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Species-mediated soil moisture availability and patchy establishment of *Pseudotsuga menziesii* in chaparral

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Abstract The occurrence of mature individuals of *Pseudotsuga menziesii* in stands of *Arctostaphylos* species mark the initial stages of mixed evergreen forest invasion into chaparral in central coastal California. We planted two cohorts of *P. menziesii* seeds at three sites under stands of two *Arctostaphylos* species and *Adenostoma fasciculatum* in order to determine whether first-year seedling emergence and survival, particularly during the regular summer drought, underlie the spatial distribution of mature trees observed in chaparral. Regardless of the chaparral species they were planted under, *P. menziesii* seeds that were not protected from vertebrate predation displayed very little emergence and no survival. In contrast, emergence of *P. menziesii* that were protected from vertebrate predators was much higher but still did not significantly differ among the three chaparral species. However, survival of protected seedlings under *Arctostaphylos glandulosa* was much greater than under *A. fasciculatum*, with intermediate survival under *Arctostaphylos montana*. While mortality of protected seedlings due to insect herbivory, fungal infection, and disturbance displayed no consistent patterns, summer drought mortality appeared to drive the patterns of survival of *P. menziesii* under the different chaparral species. These emergence, mortality, and survival data suggest that spatial patterns of *P. menziesii* recruitment in chaparral are driven by first-year summer drought seedling mortality, but only in years when seeds and seedlings are released from vertebrate predation pressure. Because the first-year drought mortality and survival patterns of *P. menziesii* seedlings differed strongly depending on the chaparral species, we examined the additional hypothesis that these patterns are associated with differences in the availability of soil moisture under different chaparral species. Both higher survival and lower drought mortality of *P. menziesii* seedlings were associated with higher soil water potential under *Arctostaphylos* stands during the summer drought, especially in the subsurface soil. The data suggest that *Arctostaphylos* stands, particularly stands of *A. glandulosa*, ameliorate xeric summer conditions to a degree that facilitates first-year establishment of *P. menziesii* and strongly influences spatial distribution of mature trees.

Key words California chaparral · *Pseudotsuga menziesii* · Soil moisture · Seedling establishment · Facilitation

Introduction

The importance of seedling emergence and early establishment to the abundance and distribution of mature plants is widely recognized (Harper 1977; Grubb 1977; Pickett and White 1985; Tilman 1988). The success of seedling establishment, as with any propagule establishment, is dependent on the presence of safe sites (sensu Harper et al. 1961). Safe site conditions can result from the influence of organisms that have direct or indirect positive effects on propagule establishment (Callaway 1992). This phenomenon has been particularly well documented for vegetation dynamics in ecosystems with harsh environments, where the establishment of some plants is spatially associated with particular vegetation types or species. Through the use of inferential or experimental evidence, these associations are often suggested to be the result of positive

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plant-plant interactions referred to as "facilitation" (Callaway 1995).

Shrubs have received considerable attention for their role in facilitating early seedling establishment of other plant species through direct amelioration of environmental extremes and through indirect effects on animal seed dispersal and herbivory. In the deserts of southwestern United States and central Mexico, the seedlings of various cactus species associate with "nurse" shrubs whose canopies reduce high temperatures and ameliorate thermic desert conditions that otherwise eliminate recruitment (e.g., Franco and Nobel 1988, 1989; Valiente-Banuet et al. 1991; Arriaga et al. 1993). In areas with Mediterranean climates such as South Africa and coastal central California, the recruitment of some tree species is associated with shrubs that may alleviate xeric summer climate, provide shade, reduce competition from grasses and forbs, reduce herbivory by cows, and provide perches for birds which disperse tree seeds (Borchert et al. 1989; Callaway 1992; Manders and Richardson 1992). Many studies focus on establishment patterns and effects associated either with a particular shrub species or with a multispecies shrub community treated as a functional group (Callaway 1995). These studies fail to elucidate the potential importance of species-specific facilitation effects (Callaway 1998) that differ among co-occurring shrub species, as explicitly demonstrated in a few systems (Hutto et al. 1986; McAuliffe 1986; Callaway and D'Antonio 1991; Jones 1995). Species-mediated differences among stands or individuals of co-occurring shrub species with respect to factors such as microclimate, nutrient availability, allelopathy, and animal and rhizosphere relationships may influence patchy establishment of other plant species.

