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Factors Influencing the Scarification and Germination of Three Montane Sierra Nevada Shrubs

Abstract

Following fires in the forested ecosystems of the northern Sierra Nevada and southern Cascade mountains, early successional communities are often dominated by shrubs that arise from seeds that have remained viable in soil seedbanks for decades, or even centuries. The germination response of seeds of three seral montane shrub species was investigated following exposure to differing types of heat (wet vs. dry), temperature levels, durations of temperature exposure, and differing lengths of stratification periods. The highest germination (>60%) of *Ceanothus integerrimus* H. & A. was observed for seeds scarified by a wet-heat (treatment) of 75-100°C for 4-8 minutes. Wet-heat treatments were more effective than dry-heat treatments in scarifying seeds at all temperatures below 100°C. At dry-heat exposures for 120°C, 68-81% of the seeds were killed. Germination was less than 2% for seeds that were not exposed to any heat (scarification) treatment. Similarly, without stratification following scarification, germination was ≤5%. However, germination of scarified seeds followed by a stratification treatment was as high as 81.3%. No significant germination was found for seeds of *Arctostaphylos viscida* Parry or for *Arctostaphylos mewukka* Merriam regardless of treatment. Seeds of these species require another chemical, physical, or environmental factor in order to break embryo dormancy or they may have inherently low germination rates.

Introduction

In the ponderosa pine (*Pinus ponderosa* Dougl. ex P & C Lawson) and mixed conifer-dominated ecosystems of North America, early successional stages are often dominated by shrub species that originate from seeds stored in soil seedbanks. These seeds are deposited in the early stages of the sere prior to conifer dominance. During periods of conifer dominance, they may remain dormant, yet viable in extremely high numbers until dormancy is broken by fire or some other disturbance. Approximately 5 million viable seeds/ha of *Ceanothus* and *Arctostaphylos* spp. were found in the soils of an 80-100 year old mixed conifer stand in California (Anderson 1985).

Following fire or some other disturbance, these seeds germinate in numbers that far exceed the carrying capacity of the site (Wells 1969, Weatherspoon 1988, Kauffman 1987). However, fire severity (i.e., levels of biomass consumption and hence heat flux into the soils) has been shown to have dramatic influences on postfire shrub seedling density. For example, Weatherspoon (1988) found that the soil seedbank of *Ceanothus velutinus* Dougl. ex Hook. (snowbrush ceanothus) was not significantly reduced by prescribed understory burns of moderate or low consumption but up to 94% were destroyed by high consumption fires. Similarly, Kauffman (1987) found a strong relationship between fuel consumption and *Ceanothus integerrimus* H. & A. (deerbrush) density. Seedling densities of this species were 216,000/ha following prescribed understory fires of high consumption (92% consumption of dead and downed fuels), and 1667/ha in understory burns of moderate consumption (58% fuel consumption). Apparently, in the high consumption burn, soil heat flux was adequate to scarify large numbers of seeds. In contrast, the lower heat flux from the moderate consumption burn did not influence large numbers of the soil seedbank.

In recently disturbed sites (e.g., following clearcut logging), surface soil temperatures exceeding 60°C are possible on hot summer days. The exposure of the soil seedbank to these temperatures has been reported to be adequate for scarification and subsequent germination (Christensen and Muller 1975, Gratkowski 1962).

Shrubs of the *Arctostaphylos* and *Ceanothus* genera serve an important function in forest ecosystems. These species provide habitat and forage for mammals and birds (Cronemiller 1959). Many *Ceanothus* species have nitrogen fixing capabilities that result in the replacement of nitrogen volatilized by the fire (Binkley *et al.* 1982, Youngberg and Wollum 1976). *Ceanothus* and *Arctostaphylos* spp. also serve as intermediate hosts of mycorrhizal fungi which can have important symbiotic relationships with conifers (Perry *et al.* 1987). Finally, they can be significant competitors with regenerating conifers in forest plantations (Conard and Radosevich 1982).

Because of the economic and ecological importance of these species, it is essential to understand the factors affecting the dynamic relationships between fire or other forest disturbances and the germination of these shrubs. Through increased understanding of these relationships, it may be possible to efficiently manipulate the abundance of these species (i.e., decrease their abundance where they are not desired or conversely, increase their abundance where they are desired). To better understand these relationships, a laboratory germination study of three montane shrub species was conducted to investigate: (1) The relationship of seed germination with varying levels and durations of temperature exposure; (2) The influences of wet versus dry-heat environment on germination; (3) The influences of stratification length on germination.

