of data (McDonald 1999). Information on plants, animals, fish, insects, fungi, and even genes will be needed in order to effectively practice ecosystem management. For plants, knowledge about species composition, density, and development often is unavailable not only for individual species, but also for the community in which they grow. In this study, seven common and widespread shrub species were quantified and evaluated both ecologically and for competitive potential. These were greenleaf manzanita (*Arctostaphylos patula* Greene), mountain whitethorn (*Ceanothus cordulatus* Kellogg), huckleberry oak (*Quercus vaccinifolia* Kellogg), bush chinquapin (*Chrysolepis sempervirens* [Kell.] Hjelmq.), bitter cherry (*Prunus emarginata* [Hook.] Walp.), western choke-cherry (*Prunus virginiana* L. var. *demissa* [Nutt.] Torrey), and Fremont silk tassel (*Garrya fremontii* Torrey). No density or developmental information could be found for five of the seven shrub species that were studied. Realistically, ecosystem management can best be accomplished if discrete units of land are identified and studied. These discrete units, called segments or land types (Miles and Goudey 1997), are the smallest units identified in the hierarchical framework of ecological units. When knowledge about many land types is available, not only will ecosystem management be enhanced on each, but it will be improved even more because these types can be joined and relationships at larger scales ascertained.

Although some anecdotal information has been recorded, knowledge about individual plant species in specific plant communities on poor sites is largely unavailable. Changes in species composition, density, and growth are often lacking, especially over a 5-year or longer period. The effect of these plant species on planted ponderosa pine seedlings, whether alone or combined, and the pine's effect on them also are poorly quantified.

This paper reports the recovery of individual shrub species, combined shrubs, and planted ponderosa pine seedlings at various intervals during a 12-year (1967-1978) period in three initial shrub density categories; documents changes in plant species composition; quantifies density, foliar cover, and height of principal shrubs; and quantifies foliar cover and height of ponderosa pine seedlings.

Methods

Location and Site Characteristics

The study area, called the Sugarloaf plantation, is located on the Downieville Ranger District of the USDA Forest Service's Tahoe National Forest in T20N, R9E, sections 13 and 14, Mt. Diablo meridian. It is situated about 6 airline miles northwest of the town of Downieville, and is located in a 750-acre brushfield. The area burned in 1924 and has been undisturbed since then. One small grove of large ponderosa pines (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) was located in a portion of the brushfield, but no other evidence was found to indicate that the area had been other than a brushfield for scores of years.

Before the study began, the vegetation consisted of mature shrub species that ranged from 3 to 8 feet tall (*fig.1*). Most abundant was greenleaf manzanita with mountain whitethorn, bush chinquapin, and huckleberry oak less abundant, but well distributed throughout the area. Western choke-cherry, bitter cherry, and Fremont silk tassel also were common, but less well distributed. Bracken fern (*Pteridium aquilinum* [L.] Kuhn var. *pubescens* L. Underw.), two perennial forbs, and no grasses were noticed in a pretreatment (fall 1962) survey (Bradshaw 1962). Scientific and common names of trees are from Little (1979) and all other vegetation follows the nomenclature of Hickman (1993).

Deer (*Odocoileus* spp.), rabbits (*Sylvilagus* spp.), and coyotes (*Canis* spp.) were common in the study area, but other than occasional nipping of some of the shrubs, damage was negligible.

Site quality of the study area is low with height of dominant mixed conifers averaging about 50 feet in 50 years (Biging and Wensel 1984). Because of its ridge-top location, the study area is subjected to high amounts of insolation and strong winds. The elevation is about 5,500 feet and the topography is gently undulating with slopes of less than 15 percent. The soils are derived from vol-

Figure 1—A portion of the study area before site preparation in 1962.

canic flows, are 2 to 36 inches deep, and generally quite stony and droughty. Occasionally, small rocky outcrops and bare gravelly areas are present. The growing season is about 90 days. Mean annual precipitation is about 80 inches with most falling as snow.

Precipitation for the January-through-June period was evaluated each year. Years with an above average amount of precipitation were 1967, 1969, 1973, and 1978. Years with below-average precipitation occurred in 1966, 1968, 1971-72, and 1976-77; and years with average precipitation were 1970, 1974, and 1975.

An early study on site preparation (Buck and Baron 1961), installed in spring 1962 through fall 1963, involved a combination of mechanical and chemical applications at different times of the year (spring and fall). The mechanical treatment involved pushing the mature shrubs into windrows with tractors equipped with a straight blade and a brushrake. The goal was to remove the shrub root crowns, but this was impossible in places because of rocks and shallow soil. About 2 inches of soil were moved, and some of it was deposited in the windrows, particularly where the blade was used. The windrows were burned shortly after piling. Two herbicides (2,4-D and 2,4,5-T) also were applied with a power sprayer as a tank mix in spring and fall in conjunction with the mechanical treatments. The treatments were applied in 12 rectangular blocks, each about 5 acres (330 by 660 feet), sandwiched between the windrows. Some treatments were effective and some were not. The net effect of all the treatments was to create a large area covered with a wide range of shrub densities that were ideal for a study whose aim was to quantify subsequent plant community-ponderosa pine relationships.

Ponderosa pine seed was from the correct zone, and seedlings were grown in the Placerville Nursery for 1 year. They were planted in spring 1964 at an intended spacing of 8 by 8 feet, which became 6 by 8 feet in places (McDonald and Oliver 1984). The weather was ideal for early seedling establishment, with rain falling before, during, and after planting. Survival after 2 years was 91 percent (McDonald 1966).

Study and Design

The current study began in summer 1965 when transects, perpendicular to planted rows of pines, were drawn on maps at 20-foot intervals in each of the 12 blocks. Two transects in each were randomly chosen and laid out on the ground. These became the center lines of sample plots. Each plot was then evaluated for shrub density and categorized as light, medium, or heavy. Consequently, six plots had a heavy shrub density, ten had a medium density, and eight had a light shrub density. At least 15,000 plants per acre separated the light, medium, and heavy designations. In effect, each category became a treatment.