In the Mt. Tamalpais watershed of central coastal California, aerial photographs and spatial analyses document that in recent decades, *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir) individuals have established in chaparral in the absence of fire. In particular, mature individuals of *P. menziesii* are primarily associated with *Arctostaphylos* species (manzanita), although there are many other chaparral species which occur in the watershed (Parker 1991; Sparling 1994). We conducted experimental seed plantings to test the hypothesis that early seedling establishment of *P. menziesii* is greater in stands of *Arctostaphylos* species than in stands of *Adenostoma fasciculatum* Hook. & Arn. (chamise), a widespread chaparral species that occurs in similar sites. To determine which early life stage events most strongly influence *P. menziesii* establishment, we examined patterns of first-year seedling emergence, survival, and three types of seedling mortality (vertebrate predation, drought mortality, and other mortality). In addition, we investigated the hypothesis that differences in summer soil moisture levels among stands of various chaparral species, within the zone where *P. menziesii* seeds are planted, are associated with differential mortality and establishment of first-year seedlings.

Materials and methods

Site characteristics

The study was conducted in 1993 and 1994 in the 9000-ha watershed associated with Mt. Tamalpais in southern coastal Marin County. The elevation ranges from 120 to 780 m, and the region has a Mediterranean climate with a seasonal summer drought and average annual precipitation of 1250 mm. The first field season spanned a 124-day summer drought (7 June to 9 October) after the wet winter of 1992–1993 (1550 mm). The second field season spanned a 107-day summer drought (8 June to 24 September) after the dry winter of 1993–1994 (790 mm). The vegetation of the watershed is composed of a mosaic of three primary vegetation types: grassland, chaparral, and mixed evergreen forest (Howell 1970). The two woody vegetation types cover about 85% of the watershed (Parker 1991). Chaparral is generally composed of a mosaic of patches dominated either by *A. fasciculatum* or *Arctostaphylos glandulosa* Eastw. (burl manzanita), with other taxa such as *Ceanothus cuneatus* (Hook.) Nutt. (California lilac) and *Quercus wislizenii* A.D.C. var. *frutescens* Engelm. (interior live oak) scattered throughout. Because they have similar habitat requirements, *A. glandulosa* and *A. fasciculatum* also occur together in mixed-species stands in some areas (Parker 1991). In the chaparral, invading mature *P. menziesii* individuals can be found in association with *Arctostaphylos* in both single-species and mixed-species stands (Sparling 1994).

Research was conducted at three sites, referred to as East Peak, Bolinas Ridge, and Rock Springs. We selected adjacent mature stands at least 200 m^2 in area of *A. glandulosa* and *A. fasciculatum* at the East Peak and Bolinas Ridge sites for 1993 and 1994 research. We used adjacent stands in order to maximize the similarity of intrasite soil, topography, and climate conditions. We used mature, primarily single-species stands in order to ensure that any vegetation effects on the microclimate and other abiotic or biotic factors would be well-developed and likely to produce differential patterns of seedling establishment. Any initial intrasite moisture differences are likely to have been swamped by short- and long-term vegetation effects on microclimate and soil properties during more than 50 years of stand development since the last major fires at these sites. Adjacent stands of the previous two species plus a nearby stand of *Arctostaphylos montana* Eastw. (serpentine manzanita) were selected for 1994 research at Rock Springs. We added an *A. montana* stand because *P. menziesii* individuals have also been found in association with this less abundant *Arctostaphylos* species (Sparling 1994). The stands of *A. glandulosa* and *A. fasciculatum* are located on Franciscan soil, while the stand of *A. montana* is on serpentine soil. At all locations, mixed evergreen forest with *P. menziesii* is within 50 m of the selected stands.