Methods

Seeds of three montane chaparral species were used in this study: *Ceanothus integerrimus* var. *californicus* (Kell.), (deerbrush ceanothus), *Arctostaphylos viscida* Parry (whiteleaf manzanita) and *arctostaphylos mewukka* Merriam (Indian manzanita). These species are common early successional constituents of mixed conifer ecosystems in the northern Sierra Nevada. Although these species have been observed to have some capacity to sprout following crown mortality (Kauffman and Martin 1990), their primary mode of regeneration following disturbance is through seed germination.

Seeds were hand collected at the time of ripening (August-September, 1983 for *C. integerrimus* and *A. viscida*, and August, 1984 for *A. mewukka*). *C. integerrimus* and *A. viscida* were collected from two early seral, shrub-dominated communities located on the Quincy Ranger District, Plumas National Forest and the Challenge Experimental Forest (also a part of the Plumas National Forest). *A. mewukka* was collected at the Challenge Experimental Forest. Elevation of these sites ranged from 1000-1350 m and mean annual precipitation ranged from 800-1800 mm.

For each species, seeds were collected from at least 25 randomly selected shrubs. After collection, seeds from all shrubs and locations were thoroughly mixed together. Lots for the germination experiments were selected from these composite samples. A sample of seeds of each species was judged for viability by a cutting test similar to that of Young *et al.* (1978). During the formation of all seed lots, criteria for the judgement of viability included seeds free of insect and mechanical damage, and of a proper shape and seedcoat texture. If shriveled, damaged or pale in color, the seed was rejected for germination. Heat treatments were applied in December, 1984. Germination trials occurred from February-May 1985.

Experiment 1. Seed Responses to Varying Temperatures and Duration of Exposure

The scarification and germination response to 24 different treatment combinations was examined in this study. As in all experiments in this paper, each treatment consisted of 3 replicates (lots) of 50 seeds each. Approximately one-half of the treatments consisted of a "wet heat" exposure and one-half consisted of a "dry heat" exposure. In the "wet heat" treatments, each seed lot was exposed to a given temperature level for a given period of time by submersion in a water bath. An oven with a modified door for rapid insertion of the seeds with minimal heat loss was utilized for the "dry heat" treatments. The temperature levels for both heat treatments included: 45°, 60°, 75°, 90°, and 100°C. In addition, a 120°C dry treatment and a control (no heat) treatment was established.

Seeds were exposed to each temperature level for 4 and 8 minutes with the exception of the 60° treatments where only a 4 min. exposure was implemented. For *C. integerrimus* and *A. viscida* at the 90° temperature level, and additional treatment with an exposure duration of 16 minutes was also examined. Following temperature exposure, all seeds were stratified by packing them in moist perlite and placing them in a cooler at 3°C for 60 days.

An additional treatment for *A. mewukka* was examined; the effect of animal digestion on seed germination. Coyote (*Canis latrans*) feces containing large amounts of *A. mewukka* seeds were collected. These samples were collected at the same sites and times as the fresh seeds. These seeds were also exposed to temperatures of 75° and 100° for 4 minutes. A control (no heat) treatment was also examined.

Experiment 2. The Effect of Stratification Length on Germination

A total of 16 treatment combinations were examined in this experiment. Seeds were exposed to wet or dry heat treatment of 90°C for a duration of 4 and 8 min. Utilizing these scarification combinations, four stratification treatments were examined: (1) 60 days stratification following scarification, (2) 90 days stratification following scarification, (3) 60 days stratification and then scarification, and (4) no stratification. Stratification temperature was 3°C for all treatments.

For the germination trial, each lot of seeds was placed in petri dishes between blotter paper and moistened with distilled water. To prevent waterlogged or dry conditions, a layer of perlite was placed between the blotter paper and the bottom of the petri dish. During germination trials, seeds were kept at a temperature of approximately 21°C, and all were exposed to approximately 11 hours of light daily. Germination was recorded weekly for 5-6 weeks. Emergence of the hypocotyl from the seed coat was the criterion for determination of germination.