Each sample plot was rectangular and contained 24 to 31 seedlings, averaging 27, surrounded by several rows of similar seedlings. No plots were located close to the windrows or near the corridors at the ends of the planted rows. Sample seedlings had to appear healthy and none that were small, misshapen, or discolored were selected. These would have been removed in the first thinning. On each of the sample seedlings, stem height (*fig*. 2) and 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]) were measured. These seedlings also were checked for possible injury from both biotic and abiotic sources. Damage was recorded only if the seedling stem was injured or the top was killed. Sampling for shrubs and other vegetation was by four systematically selected subplots located near the center of each plot. Subplots were square and contained 1 milacre (0.001 acre or 43.56 ft^2). The most abundant species were measured for density, foliar cover, and height. More specifically, density was the number of plants on each subplot, presented on a per-acre basis. Foliar cover was an ocular estimate, checked by a foot-square wire frame and a measuring

Figure 2—Measuring height on a ponderosa pine seedling in a low shrub density area, September 1965. Note the rocky soil.

tape, and also presented on a per-acre basis. If less than 0.5 ft^2, foliar cover was denoted as a trace (T). Height was calculated as the average of the three tallest stems per species in the milacre subplots. It was measured from mean ground line to top of plant.

Sampling

Detailed sampling of pine seedlings and woody vegetation by species did not begin until 1966, but these data are not presented here because of lingering effects from the site preparation spraying. Consequently, sampling of the most abundant species began in 1967 and took place in late summer or early fall at various yearly intervals, which were close together early in the study and widened at the end. All species on study plots were recorded at the beginning and end of the study, and some of the forbs, ferns, and grasses were quantified at the end of the study in 1978.

Early surveys showed that total shrub density was huge (up to 97,000 plants per acre) and shrub growth was vigorous. Thus, a decision was made to release the pines from the shrubs in early October 1967. Sampling had already been completed. Release involved aerially spraying the study area with 2,4,5-T at a rate of 3 pounds acid equivalent per acre.

Because the three treatments (categories) had an uneven number of plots in them, an unbalanced form of analysis of variance was used, along with a Bonferroni "t" test (SAS Institute 1988). Significance in all tests was at α= 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 in 1967 consisted of 29 species including 1 conifer, 1 hardwood, 11 shrubs, 15 forbs, and 1 fern. At the end of the study in fall 1978, the plant community was composed of 1 conifer, 1 hardwood, 10 shrubs, 12 forbs, 1 graminoid, and 1 fern, for a total of 26 species. The total number of plant species recorded during the study period was 32 (*table 1*). The graminoid (*Achnatherum nelsonii* [Scribner] Barkworth), which is a species of

Table 1—*Natural vegetation in study plots, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Vegetation category	Scientific name	Common name	1967	1978
Conifers				
	Abies concolor var. *lowiana*	California white fir	X	X
Hardwoods				
	Quercus kelloggii	California black oak	X	X
Shrubs				
	Arctostaphylos patula	greenleaf manzanita	X	X
	Amelanchier utahensis	service-berry	X	X
	Ceanothus cordulatus	mountain whitethorn	X	X
	Chrysolepis sempervirens	bush chinquapin	X	X
	Garrya fremontii	Fremont silk tassel	X	X
	Prunus emarginata	bitter cherry	X	X
	Prunus virginiana var. *demissa*	western choke-cherry	X	X
	Quercus vaccinifolia	huckleberry oak	X	X
	Ribes roezlii	Sierra gooseberry	X	X
	Rosa gymnocarpa	wood rose	X	--
	Symphoricarpos mollis	creeping snowberry	X	X
Forbs				
	Calyptridium umbellatum	pussypaws	X	X
	Eriophyllum lanatum	woolly sunflower	X	X
	Eriophyllum spp.	woolly sunflower	X	X
	Gayophytum diffusum	---	X	X
	Kelloggia galioides	---	X	--
	Lilium washingtonianum	Washington lily	X	X
	Lupinus spp.	lupine	--	X
	Nama lobbii	purple mat	X	X
	Penstemon spp.	beardtongue	X	X
	Smilacina racemosa	false Solomon's seal	X	X
	Solanum xanti	nightshade	X	--
	Trientalis latifolia	starflower	--	X
	Unknown	---	X	--
	Unknown	---	X	--
	Unknown	---	X	--
	Unknown	---	X	X
	Unknown	---	X	X
Graminoids				
	Achnatherum nelsonii	needlegrass	--	X
Fern				
	Pteridium aquilinum var. *pubescens*	bracken	X	X

Figure 3—Invasion of needlegrass in the study area.

needlegrass, is common at lower elevations, but was not present in the study area before site preparation. It became established near the road that passed through the plantation, and eventually spread into the study plots (*fig. 3*). Pickups and cattle trucks travel this road and seed probably blew off them. In 1978, several classes of non-woody and semi-woody vegetation were present on the milacre subplots. Their mean density and height were:

Category	Density	Height
	plants/acre	*ft*
Most abundant forbs	12,459	0.7
Woolly nama	3,302	0.3
Bracken fern	1,417	1.1
Needlegrass	4,323	1.8

Because plants were poorly distributed, standard errors are meaningless and not presented.

Woolly nama (*Nama lobbii* A. Gray) is a prostrate perennial that becomes established on bare areas in bright sunlight (*fig. 4*). It spreads rapidly from elongating roots and forms dense masses of vegetation. These dense masses suppress germination of dormant shrub seeds in the soil, and serve as a means of biological control. Hence, it was sampled separately. However, it was impossible to delineate a "plant" because of its spreading habit. Consequently, density for this species is conservative and defined as number of clumps, rather than number of plants. Bracken fern spreads across the landscape from underground rhizomes and defining a "plant" also is difficult. Hence, its density was recorded in terms of number of fronds.

Dodder (*Cuscuta* spp.), which is an annual parasitic vine, became present in the plantation in 1966 and became dense in places. It tended to form a net over some plants, particularly greenleaf manzanita, and killed several of them. By the end of the study, however, it had almost disappeared from the study area.

Figure 4—This ponderosa pine seedling is surrounded by woolly nama and a few shrubs.

Effect of Release Spray

The effect of the October 1967 release spray is best described as variable both as to area and plant species affected (*tables 2-9*). Some portions of the study area were not affected; some were moderately influenced; and a small portion, particularly where the soil was poorest, was heavily affected. In affected portions of the plantation, mountain whitethorn was damaged most with greenleaf manzanita second. Many plants of these two species died. Bush chinquapin and huckleberry oak lost almost all of their leaves and stems, but resprouted at ground line in most instances. Fremont silk tassel lost most of its outer leaves, but the inner leaves were untouched. Only a few plants of these species died from the spray. Western choke-cherry was only lightly affected by the spray and bitter cherry was unaffected. Dieback and sprouting from the root crown almost always resulted. Woolly nama and dodder virtually disappeared from the study area, but reappeared the next year and colonized vigorously for 2 additional years.