Seed preparation and planting

We purchased *P. menziesii* seeds, collected in 1982 at 1050 m from a nearby region in northern central California, from the Pacific Forest Seeds Company (Eagle Point, Ore.). We chose not to use local seeds because two previous years of collection attempts yielded very few viable seeds. Use of either type of seed source has potential drawbacks. Had local seed sources been used, we might have inadvertently used seeds from trees that previously established under *Arctostaphylos* and had experienced ecotypic adjustment or adaptation to those conditions, leaving it unclear to what degree establishment patterns were a result of local *P. menziesii* population characteristics versus other factors. On the other hand, non-local seeds may show different amounts of establishment to local seed sources. However, this was of little concern since our focus was to compare patterns and processes of seedling establishment under several chaparral species rather than documenting accurate local rates of establishment.

The seeds were packed in peat moss and cold stratified for at least 30 days. Prior to planting, seeds were washed with distilled water and a 3% solution of the fungicide Amphyl, soaked in a 10% bleach solution for 10 min, and soaked in distilled water for 2 min. Floating seeds were discarded. A single field plot consisted of 30 seeds that were planted in an area of 0.5 m^2. The litter layer was scraped away and the seeds were placed 2–3 cm below the surface of the soil, with as little disturbance to the soil as possible. The litter layer was replaced, and the plots were then covered by small cages made of 6.5-mm wire mesh screen, which were staked down to inhibit vertebrate predation.

On 22 January 1993, five plots each were randomly planted under a stand of *A. glandulosa* and a stand of *A. fasciculatum* at East Peak, and three plots each were similarly planted under two Bolinas Ridge stands. On 26–27 January 1994, four plots each were randomly planted under the two chaparral stands at all three sites. An additional four plots were planted under a stand of *A. montana* at Rock Springs. To investigate vertebrate predation effects, we planted 30 uncaged seeds near each 1994 plot. The 1994 Bolinas Ridge plots were abandoned after 2 months when rodents dug into half of the cages and destroyed most seeds and seedlings. In total, we report on the first-year fate of 2160 seeds.

Seedling monitoring

The plots were monitored for newly emergent seedlings every 2–3 weeks starting in March of both field seasons and continuing until there was no new emergence. In this study, "total emergence" refers to the total number of seedlings, as a proportion of planted seeds, that broke the soil surface during their first growing season. The number of live seedlings per plot was monitored every 2–3 weeks from March until November and occasionally thereafter for several more months. By the end of November in each year, approximately 2 months after the summer drought ended, first-year seedling mortality dropped to one or fewer deaths per chaparral stand per month. "Total survival" for each cohort refers to the number of seedlings alive as of 24 November as a proportion of total emergence for that year.

The number of dead seedlings and the type of mortality were recorded at the same times as the number of live seedlings. Type of mortality was categorized either as "non-drought mortality" or "apparent drought mortality." Non-drought mortality was attributable primarily to predation or pathogen events (e.g., damping-off by fungi, insect herbivory), but was also occasionally caused by disturbance events (e.g., deer stepping on cages). Seedlings classified with apparent drought mortality were observed to wilt, dry, and become necrotic, and were recorded as dead when there was no more visible chlorophyll. This type of mortality is henceforth referred to as "drought mortality." In general, non-drought mortality occurred in the first 5 months after planting (February to June), while drought mortality started in mid-summer and continued for a month past the drought (July to October). Total non-drought mortality as of 24 November was converted to a proportion of total emergence, and total drought mortality was similarly converted with adjustments for prior non-drought mortality, since the available pool of seedlings was made smaller by earlier deaths. This adjustment results in $>100\%$ apparent total mortality in some plots.

Monitoring of soil water potential

To determine soil water potential within the chaparral stands, a pair of thermocouple psychrometers, model PCT-55 (Wescor, Logan, Utah) were buried next to each caged seedling plot. All sensors were individually calibrated and pairs were placed through 30-cm-long, 5-cm-diameter insulation-filled PVC tubes. The tubes were buried prior to seed planting with one sensor inserted at 7 cm soil depth and one at 20 cm. Psychrometer voltage was measured using a dew point microvoltmeter on psychrometric mode (model HR-33 T, Wescor) on the same days that seedlings were monitored through November of each field season. Measurements occurred between 10:00 a.m. and 2:00 p.m. Calibration and setup of the psychrometers followed Fonteyn et al. (1987) to maximize accuracy in a dry ecosystem.