During germination trials, the number of *C. integerrimus* seeds that imbibed water (i.e., were scarified) and those that died were recorded to assess the treatment effects on these variables. Mortality was recorded when the seed was obviously rotted. These were easily separated from living seeds which did not become moldy and remained firm. Death and water uptake (imbibition) were not discernible for the *Arctostaphylos* spp.

It was estimated that greater than 95% of the seeds utilized were viable. Data were analyzed utilizing Analysis of Variance. If significant, a multiple comparison test (Student-Newman-Keuls') was utilized to determine significant differences among treatments.

Results and Discussion

Ceanothus integerrimus

Temperature Effects on Scarification and Germination

The highest levels of germination occurred following exposure to the 75°C, 90°C and 100°C treatments (Table 1). In the wet-heat treatments, germination was greatest when seeds were exposed to 90°C for 4 and 8 minutes (73-75% germination), but declined in lots exposed for 16 minutes (46.7%). The highest rate of germination in dry treatments was in lots exposed to 100°C for 4 and 8 minutes (52-53%).

There were large differences in the percent of germination between wet and dry-heat treatments at all temperatures below 100°C (Table 1). For example, germination was greater than 32% for all of the wet-heat treatments below 100°C. In contrast, there was little or no germination in dry heat treatments of 45°C or 60°C. Seed germination was significantly higher in wet treatments over dry treatments at exposures of 60°C, 75°C and 90°C temperature levels (Table 1).

Following exposures of 60°C for four minutes, 100% of seeds exposed to wet heat and 27% of seeds exposed to dry heat were scarified. Germination was 48% and 2% for the wet and dry heat, respectively. This indicates that the environment surrounding the seeds will dramatically influence rates of scarification and hence, germination. Under natural conditions, if surface soil temperatures are ~45-60°C when soils are saturated, thermal scarification from solar insulation is possible. Conversely, when soils are dry, temperatures of 90°C may be required to achieve these same levels of scarification (Table 1).

The percentage of seeds that were scarified was significantly different among seeds exposed to wet or dry heat. In wet-heat treatments, all treatments above 45°C had a 100% level of scarification. In contrast, of all the dry-heat treatments, only exposure to 120°C resulted in 100% scarification (Table 1).

The processs for germination is initiated in *Ceanothus* species when gas and water exchange occurs through the hilar fissure; an opening that bisects the hilum of the seed apex (Gratkowski 1962). In mature dormant *Ceanothus* seeds, the hilar fissure is sealed by opposing pressures of the two edges of this fissure against each other. Heat (scarification) in *Ceanothus* opens the hilar fissure allowing for gas and water exchange to occur between the surrounding environment and the endosperm and embryo of the seed. In studies of *C. velutinus* seeds, Gratkowski (1962) reported that heat affected only the hilum of seeds rendering it permeable to moisture; the rest of the seed coat was not affected and remained impermeable. From examination of scarified *C. integerrimus* seeds, heat appeared to only affect the hilum. After imbibition,

TABLE 1. Percent germination, death, and scarification for *Ceanothus integerrimus* seeds exposed to differing temperatures, lengths of exposure and different heat sources. Stratification period was for 60 days. Data are mean and standard error (in parentheses).

Temperature °C	Duration of Exposure (min)	Heat Source					
		Wet (Water bath)			Dry (Oven)		
		% Germination	% Dead	% Scarification	% Germination	% Dead	% Scarification
Control—no heat treatment		1 (1)	11 (1)	15 (1)	–	–	–
45°	4	33 (7)	17 (5)	69 (8)	3 (1)	13 (3)	25 (5)
	8	33 (15)	5 (1)	86 (3)	1 (1)	14 (2)	25 (1)
60°	4	48 (14)	9 (2)	100 (0)	2 (1)	16 (4)	27 (6)
	8	–	–	–	9 (1)	14 (4)	29 (2)
75°	4	68 (16)	19 (6)	100 (0)	27 (10)	11 (3)	48 (4)
	8	63 (13)	19 (8)	100 (0)	16 (4)	11 (3)	50 (5)
90°	4	75 (7)	23 (5)	100 (0)	23 (12)	13 (2)	70 (34)
	8	73 (4)	19 (6)	100 (0)	36 (14)	15 (2)	72 (5)
	16	47 (5)	28 (11)	100 (0)	27 (11)	12 (5)	68 (9)
100°	4	67 (8)	27 (7)	100 (0)	53 (8)	15 (3)	87 (1)
	8	45 (1)	41 (10)	100 (0)	52 (10)	19 (8)	85 (2)
120°	4	–	–	–	11 (1)	68 (13)	100 (0)
	8	–	–	–	8 (4)	81 (17)	100 (0)

openings along the hilar fissure were apparent with the naked eye. In addition, emergence of the radical always originated through the hilar fissure.