Visual observations and diary records noted that the timing of death differed among species as well. Most mountain whitethorn plants died outright, although a few sprouted from ground line the next spring. In contrast, greenleaf manzanita continued to die from spray damage through 1970. Some plants died outright, others died back to ground line, and still others lost most of their leaves and stems. Many lingered in this condition for 2 or 3 years. Some recovered and some died. Mortality of manzanita was greatest the first year after spraying and tapered off during the next 2 years. For mountain whitethorn, density decreased 53 percent between 1967 and 1970; for greenleaf manzanita, the decrease in density was 56 percent. Certainly, some of this decrease can be ascribed to mortality from spraying, but not all. Early density values for some species were high—too high. They are unsustainable and high natural mortality during the first few years is the normal trend. Corresponding decreases in foliar cover for whitethorn and manzanita were 46 and 57 percent, respectively. Because plants tend to become larger from the beginning, foliar cover tends to increase. Thus, the decrease in foliar cover during the first few years is likely to be more a consequence of the spraying than is density.

Greenleaf Manzanita

This evergreen, fast-growing shrub was the most abundant species in the plantation. After site preparation, viable seeds in the soil germinated by the thousands, and averaged more than 64,000 plants per acre in the high shrub category. Corresponding values in the medium and low shrub categories were 26,580 and 7,975 plants per acre, respectively. These values differed statistically (p = 0.001) (*table 2*). Manzanita density in the high and medium categories then decreased markedly through the end of the study in 1978. In the low category, however, density decreased through 1971 and then increased. Foliar cover was more consistent among shrub density categories. In all three categories it decreased through 1969 and then increased through 1978. For the high category foliar

Table 2—*Average density, foliar cover, and height of greenleaf manzanita by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	64,783 a[1]	2,900 a	0.8 a
	Medium	26,580 b	1,400 b	0.8 a
	Low	7,975 c	588 c	0.8 a
	Root mse[2]	10,300	885	0.29
	F	35.60	7.88	0.51
	P	0.001	0.001	0.679
1969	High	29,917 a	1,250 a	0.8 a
	Medium	12,670 a	740 a	0.8 a
	Low	5,613 a	238 a	0.5 a
	Root mse	15,999	994	0.35
	F	3.02	1.62	1.65
	P	0.054	0.216	0.210
1971	High	26,317 a	3,483 a	1.3 a
	Medium	12,750 a	2,430 a	1.3 a
	Low	5,325 a	688 a	1.1 a
	Root mse	14,615	2,203	0.46
	F	2.78	2.06	0.62
	P	0.068	0.138	0.608
1974	High	21,733 a	6,100 a	2.2 a
	Medium	11,180 a	4,930 ab	2.1 a
	Low	6,500 a	1,575 b	1.6 a
	Root mse	11,625	2,941	0.75
	F	2.46	3.29	1.19
	P	0.094	0.042	0.339
1978	High	16,583 a	9,183 a	3.1 a
	Medium	8,980 a	7,980 a	3.1 a
	Low	5,812 a	2,437 b	2.8 a
	Root mse	8,218	3,675	0.79
	F	2.32	4.97	0.94
	P	0.105	0.010	0.440

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test ($\alpha = 0.05$).
[2] Root mse is root mean square error.

averaged 2,900 ft^2 in 1967 and increased 217 percent through 1978; for the medium category, it was 1,400 ft^2 in 1967 and increased 470 percent; in the low category, foliar cover of manzanita in 1967 averaged 588 ft^2 per acre and increased 314 percent through 1978. In general, foliar cover differed statistically between the high and low shrub density categories during the study. Mean height of manzanita generally increased throughout the study in all three categories. It ranged from 0.8 foot in 1967 to about 3 feet in 1978 with no statistical difference among categories.

Mountain Whitethorn

Although never abundant, this species was well distributed throughout the study area and was an important part of the shrub community. In 1967, whitethorn density averaged between 350 and 925 plants per acre among shrub categories (*table 3*). Density then declined through 1969, recovered slightly in 1971, and decreased drastically between 1974 and 1978. In 1978, density averaged between 100 and 312 plants per acre in the three shrub categories. The trend in foliar cover was to decrease in 1969, and to recover somewhat by the end of the study. In 1978 foliar cover averaged between 330 and 917 ft^2 per acre among shrub categories. Height of mountain whitethorn generally increased during the study, and in 1978 ranged between 1.3 and 1.9 feet. At no time did mean density, foliar cover, or height differ statistically among shrub categories.

Huckleberry Oak

This oak is a small, compact, deciduous shrub, 1 to 4 feet tall, that inhabits mountain ridges and rocky areas at higher elevations. It extends from southern Oregon southward in the North Coast and Klamath Mountains and through the Sierra Nevada to the vicinity of Yosemite National Park (McMinn 1939, Pavlik and others 1991). In 1967, mean density of this oak ranged from 88 to 840 plants per acre among shrub categories (*table 4*). In 1978, density ranged from 162 to 950 plants per acre among shrub categories with no real trend in intervening years. Foliar cover also showed no meaningful trends and ranged from 250 to 860 ft^2 per acre in 1967 to 188 to 1,000 ft^2 per acre in 1978. For all density classes, mean height ranged from an average of 1.8 feet in 1967 to an average of 1.3 feet in 1978. No statistical differences were found among shrub categories for density, foliar cover, or height during the 1967- to 1978-period.

Bush Chinquapin

This low, spreading, evergreen shrub, 1 to 8 feet tall, often forms thickets on dry mountain ridges and in rocky places in open forests in several mountain ranges in California, western Nevada, and southern Oregon (McMinn 1939). In this study, mean density generally declined in all density classes between 1967 and 1978 (*table 5*). In 1978, statistically more plants per acre were present in the medium category than in the low category (322 versus 62 plants). Foliar cover decreased erratically in the high and low density categories, and then after an early decline, increased steadily in the medium category. In 1978 it ranged from 600 ft^2 per acre in the high category to 1,944 ft^2 per acre in the medium category. Height generally increased throughout the study in all density categories, and by the study's end ranged from 2.6 to 4.5 feet.