Statistical analyses

For proportions of total seedling emergence and seedling survival, arcsine square root transformations were conducted in addition to Bartlett's transformation for proportions of 0 and 1 to equalize variance prior to conducting ANOVAs (Zar 1984). We compared multiple treatment means using Tukey HSD tests. Soil water potential means at different depth and dates were subjected to independent ANOVAs. Bartlett's test was used to examine homogeneity of variances. Analysis of mortality, survival trends, and uncaged seed data is by inspection only. All statistics were conducted using SYSTAT software.

Results

Seedling establishment

In both years, there was no significant difference in emergence of caged *P. menziesii* seedlings under *A. glandulosa* versus *A. fasciculatum* or between sites (1993 ANOVA, $P_{\text{species}} = 0.541$, $P_{\text{site}} = 0.095$; 1994 ANOVA, $P_{\text{species}} = 0.216$, $P_{\text{site}} = 0.295$). Total emergence ranged from about 60 to 70% of seeds planted under both species and during both years (Fig. 1a). In contrast, survival of emergent seedlings after the first drought season was much higher under *A. glandulosa* (19–24%) than under *A. fasciculatum* (0–3%), although there were no significant site differences (1993 ANOVA, $P_{\text{species}} = 0.060$, $P_{\text{site}} = 0.178$; 1994 ANOVA, $P_{\text{species}} = 0.001$, $P_{\text{site}} = 0.403$). Drought mortality of *P. menziesii* seedlings was greater than non-drought mortality under both chaparral species in both years and was also greater under *A. fasciculatum* (95–100%) than *A. glandulosa* (75–79%; Fig. 1c). There was no consistent pattern in non-drought mortality, with a higher rate under *A. glandulosa* than under *A. fasciculatum* in 1993 (26 vs 13%) and a lower rate in 1994 (6 vs 13%).

At Rock Springs, total emergence of caged *P. menziesii* under *A. montana* was not significantly different from the other two species (ANOVA, $P_{\text{species}} = 0.545$). However, seedling survival under *A. montana* was intermediate to survival under the other two species (Fig. 1b), although the differences are not statistically significant (ANOVA, $P_{\text{species}} = 0.137$). Drought mortality was much greater under all three species than non-drought mortality, with drought mortality under *A. montana* intermediate to the other two species (Fig. 1d). Non-drought mortality was similar under the two *Arctostaphylos* species and higher under *A. fasciculatum*.

Uncaged *P. menziesii* seeds planted in 1994 exhibited extremely low emergence and no survival. In this case, emergence should be considered "apparent" rather than "total," since we were unable to distinguish between mortality events on seeds and seedlings. Emergence was lowest under *A. montana* (0%) and *A. fasciculatum* (0.4 ± 0.4%), with slightly higher emergence under *A. glandulosa* (4.6 ± 2.1%).

In both years, under *A. glandulosa* and *A. fasciculatum*, the percentage of live caged *P. menziesii* seedlings