The difference in percent of seeds that were scarified at lower temperatures indicates that exposure to wet-heat is more efficient in opening the hilar fissure than the dry-heat. Whether this was a result of increased thermal conductivity in a water medium or some chemical-mechanical reaction due to contact with water is unknown.

Seed mortality did not significantly differ in all dry-heat treatments from 45-100°C. However, in the 120°C treatments, mortality significantly increased and was over 4 times greater than in the 100°C treatments. There was also a relationship between duration of heat and seed mortality at the 100°C level. For example, in the 100°C wet-heat treatments, mortality following 8 minutes of heat exposure was 14% greater than mortality following 4 minutes of exposure. Similar results were reported by Quick (1959) who found the highest germination of *Ceanothus* spp. occurred when boiled for 5 minutes. Germination declined when boiled for longer periods. Quick and Quick (1961) predicted a 4.2% drop in germination would occur for each minute *C. integerrimus* was immersed in boiling water.

Effects of Varying Durations of Stratification

After scarification, gas exchange at lower temperatures is necessary for seeds to overcome certain biochemical inhibitions to germination. Abscisic acid has been identified in the seeds of several species as an inhibitor of germination and has been found to decrease during chilling periods (Arias *et al.* 1976, Wareing *et al.* 1973). Concomitant with the decrease in abscisic acid, Wareing *et al.* (1973) and Arias *et al.* (1976) reported increases in cytokinins and gibberellins which have been found to promote germination. In this study we found that little or no germination occurred in seeds that were not stratified following scarification nor was there appreciable (< 1%) germination in seeds exposed to cold periods prior to scarification (Table 2). In contrast, germination was as high as 81% for scarified seeds with a 90 day stratification (Table 2).

Stratification resulted in highly significant increases in germination. In addition, the sample means were consistently higher in the 90 day stratification treatment in comparison to the 60 day stratification treatment. This is particularly true in the dry-heat treatments where germination rates increased from 22.9 to 54.7% in 4-min treatments and from 36.0 to 52.7% in 8-min treatments

TABLE 2. The percent germination of *Ceanothus integerrimus* resulting from four different stratification treatments. Seeds were exposed to heat treatments of 90°C for 4 or 8 minutes prior to stratification. Data are the mean percent germination and standard error (in parentheses). Different superscripted letters denote a significant difference ($P \leq 0.05$) in means between all treatments.

Treatment	Length of Exposure (min)	Heat Source	
		Wet (water bath)	dry (Oven)
60 d	4	75^c (7)	23^b (12)
	8	73^c (4)	36^b (14)
90 d	4	81^c (2)	55^b (7)
	8	79^c (9)	53^b (4)
60 d prior to scarification	4	1^a (1)	1^a (1)
	8	0^a (1)	0^a (0)
no stratification	4	1^a (1)	1^a (1)
	8	5^a (4)	1^a (1)

(Table 2). In both the 60 day and 90 day stratification treatments exposure of seeds to the wet-heat treatment at 90°C resulted in significantly higher levels of germination than identical exposures to dry-heat treatments.

In mixed conifer ecosystems, hundreds of thousands of shrub seedlings/ha have emerged the first postfire spring (Kauffman 1987). Following fire or other disturbance, rapid germination is a competitive advantage facilitating exploitation of limiting resources. For all of the 60 and 90 day stratification treatments, greater than 90% of the seeds that germinated did so in the first week (Figure 1). From examination of Figure 1, it is apparent that stratification requirements of the response of seeds in this species are only met with cool-moist conditions. This can be evidenced through examination of the response of seeds in