Bitter Cherry

This cherry, one of seven species in California, is a deciduous shrub, 4 to 12 feet tall, that often forms dense thickets in the Coast Ranges and the mountains of the Sierra Nevada (McMinn 1939). Average density of this species in 1967

Table 3—*Average density, foliar cover, and height of mountain whitethorn by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	350 a[1]	50 a	0.5 a
	Medium	630 a	510 a	0.8 a
	Low	925 a	725 a	1.8 a
	Root mse[2]	927	869	0.34
	F	0.49	0.72	2.09
	P	0.694	0.553	0.155
1969	High	200 a	T[3] a	0.5 a
	Medium	210 a	320 a	0.9 a
	Low	500 a	412 a	0.9 a
	Root mse	541	530	0.45
	F	1.71	0.78	0.80
	P	0.198	0.519	0.536
1971	High	300 a	T a	0.7 a
	Medium	400 a	400 a	0.8 a
	Low	588 a	825 a	1.0 a
	Root mse	676	985	0.39
	F	0.57	0.93	0.93
	P	0.641	0.444	0.481
1974	High	467 a	500 a	1.1 a
	Medium	400 a	250 a	0.7 a
	Low	500 a	400 a	1.0 a
	Root mse	700	601	0.47
	F	0.04	0.29	0.46
	P	0.987	0.832	0.724
1978	High	150 a	917 a	1.9 a
	Medium	100 a	330 a	1.9 a
	Low	312 a	750 a	1.3 a
	Root mse	331	1,272	0.63
	F	1.02	0.39	0.54
	P	0.406	0.760	0.681

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α = 0.05).
[2] Root mse is root mean square error.
[3] T equals trace.

Table 4—*Average density, foliar cover, and height of huckleberry oak by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	717 a[1]	833 a	3.2 a
	Medium	840 a	860 a	0.4 a
	Low	88 a	250 a	1.8 a
	Root mse[2]	900	1,043	2.14
	F	1.27	1.23	1.28
	P	0.310	0.324	0.352
1969	High	550 a	417 a	1.2 a
	Medium	560 a	410 a	0.5 a
	Low	88 a	125 a	0.7 a
	Root mse	728	844	0.33
	F	0.98	0.54	3.38
	P	0.422	0.663	0.084
1971	High	550 a	1,200 a	1.2 a
	Medium	490 a	930 a	1.0 a
	Low	88 a	250 a	0.9 a
	Root mse	728	1,515	0.25
	F	0.93	0.77	1.42
	P	0.442	0.522	0.325
1974	High	1,000 a	1,717 a	1.5 a
	Medium	600 a	960 a	1.2 a
	Low	88 a	250 a	1.2 a
	Root mse	1,120	1,744	0.29
	F	0.89	0.86	1.59
	P	0.462	0.477	0.302
1978	High	950 a	1,000 a	1.6 a
	Medium	750 a	930 a	1.5 a
	Low	162 a	188 a	0.9 a
	Root mse	1,102	1,372	0.34
	F	0.73	0.63	2.88
	P	0.548	0.605	0.142

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.

Table 5—*Average density, foliar cover, and height of bush chinquapin by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	333 a[1]	1,217 a	1.3 a
	Medium	788 a	750 a	0.9 a
	Low	290 a	1,250 a	1.2 a
	Root mse[2]	1,048	1,830	0.51
	F	0.49	0.14	0.62
	P	0.695	0.933	0.627
1969	High	283 a	333 a	1.0 a
	Medium	210 a	250 a	1.0 a
	Low	625 a	538 a	1.6 a
	Root mse	988	797	0.64
	F	0.34	0.22	0.66
	P	0.799	0.880	0.629
1971	High	200 a	500 a	2.2 a
	Medium	210 a	700 a	2.1 a
	Low	662 a	1,100 a	2.3 a
	Root mse	1,043	1,674	0.99
	F	0.43	0.16	0.03
	P	0.735	0.921	0.990
1974	High	200 a	767 a	2.5 a
	Medium	180 a	1,100 a	2.5 a
	Low	62 a	625 a	3.5 a
	Root mse	336	2,182	0.35
	F	0.69	0.16	5.37
	P	0.566	0.922	0.305
1978	High	167 ab	600 a	3.1 a
	Medium	322 a	1,944 a	2.6 a
	Low	62 b	875 a	4.5 a
	Root mse	297	3,038	1.46
	F	5.25	0.42	1.41
	P	0.008	0.742	0.440

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α = 0.05).
[2] Root mse is root mean square error.

ranged from 267 plants per acre in the high shrub category to 562 per acre in the low shrub category, and in general increased throughout the study period (*table 6*). In 1978, density ranged from 960 to 1,783 plants per acre. Foliar cover increased erratically throughout the study in the high density category and-steadily in the medium and low categories. At the study's end, mean foliar cover was 300 ft^2 per acre in the high category and 2,000 or more square feet per acre in the medium and low categories. Mean height ranged from 2.3 to 3.3 feet at the end of the study. No statistical differences were found among shrub categories for density, foliar cover, or height during the study period.

Western Choke-Cherry

Like bitter cherry, this species is one of the seven species of *Prunus* in California. It is an erect deciduous shrub, 3 to 12 feet tall, that is widely distributed throughout the mountains of California (McMinn 1939). Average density, foliar cover, and height of this species all increased erratically in all density classes from the beginning of the study in 1967 to its end in 1978 (*table 7*). At the end of the study, density ranged from 90 to 262 plants per acre, foliar cover from a trace to 1,962 ft^2 per acre, and height from 0.4 to 5.4 feet. The lower number reflects the height of new recruits entering the medium shrub category. Mean height was statistically lower than counterparts in the high shrub category.

Fremont Silk Tassel

This erect, evergreen shrub, which grows in chaparral and forest areas in most mountain ranges in California (McMinn 1939), ranges from 4 to 10 feet tall. It resembles greenleaf manzanita in many ways, except that it has dark green leaves arranged opposite each other on the stem. No plants were present during the study in the high density category (*table 8*). In the medium and low categories, density ranged from 112 to 340 plants per acre in 1967 to 175 to 340 plants per acre in 1978. Only in the low category was density increasing. Mean foliar cover in the medium category decreased initially and then increased to 950 ft^2 per acre in 1978. It was 750 ft^2 per acre in the low category at the beginning and end of the study. Height increased in both the medium and low categories throughout the study, and was about 2.8 feet tall in 1978.