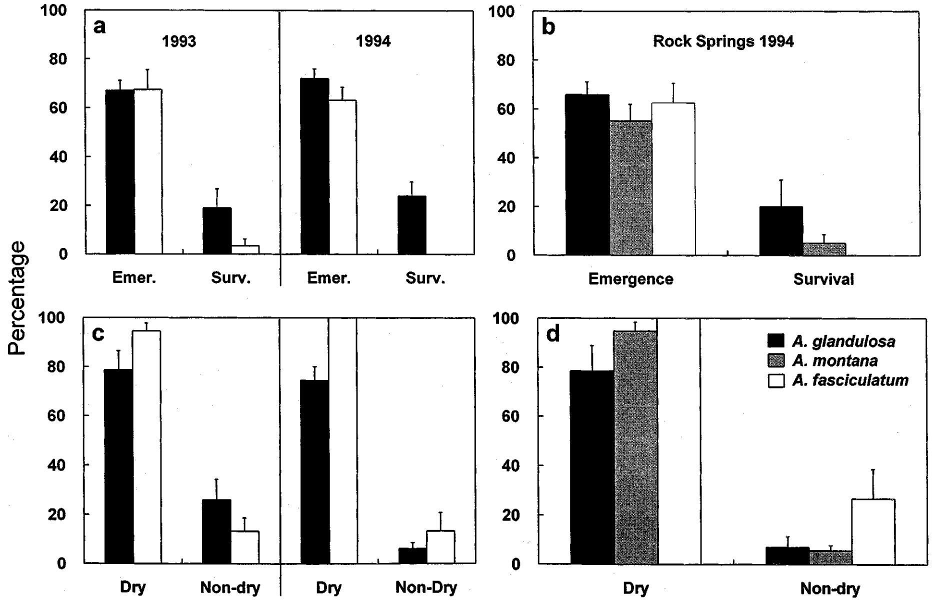

Fig. 1a–d First-season emergence, survival, and apparent causes of mortality of *Psuedotsuga menziesii* seedlings under chaparral. **a,c** Combined results from two sites for two annual cohorts of seedlings planted under *Arctostaphylos glandulosa* and *Adenostoma fasciculatum*, respectively ($n = 8$). **b,d** Results from Rock Springs in 1994 for seedlings planted under the previous two species and *Arctostaphylos montana* ($n = 4$). **a,b** Total seedling emergence (*Emer.*) and survival (*Surv.*). **c,d** Total seedling non-drought (*Non-dry*) and drought (*Dry*) mortality

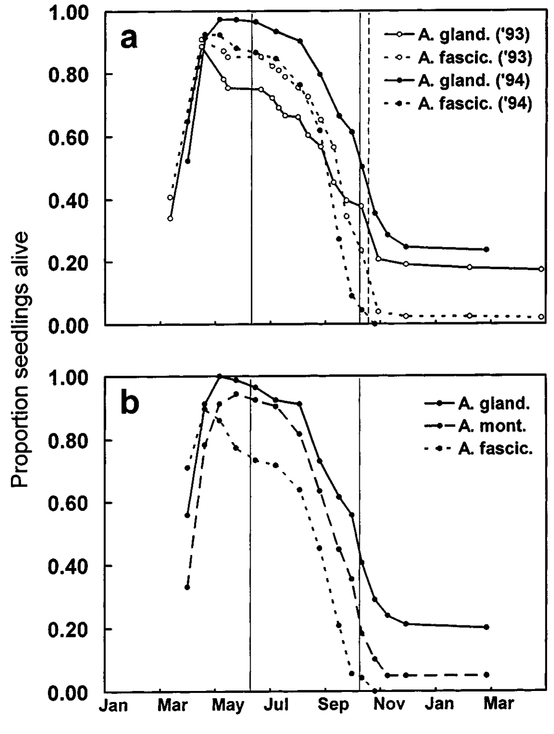

Fig. 2a,b First-year survival curves of *P. menziesii* seedlings in chaparral, shown as the proportion of live seedlings to total emergent seedlings. **a** Survival combined for two sites for two cohorts of seedlings planted under *A. glandulosa* and *A. fasciculatum*. The *vertical solid lines* indicate the period of summer drought in 1994, and the *first solid line* and the *dashed line* indicate the period of summer drought in 1993. **b** Survival at Rock Springs in 1994 under the previous two species and *A. montana*. Summer drought period indicated by *solid lines*

peaked at 88–98% during a 6- to 8-week period prior to the start of the summer drought (Fig. 2a). In all cases, declines in survival were gradual but steady for the first half of the summer drought and precipitous during the last half of the summer drought. Following the summer drought, seedling survival either dropped immediately to 0 or quickly stabilized at low levels. The final pattern of greater seedling survival under *A. glandulosa* in 1994 emerged prior to the onset of the summer drought, with the gap steadily widening during the drought. However, in 1993, there was greater survival under *A. fasciculatum* prior to the drought and during the first 3 drought months. It was not until the final drought month that seedling survival under *A. fasciculatum* plummeted lower than survival under *A. glandulosa*. At Rock Springs, survival under *A. montana* followed a trend intermediate to survival under the other two species starting a month prior to the drought and continuing through the end of the monitoring period (Fig. 2b).