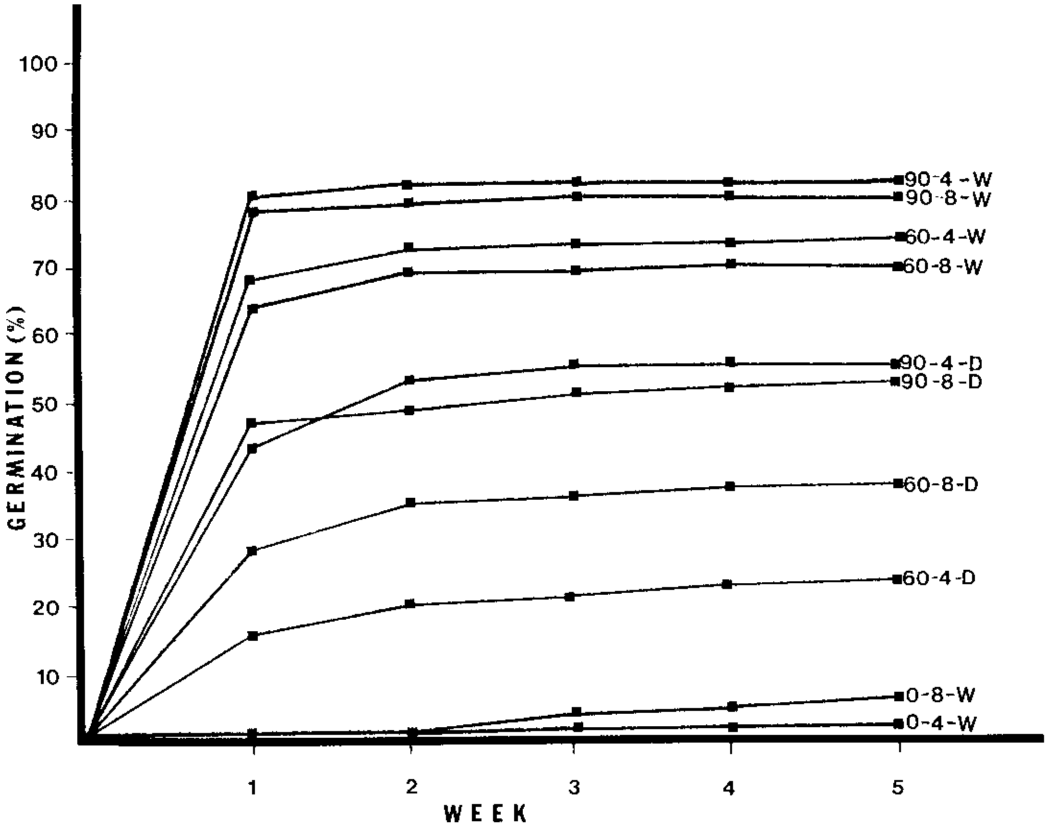

Figure 1. Weekly germination of *C. integerrimus* seeds that were exposed to 90°C for 4 and 8 min. and subjected to 3 different stratification treatments. The first number refers to the length of stratification period (0, 60 or 90 days). The second number refers to the duration of heat exposure (4 or 8 min.). The W refers to the wet heat treatment and the D refers to the dry heat treatment.

TABLE 3. The germination of *Arctostaphylos viscida* and *Arctostaphylos mewukka* following different temperatures and duration of exposure. Numbers are mean and standard error (in parentheses). Stratification length was 60 days. There were no significant differences ($P \leq 0.05$) in germination among treatments.

		A. viscida		*A. mewukka*	
Treatment	Duration of Exposure (min)	Wet (Water bath) % Germination	Dry (Oven) % Germination	Wet (Water bath) % Germination	digested/wet+ % Germination
control—no heat treatment		0 (0)	0 (0)	1 (1)	1 (1)
45°	4	0 (0)	0 (0)	4 (2)	–*
	8	1 (1)	1 (1)	0 (0)	–
60°	4	0 (0)	0 (0)	3 (1)	–
75°	4	1 (1)	0 (0)	3 (1)	8 (3)
	8	0 (0)	0 (0)	5 (1)	–
90°	4	0 (0)	1 (1)	5 (3)	–
	8	1 (1)	2 (1)	4 (4)	–
	16	0 (0)	1 (1)	0 (0)	–
100°	4	0 (0)	0 (0)	0 (0)	4 (2)
	8	0 (0)	2 (1)	0 (0)	–

+seeds collected from fresh fecal samples of *Canis latrans*

*—denotes that no trial conducted under this treatment combination

the unstratified treatments that had no increases in germination after exposure to 4-5 weeks of warm-moist conditions (i.e., the later stages of the germination trials).