Combined Shrubs

When combined, the seven principal shrub species in this study constituted a hardy, vigorous, dominant component of the plant community. Initial mean densities of 66,533 plants per acre in the high category and 29,240 plants per acre in the medium category generally decreased throughout the study and ended with 19,800 and 11,542 plants per acre, respectively (*table 9*). Density in the low category decreased through 1971 and then increased to more than 8,300 plants per acre, which was a decrease of 18 percent from the initial value (10,625 plants per acre). The trend in foliar cover was consistent in all categories: decreasing in 1969 and then steadily increasing through 1978. For the high category, foliar cover averaged 5,333 ft^2 per acre in 1967 and increased 135 percent by the end of the study in 1978. In the medium category, cover in 1967 was 4,370 ft^2 per acre and in 1978 was 14,184 ft^2 per acre for a 225 percent increase. For the low category, cover increased 94 percent to 8,962 ft^2 per acre through 1978. Average height increased over initial values in all categories and by the end of the study ranged from 2.5 to 2.8 feet.

Table 6—*Average density, foliar cover, and height of bitter cherry by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft^2/acre*	*ft*
1967	High	267 a[1]	83 a	0.7 a
	Medium	560 a	400 a	1.0 a
	Low	562 a	288 a	1.3 a
	Root mse[2]	1,251	944	0.53
	F	0.10	0.22	0.71
	P	0.957	0.883	0.584
1969	High	267 a	T[3] a	1.1 a
	Medium	540 a	650 a	1.7 a
	Low	825 a	688 a	2.1 a
	Root mse	1,577	1,615	0.68
	F	0.16	0.30	0.88
	P	0.920	0.827	0.525
1971	High	233 a	267 a	1.2 a
	Medium	530 a	1,020 a	1.5 a
	Low	900 a	1,350 a	2.3 a
	Root mse	1,590	2,674	1.19
	F	0.26	0.19	0.54
	P	0.852	0.900	0.668
1974	High	667 a	333 a	1.5 a
	Medium	880 a	1,430 a	1.6 a
	Low	1,325 a	1,588 a	2.9 a
	Root mse	1,881	3,477	1.04
	F	0.17	0.17	1.19
	P	0.916	0.914	0.391
1978	High	1,783 a	300 a	2.5 a
	Medium	960 a	2,050 a	2.3 a
	Low	1,562 a	2,000 a	3.3 a
	Root mse	2,243	4,086	1.25
	F	0.20	0.27	0.47
	P	0.895	0.847	0.716

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.
[3] T equals trace.

Table 7—*Average density, foliar cover, and height of western choke-cherry by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	83 a[1]	250 a	2.0 a
	Medium	0 a	0 a	-
	Low	175 a	775 a	2.7 a
	Root mse[2]	256	885	1.06
	F	1.36	2.12	0.33
	P	0.284	0.130	0.667
1969	High	83 a	167 a	2.4 a
	Medium	20 a	10 a	2.0 a
	Low	200 a	275 a	2.3 a
	Root mse	223	360	0.42
	F	2.35	1.82	0.04
	P	0.104	0.175	0.879
1971	High	83 a	417 a	2.8 a
	Medium	0 a	0 a	-
	Low	150 a	688 a	2.2 a
	Root mse	160	879	0.49
	F	2.05	1.90	14.05
	P	0.140	0.162	0.185
1974	High	83 a	583 a	3.2 a
	Medium	20 a	T[3] a	0.2 a
	Low	250 a	1,312 a	2.8 a
	Root mse	238	1,542	0.28
	F	2.05	1.79	33.80
	P	0.139	0.181	0.126
1978	High	167 a	550 a	5.4 b
	Medium	90 a	T a	0.4 a
	Low	262 a	1,962 a	2.9 a
	Root mse	300	2,092	0.49
	F	1.46	1.98	30.31
	P	0.256	0.149	0.010

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.
[3] T equals trace.

Table 8—*Average density, foliar cover, and height of Fremont silk tassel by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft^2/acre*	*ft*
1967	High	0 a[1]	0 a	-
	Medium	340 a	450 a	1.1 a
	Low	112 a	750 a	1.3 a
	Root mse[2]	663	1,018	0.15
	F	0.80	1.92	1.50
	P	0.501	0.160	0.308
1969	High	0 a	0 a	-
	Medium	340 a	350 a	1.3 a
	Low	112 a	500 a	1.3 a
	Root mse	662	633	0.27
	F	0.80	2.41	0.02
	P	0.501	0.097	0 .903
1971	High	0 a	0 a	-
	Medium	340 a	520 a	1.7 a
	Low	112 a	1,125 a	1.7 a
	Root mse	663	1,159	0.61
	F	0.80	2.97	0.01
	P	0.507	0.056	0.956
1974	High	0 a	0 a	-
	Medium	340 a	850 a	2.0 a
	Low	188 a	50 a	1.8 a
	Root mse	671	1,311	0.54
	F	0.90	1.96	0.26
	P	0.459	0.152	0.645
1978	High	0 a	0 a	-
	Medium	340 a	950 a	2.8 a
	Low	175 a	750 a	2.9 a
	Root mse	665	1,390	0.59
	F	0.79	2.00	4.17
	P	0.516	0.147	0.136

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.

Table 9—*Average density, foliar cover, and height of combined shrubs by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Density	Cover	Height
		plants/acre	*ft²/acre*	*ft*
1967	High	66,533 a[1]	5,333 a	1.2 a
	Medium	29,240 b	4,370 a	0.8 a
	Low	10,625 c	4,626 a	1.0 a
	Root mse[2]	10,230	1,018	0.15
	F	34.78	1.92	1.50
	P	0.001	0.160	0.308
1969	High	31,300 a	2,167 a	1.0 a
	Medium	14,550 a	2,730 a	0.9 a
	Low	7,962 a	2,776 a	1.1 a
	Root mse	16,548	633	0.27
	F	2.56	2.41	0.02
	P	0.083	0.097	0.903
1971	High	27,683 a	5,867 a	1.3 a
	Medium	14,720 a	6,000 a	1.4 a
	Low	7,825 a	6,025 a	1.5 a
	Root mse	15,371	1,159	0.61
	F	2.21	2.97	0.01
	P	0.118	0.056	0.956
1974	High	24,150 a	10,000 a	1.8 a
	Medium	13,600 a	9,520 a	1.8 a
	Low	8,913 a	6,500 a	2.1 a
	Root mse	12,285	1,311	0.54
	F	2.18	1.96	0.26
	P	0.123	0.152	0.645
1978	High	19,800 a	12,550 a	2.6 a
	Medium	11,542 a	14,184 a	2.5 a
	Low	8,347 a	8,962 a	2.8 a
	Root mse	8,592	1,390	0.59
	F	2.40	2.00	4.17
	P	0.098	0.147	0.136

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.