Soil water potential

Prior to the beginning of the summer drought in both years, soil water potential at 7- and 20-cm depths remained above −1.0 MPa at all sites and under all chaparral stands monitored. In general, soil water potential declined rapidly during the summer drought, and either stabilized at −7.5 to −8.0 MPa, or failed to reach this apparent lowest soil water potential range prior to autumn rehydration. Overall, soil water potential was lowest at 7 cm, under *A. fasciculatum*, and in 1994 (Fig. 3a,c). While soil water potential at 7 and 20 cm under both species was similar prior to and for a week following the start of the summer drought, soil at 7 cm experienced sharper decreases and reached lower water potential levels than soil at 20 cm during the drought. Soil water potential under any given stand at 7 cm tended to reach a stable, low range of values 6–10 weeks prior to the end of the drought, while soil at 20 cm displayed more gradual declines that continued until the drought ended.

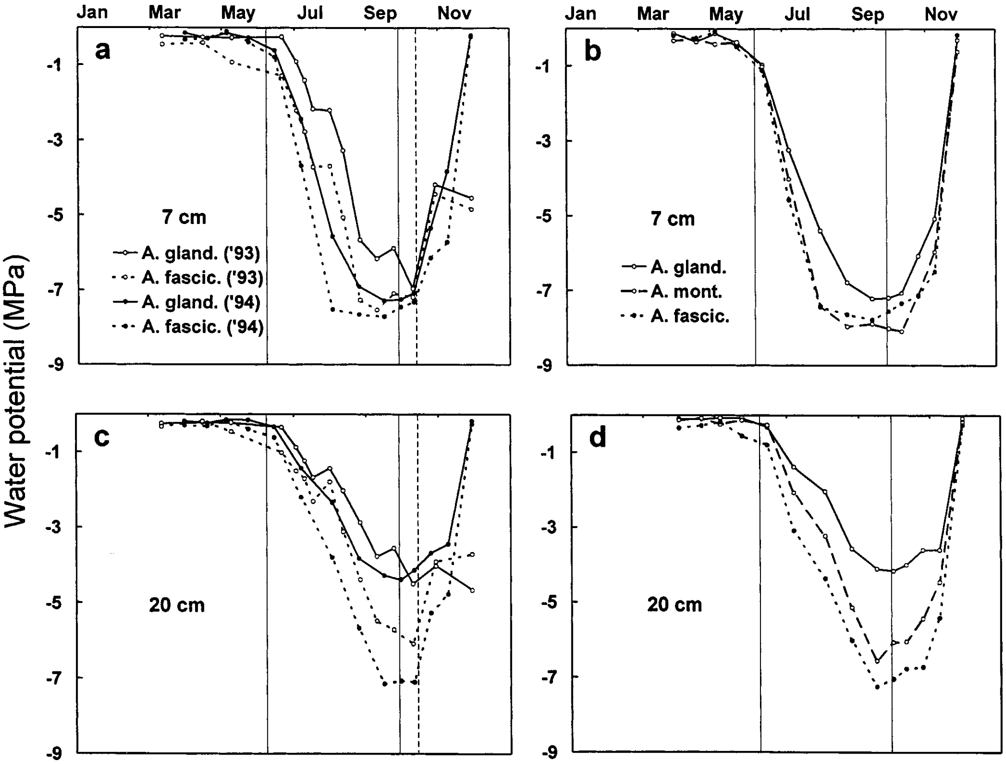

Fig. 3a–d Soil water potential at 7 cm and 20 cm, under chaparral. Statistics are presented in the text and Tables 1 and 2. **a,c** Combined results from two sites for 2 years under *A. glandulosa* and *A. fasciculatum*. The *vertical solid lines* indicate the period of summer drought in 1994, and the *first solid line* and the *dashed line* indicate the period of summer drought in 1993. **b,d** Results from Rock Springs in 1994 under the previous two species and *A. montana*. Summer drought period indicated by *solid lines*