Response of the *Arctostaphylos* spp.

Regardless of scarification treatment, germination rates were low for both *Arctostaphylos* species (Table 3). There were no significant differences in germination among treatments. The various stratification treatments also resulted in no differences in germination success. For *A. viscida*, the 90°C wet-heat scarification treatment with 60 days of stratification was replicated in 1985 with another seed source. The mean germination of this 1984 seed source was 10.6% ± 1.3. This was significantly greater than the 1983 seed source reported in Table 3. Although germination was significantly different, the percentage of seed viability before scarification treatments was not. However, the seeds collected in 1984 were generally larger in size and mass than the seeds produced the previous year.

None of the various combinations of heat or stratification resulted in high percentages of germination of *A. mewukka* seeds. Although slightly higher than that of fresh seed, germination of seeds found in the feces of coyotes was relatively low (≤8%) (Table 3). Therefore, animal digestion by mammals did not appear to be a significant factor in breaking seed dormancy of this species. However, during the season in which fruits are ripe, large numbers of *Arctostaphylos* seeds are widely dispersed throughout the region via fecal deposition. Thus, it is apparent that consumption of the *Arctostaphylos* fruits by mammals represents an effective means of seed dispersal.

While these species did not respond to these germination treatments, other species of *Arctostaphylos* have been reported to respond to heat treatments (Keeley 1977, Quick 1959). *Arctostaphylos patula* Greene is commonly associated with these species in the mixed conifer zone of the Sierra Nevada. Seeds of *A. patula* were observed to germinate in densities as high as 25,233/ha following fires in the northern Sierra Nevada (Kauffman 1987). Although seedlings of *A. viscida* in densities as high as 1,567/ha were present after fires, their numbers were exponentially less than those of *A. patula* (Kauffman 1987). Although seedling density of *A. viscida* significantly increases following high consumption fires, it is apparent that neither heat nor chemical changes (pH, nutrients, toxins, etc.) in the postfire environment are factors which induce the heavy simultaneous amounts of germination observed for *C. integerrimus* or *A. patula*. Similar results of low germination in laboratory tests of *A. viscida* were reported by Rogers (1949).

Based upon field observations of recently logged sites containing abundant *A. viscida* and *A. mewukka* seedlings, it appears that dormancy is often broken by mechanical scarification of the seed coat. In logged areas, it is frequently observed that *A. viscida* densities are highest where logging equipment has heavily impacted the soil. Areas of impact such as harvested stands in which logging slash has been piled will frequently have higher densities of *A. viscida* than harvested stands in which logging slash was left in place (i.e., areas of less mechanical disturbance). Conversely, logged areas in which slash is left in place and broadcast burned has been observed to have lower densities of *A. viscida* but higher densities of *C. integerrimus.*

Conclusion

The results of this laboratory study aid in the explanation of the mechanisms responsible for the increased densities of *C. integerrimus* in burned areas. Although high densities of *A. viscida* and *A. mewukka* have been observed following anthropogenic disturbances in mixed conifer ecosystems, additional research is needed to determine those physical, chemical, and biological mechanisms responsible for initiating germination.

Seeds of *C. integerrimus* were scarified by heat and required a cool-moist stratification period to break embryo dormancy. Optimum scarification temperatures were 75-100°C. At temperatures less than 100°C with either a 4 or 8 minute period of exposure, wet-heat was significantly more effective at seed scarification and initiation of germination than dry-heat. Seed exposure to a temperature of 120°C for 4 or 8 minutes exponentially increased mortality. Following stratification periods, germination is almost simultaneous with 80-90% of all germination occurring in the first week. In contrast, there was no germination response to thermal scarification by *A. viscida* or *A. mewukka* in this study.

Results of this study would infer that prescribed broadcast burning or wildfires would stimulate germination of *C. integerrimus* but not *A. viscida* or *A. mewukka.* These plant species are important in the ecological functioning of mixed conifer ecosystems and also are of aesthetic and economic significance.

An increased understanding of the germination requirements may allow for successful establishment of these species where desired. Conversely, this information could also aid in controlling densities of these shrubs in situations where unacceptable levels of competition with young conifers in managed plantations exist.

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