Ponderosa Pine

Pine seedlings led a precarious existence during most of this study and were constantly recovering from a host of biotic and abiotic agents. Destructive biological agents were humans, insects and disease; abiotic agents were wind and snow. Damage by humans was caused by the release spray. An unknown tip moth killed the tops of ponderosa pine seedlings in 1969, 1970, and 1976. Damage was confined to small, weak seedlings that were shaded by the surrounding shrubs. Death almost always resulted. Snow mold (*Neopeckia colteri* [Pk.] Sacc.) killed several pine seedlings in 1967 and 1968 and damaged others in 1969. Damage seemed to relate more to the persistent snowdrifts of a cool, late spring than to a winter with a heavy snow pack.

Wind in this ridge-top study was strong and pervasive. Its damage took the form of wind cupping and winterburn. Wind cupping causes a funnel-shaped depression in the soil around seedling stems. Normally, when this happens, the depression is small, and little or no damage results. In this study, however, the depression was so large that many pine seedlings leaned 60 degrees or more (*fig. 5*). Years 1966 and 1970 were particularly bad for wind cupping. Most pines eventually recovered, but some developed a crooked bole. Winterburn takes place when the ground is frozen, water uptake is low, and strong winds dehydrate the needles, especially in the upper part of the seedling. This took place in 1969, 1970, and 1974. Its effect was to weaken most of the seedlings and kill a few of them. Damage from snow took the form of weighting down pine branches and boles to the point that the branches were actually pulled out of the bole or the boles were either split open or broken off (*fig. 6*). Snow damage occurred in the plantation where large drifts were formed. In the spring, the snow became ice and its weight was tremendous. Many seedlings were deformed from this damage and some eventually died. This form of damage was prevalent in 1971 and 1978.

Damage from the aerially applied herbicide was worse the first season after spraying (1968), and continued for the next 2 years. Not many seedlings died, but many were deformed. Some lost their tops and others formed a spindle-shaped leader with a few twisted needles on top. Most of these tops died. On many seedlings, a branch turned upward and became a new bole.

Diary entries noted “seedlings recovering from damage” almost every year. In 1974, the comment was that “pine seedlings are beginning to look like young trees” (*fig. 7*). In 1978 observers noted that “for the first time, the area is beginning to look like a plantation.” This was because the proportion of deformed pines had lessened dramatically in every shrub density category:

Category	**1974**	**1978**
	- - - - - -percent	- - - - -
High	25	7
Medium	24	2
Low	19	3

Pine seedling mortality during the 12-year study by shrub category was high, 7 percent; medium, 16 percent; and low, 9 percent. Overall, mortality was 12 percent, making survival 88 percent. The primary cause of seedling mortality was injury-related/competition-induced drought. From mid-July to the first rain in the fall, the soil was dry and its moisture content was at or below the wilting point. Shrubs often lost most of their leaves and pines all but current-year needles by mid-August.

Figure 5—Because of wind cupping at the base of the stem, this pine seedling has a severe lean, May 1970.

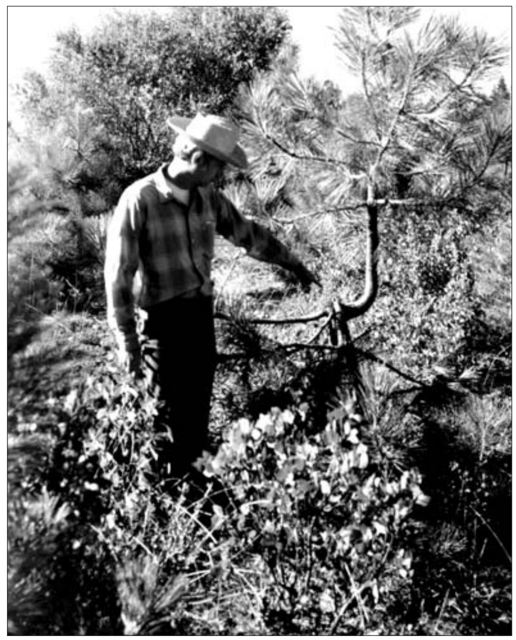

Figure 6—Typical snow damage to a ponderosa pine seedling in the study area, September 1978.

Figure 7—Now straight and tall, the pine on the right once had a damaged stem, August 1974.

Figure 8—A contrast in ponderosa pine foliar cover in 1978 (A) low initial shrub density, and (B) high initial shrub density. (The tip of one pine is just to the right of the man's shoulder.)

A

B

Average foliar cover of pine seedlings in all three shrub categories increased steadily throughout the study period (*table 10*). Values in 1978 by shrub category were high, 5,933 ft^2 per acre; medium, 7,780 ft^2 per acre; and low, 12,550 ft^2 per acre. By fall 1974, pine cover in the low shrub category was significantly larger than that in the high and medium categories. In 1978, foliar cover of pines in the low shrub category was significantly greater than that of counterparts in the high category (*fig. 8*). This relationship is likely to continue (*fig. 9*). Height also increased steadily in all categories from 1967 through 1978, when pines in the high shrub category averaged 5.8 feet tall; those in the medium category, 6.2 feet; and those in the low category, 8.1 feet tall (*table 10*). In 1974, pine height in the low shrub category was significantly greater than that of counterparts in the high category. This relationship not only is likely to continue, but it also is likely to accelerate (*fig. 10*), and to again become statistically significant as it was in 1974.

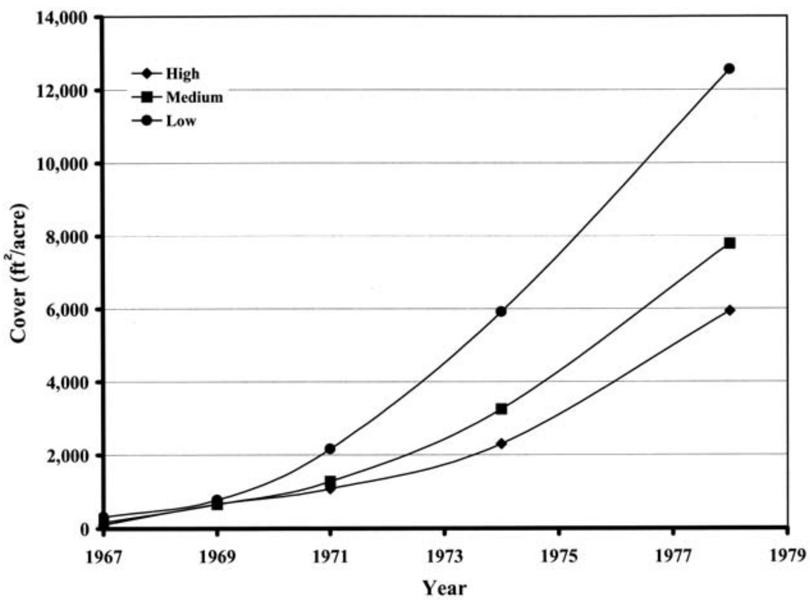

Figure 9—Trend of average foliar cover in three initial shrub density categories for ponderosa pine seedlings, Sugarloaf plantation, Tahoe National Forest, 1967-1978.