At both depths in both years, soil water potential under *A. glandulosa* remained higher than soil water potential under *A. fasciculatum* throughout the summer drought. At 7 cm, *A. fasciculatum* soils reached lowest average values of −7.5 and −7.7 MPa in 1993 and 1994 compared to −7.0 and −7.3 MPa in soils under *A. glandulosa* (Fig. 3a). Much greater species differences were recorded at 20 cm, with lows of −6.1 and −7.2 MPa reached under *A. fasciculatum* in 1993 and 1994 compared to only −4.5 and −4.4 MPa under *A. glandulosa* (Fig. 3c). During the drought, species differences in soil water potential at 20 cm in 1993 and at both depths in 1994 steadily widened until the soil under *A. fasciculatum* reached a stable low value. At that point, soil under *A. glandulosa* continued to dry, reducing the difference between species during the final drought weeks. A different trend was expressed at 7 cm in 1993, when soil drying appeared to proceed at the same rate under the two species throughout the drought, with more rapid predrought drying under *A. fasciculatum* setting the pattern of difference between species (Fig. 3a).

ANOVAs used to examine site and species differences in soil water potential on each observation day revealed that there were very few significant interaction effects, and that East Peak sometimes had significantly higher soil water potential than the other two sites during the summer droughts (data not shown). We focus here on the strong patterns of significant differences between species. At 7 cm, soil moisture was significantly or marginally significantly ($P \leq 0.1$) greater under *A. glandulosa* than under *A. fasciculatum* on the first 9 of 10 observation days during the 1993 summer drought and on the last 4 of 5 drought observation days in 1994 (Table 1). At 20 cm, soil water potential was significantly or marginally significantly greater under *A. glandulosa* on all drought observation days in both years.

At Rock Springs, soil water potential trends at 7 and 20 cm reflect the overall trends for 1994 described previously, with lowest average soil water potential at 7 cm and under *A. fasciculatum* (Fig. 3b,d). At 7 cm, soil water potential under *A. montana* was almost identical to soil water potential under *A. fasciculatum* (Fig. 3b). The lowest average 7-cm soil water potentials reached were −7.2 MPa (*A. glandulosa*), −7.8 MPa (*A. fasciculatum*), and −8.1 MPa (*A. montana*), the final number representing the lowest average soil water potential recorded under any stand during the study. At 20 cm, soil water potential under *A. montana* followed an intermediate trend (Fig. 3d). The lowest average 20-cm soil water potentials reached were −4.2 MPa (*A. glandulosa*), −6.6 MPa (*A. montana*), and −7.2 MPa (*A. fasciculatum*).

At 7 cm at Rock Springs, there were significant species differences in soil water potential on only 2 of 5 drought observation days (data not shown). However, at 20 cm, many significant species differences among all three species-pairings were assessed for 10 observation days spanning 23 May to 4 November (Table 2). The most significant differences within a species pair were due to the higher soil water potential under *A. glandulosa* than under *A. fasciculatum* on all 10 days. Soil water potential under *A. montana* was significantly or

Table 1 Partial summary of two-factor ANOVA (species, site) outputs for differences in soil water potential under *Arctostaphylos glandulosa* versus *Adenostoma fasciculatum* at two soil depths. Individual dates were subjected to separate ANOVAs. Summer drought dates are demarcated by spaces between the data. Data are *F*-values for differences between species. All values with $P \leq 0.1$ are shown