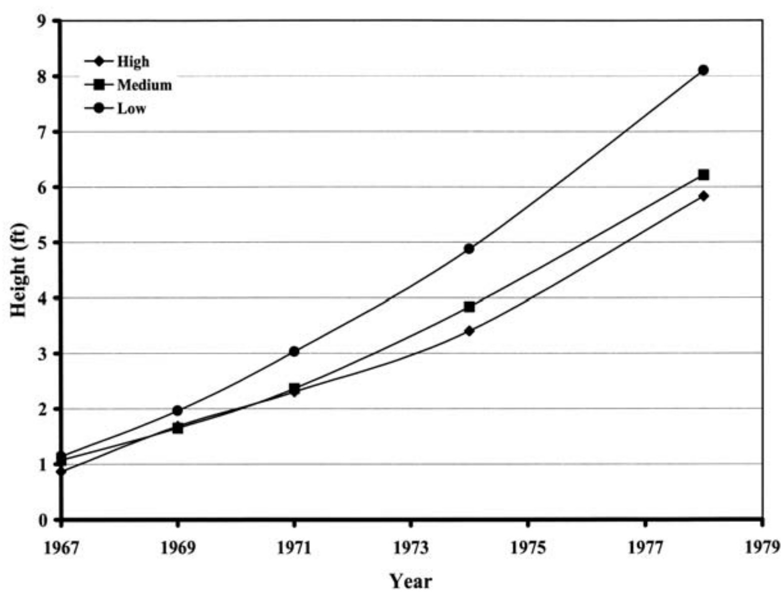

Figure 10—Trend of average stem height in three initial shrub density categories for ponderosa pine seedlings, Sugarloaf plantation, Tahoe National Forest, 1967-1978.

Discussion and Conclusions

Recovery was an important and ongoing process for almost all the vegetation in the study area. Pines in particular, and shrubs to a lesser extent, were recovering from some form of damage almost every year. Even bracken fern was affected. Wind cupping in 1967 had many ferns lying on their side. Notable was the almost complete recovery of the vegetation in 1978. Diary records noted the "unbelievable recovery of the pines" and the healthy appearance and vigorous growth of the shrubs. Indeed, "enormous" seed crops of bitter cherry, choke-cherry, greenleaf manzanita (*fig. 11*), Fremont silk tassel, and bush chinquapin were noted that fall.

The overall effect of the October 1967 release spray with the herbicide 2,4,5-T is best described as marginal. Timing, not the herbicide, was the primary reason for its ineffectiveness. First of all, the shrubs had grown for several years after the site preparation spray and were large and healthy. Had the release spray been applied in 1965, when the shrubs were still recovering from the first spray, the release spray probably would have been more effective. Secondly, the release spray was applied too late in the fall. Best results generally are attained when shrubs such as these are actively growing and transpiring (Stewart and others 1984). At the elevation of the study site, temperatures were becoming low in October, and most plants were hardened off and in a ready-for-winter mode. Many had lost at least some of their leaves and bitter cherry had lost all of its leaves. Although mountain whitethorn was affected most by the spray and thousands of greenleaf manzanita plants were damaged or killed, the overall effect of spraying on the shrub community was small. For example, before spraying in 1967, mountain whitethorn constituted about 2 percent of the total shrub community and retained this proportion in 1970. Greenleaf manzanita constituted about 93 percent of the community in 1967 and 89 percent in 1970. These proportions, however, are close, but only approximate, because recruitment from the seed bank in the soil took place each year, especially where mortality was heavy and the ground had become devoid, or nearly devoid, of vegetation. New shrub seedlings, mostly of manzanita, emerged by the hundreds. Many died, but those that did live became established and lowered mortality.

Figure 11—A heavy seed crop on greenleaf manzanita in the study area, September 1978.

Most plant species recovered by regrowth from burls or rhizomes plus a few recruits from seed. Greenleaf manzanita, however, recovered almost entirely by producing new seedlings from dormant seed in the soil. Diary records noted many new seedlings of this species each year from 1967 through 1972.

Ecologically, *tables 2* through *9* provide within-species and among-species relationships that suggest trends in early plant succession and the composition of the future plant community. Greenleaf manzanita was the most abundant species before the study began and continued to be the most abundant species at the end of the study. Its early densities in the high shrub category (64,783 plants per acre) and medium category (26,580 plants per acre) were not sustainable, and density continued to decline to a more sustainable level (16,583 and 8,980 plants per acre, respectively) in 1978. The release spray probably did little more than reduce inevitable mortality. Even with the decline, manzanita density in all categories was 70 to 84 percent of total shrub density at the end of the study. Foliar cover was affected by the release spray as well, but that too was inconsequential. In 1978, foliar cover of manzanita ranged from 73 percent of total shrub cover in the high category to 27 percent in the low category. At the end of the study, density was lower, but foliar cover and height were higher. Altogether, greenleaf manzanita should be both abundant and dominant in the study area for years to come.

Of all the shrub species, bitter cherry was the only one to increase in density, foliar cover, and height in all categories during the study. It was unaffected by biotic and abiotic agents, as well as the release spray, and showed large increases in cover in the medium and low categories. Western choke-cherry also was increasing in most categories during the study. It recovered from the release spray of 1967 and browsing in 1971 and was the tallest shrub in the study. Fremont silk tassel also recovered from the release spray, and in general was maintaining its density and foliar cover, and was increasing slightly in height. All three of these species should be present in the future plant community in the study area.

The future of huckleberry oak in the future plant community is not clear. From the beginning to the end of the study, its density, foliar cover, and height were generally increasing in the high and medium categories, but cover and height were decreasing in the low category. Its low average height in all categories (0.9 to 1.6 ft) in 1978 makes it vulnerable to increasing shade from taller shrubs and pines.

Mountain whitethorn appears to be the least competitive of the shrub species in the study. Its decreasing density from beginning to end of study in all three shrub categories and mixed gains and losses in foliar cover suggest that it will be relegated to only a minor presence in the plant community of the future. Bush chinquapin is another species with similar trends during the study period, and it too appears to be in decline. However, its robust height (2.6 to 4.5 feet) should help it to retain its presence in the plant community of the future.

For combined shrubs, some relationships are noteworthy. Foliar cover, which is recognized as providing a conservative expression of horizontal development, was low. At the end of the study, foliar cover ranged from 21 percent in the low category to 33 percent in the medium category. Crowns of the most abundant species, greenleaf manzanita, tended to be narrow and skimpy, with bare ground between them. It is likely on this poor site that shrub roots of manzanita and other species had larger radii than crowns and that they were present beneath much of this bare area. Another finding noted in diaries and to some extent in the data was that where manzanita was abundant and well developed, other shrub species were less abundant and poorly developed. For example, in the high category in 1978, shrubs other than manzanita had an average cover value of 8 percent relative to manzanita's 21 percent; in the low category, however, shrubs other than manzanita had an average value of 15 percent while manzanita had a cover value of only 6 percent. Indeed, foliar cover of bush chinquapin, bittercherry, and western choke-cherry was higher in the low category than in the high category at the end of the study.

Not only was foliar cover low, so was average height. Height values of combined shrubs of 2.5 to 2.8 feet in the three shrub categories in 1978 do not accurately portray the amount of competition that the shrubs gave to the pine seedlings. Although all the shrubs furnish competition, the tallest and widest ones probably furnish more. In this study, the tallest plants of most shrub species ranged from 4 to 7 feet (*fig. 8B*).

"Remarkable" best describes pine survival and recovery from damage. From 1966 through 1978, 88 percent of pine seedlings in the study survived in spite of almost chronic damage by a host of biotic and abiotic agents. Dead tops and crooked stems were common during the study, but many seedlings turned a branch upward and it became the new bole. Damage decreased from 23 percent of living trees in 1974 to 4 percent of living trees in 1978.

By 1974, the effect of competition on pine seedlings was becoming manifest among the three shrub density categories. Not only were differences among density classes becoming statistically significant (*table 10*), but trends in foliar cover and height were strengthening (*figures 9 and 10*). The slope of the fitted curves of pine foliar cover and height in the low shrub category in 1978 is greater than that of the curves in the medium category, indicating that the separation in growth will continue. The slope of the curve for foliar cover in the medium shrub category and its separation from the high category indicate that increasingly better growth will accrue to pines in the medium category as well. Plainly, the lower the amount of competition, the better the growth of ponderosa pine seedlings. Where the site preparation trials were effective, the competition was reduced early in the life of the seedlings, and that gave them an advantage that was maintained throughout the study.

The future of the pine seedlings in the high shrub category is problematical. The slope of the curves in *figures 9 and 10* indicate an upward trend, but the photo (*fig. 8B*) indicates heavy competition and skinny pine stems and narrow crowns. Tall, skinny stems are typical of pine seedlings striving to remain taller than the competition. To do so, stem diameter, crown development, and needle number and length are sacrificed to bolster stem height. This sacrifice is not sustainable, however, and at some point height growth slows, the pine seedlings become shaded, and soon die. Thus, height alone is a poor indicator of future pine seedling growth. In a similar study on a poor site (McDonald and Abbott 1997), the already-slow growth rate of pines with heavy competition continued for another 14 years, and was below minimum acceptable growth standards.

On a harsh, dry site in southwestern Oregon, Hanson (1997) studied the relationship between various densities of whiteleaf manzanita (*Arctostaphylos viscida* C. Parry) and the growth of ponderosa pine seedlings over a 13-year period. His data indicated that the biomass of whiteleaf manzanita expanded each year from seed during this period and will continue to do so for years to come. For pine seedlings, he found that the variation in height growth among the several manzanita densities correlated to both timing of departure and degree of departure from shrub-free conditions. In general, pines growing with manzanita continued to fall behind those without manzanita each year. He postulated that this trend in growth will continue until the trees reach economic maturity. Without release, trees growing with manzanita probably will grow slowly or succumb, leaving a near-continuous manzanita brushfield.

Vegetation managers never cease to look for "good" plant species that suppress "bad" species, and thus serve as a biological control. In the case of woolly nama, it had strong potential to be a good species because it virtually eliminated the aggressive shrub species. However, it requires full sunlight. Decline is inevitable as crowns of other vegetation develop and coalesce. Nord and Leiser (1974) noted that woolly nama grew well and formed dense cover in full sunlight. In this study, milacre subplots that initially had a dense cover of this species remained free of woody shrubs for the length of the study. Thus, woolly nama is worth considering as an early, but ephemeral, biological control species.

Before this study began, the area was a brushfield, and likely would have remained a brushfield for scores of years. The shrubs were large, well established, and covered the area to the point that access was limited. After site preparation, the planting of ponderosa pine seedlings, and their recovery from a release spray and several damaging agents, the area is poised to become a forest, at least in that area where competition was low. By reestablishing ponderosa pine, an important arborescent component has been restored to the plant community.

Table 10—*Average foliar cover and height of ponderosa pine seedlings by shrub category, Sugarloaf plantation, Tahoe National Forest, 1967-1978*

Year	Category	Cover	Height
		ft²/acre	*ft*
1967	High	100 a[1]	0.9 a
	Medium	170 a	1.1 a
	Low	312 a	1.1 a
	Root mse[2]	331	0.30
	F	0.92	1.08
	P	0.451	0.380
1969	High	667 a	1.7 a
	Medium	660 a	1.6 a
	Low	775 a	2.0 a
	Root mse	394	0.48
	F	1.78	0.71
	P	0.182	0.557
1971	High	1,083 a	2.3 a
	Medium	1,280 a	2.4 a
	Low	2,162 a	3.0 a
	Root mse	997	0.66
	F	1.70	2.02
	P	0.198	0.144
1974	High	2,300 a	3.4 a
	Medium	3,250 a	3.8 ab
	Low	5,912 b	4.9 b
	Root mse	2,126	1.04
	F	3.85	2.66
	P	0.025	0.076
1978	High	5,933 a	5.8 a
	Medium	7,780 ab	6.2 a
	Low	12,550 b	8.1 a
	Root mse	3,993	1.84
	F	3.70	2.57
	P	0.029	0.083

[1] For each year, treatment means in each column followed by the same letter do not differ significantly according to a Bonferroni test (α= 0.05).
[2] Root mse is root mean square error.

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Development of a Mixed-Shrub–Planted Ponderosa Pine Community on a Poor Site After Site Preparation and Release