1993	7 cm	20 cm	1994	7 cm	20 cm
12 March	NS	NS	31 March	4.17	NS
15 April	NS	NS	19 April	NS	NS
9 May	12.15**	6.41*	5 May	NS	NS
			23 May	NS	6.77*
19 June	10.59**	10.90**			
1 July	10.09**	12.88**	13 June	NS	7.26*
8 July	8.29*	8.05*	5 July	25.79*	12.36**
15 July	9.73**	10.23*	31 July	74.13***	38.19***
29 July	4.98*	3.51	22 August	11.85**	53.94***
9 August	35.84***	21.76***	12 September	3.84	175.99***
23 August	45.85***	28.56***			
6 September	20.80***	31.87***	26 September	NS	137.07***
20 September	30.54***	25.15***	7 October	NS	123.74***
6 October	NS	13.34**	21 October	3.81	53.07***
			4 November	14.24**	31.30***
25 October	4.17	NS	24 November	NS	NS
24 November	3.28	12.98**			

$^*P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$; *NS* not significant

Table 2 *P*-values for Tukey multiple-comparison tests for significant differences in soil water potential at 20 cm among three chaparral species at Rock Springs in 1994. Individual dates were subjected to separate tests. Summer drought dates are demarcated by spaces

	A. glandulosa/ A. fasciculatum	*A. fasciculatum/ A. montana*	*A. montana/ A. glandulosa*
31 March	NS	NS	NS
19 April	NS	NS	NS
5 May	NS	NS	NS
23 May	0.004	0.008	NS
13 June	0.028	0.016	NS
5 July	0.004	0.059	NS
31 July	≤0.001	0.019	0.016
22 August	≤0.001	0.040	≤0.001
12 September	≤0.001	0.098	≤0.001
26 September	≤0.001	0.027	≤0.001
7 October	≤0.001	NS	0.002
21 October	≤0.001	0.065	0.014
4 November	0.008	NS	NS
24 November	NS	NS	NS

marginally significantly higher than under *A. fasciculatum* on the 7 observation days from 23 May to 26 September, with significantly higher water potential under *A. glandulosa* than *A. montana* on the 6 observation days from 31 July to 21 October.

Discussion

Although there were no significant differences in emergence of protected *P. menziesii* seedlings among different chaparral stands, survival of emergent seedlings was much greater under *A. glandulosa* and slightly greater under *A. montana* than under *A. fasciculatum*, where almost no seedlings survived their first summer drought. This pattern of first-year seedling survival, which expands on and corroborates an earlier *P. menziesii* seedling study in this ecosystem (Horton 1992), is consistent with the distribution of mature *P. menziesii* individuals in chaparral in the Mt. Tamalpais watershed, where they are found almost exclusively in association with *Arctostaphylos* species (Sparling 1994). The seedling emergence and survival results suggest that the critical period of differential *P. menziesii* establishment within chaparral stands occurs during the last 2 months of the 4-month drought when seedling mortality accelerates.

While differential drought mortality of first-year seedlings appears to determine the spatial pattern of *P. menziesii* distribution in chaparral, the temporal pattern of successful recruitment events appears to be driven by other factors. At our study sites, the almost total mortality of unprotected seeds and seedlings under all chaparral stands within the first 4 months of seed planting suggests that in some years, overwhelming predation of seeds and very young seedlings by vertebrates may prevent any conifer establishment in chaparral. In our research area, tree-ring data indicate that since 1945, when the last major fire occurred, establishment of *P. menziesii* occurred primarily in only three tightly constrained temporal clusters (Sparling 1994). One hypothesis is that years of successful recruitment correlate with large seed output and/or low populations of seed predators, and vice versa for unsuccessful recruitment years. The importance of vertebrate seed and seedling predation in reducing or preventing *P. menziesii* recruitment has been demonstrated in other habitats (e.g., Isaac 1938; Krauch 1938; Gashwiler 1970; Sullivan 1979).

Because our study primarily investigated spatial demographic patterns, we focus on potential spatially related mechanisms. Given enough seedlings that survive early predation, the patterns of seedling establishment in this study suggest that the environment within *Arctostaphylos* stands, especially *A. glandulosa*, is more favorable for early *P. menziesii* seedling establishment than the environment within *A. fasciculatum* stands. In summer drought-stressed Mediterranean climates, soil moisture availability is often crucial to establishment of trees in other vegetation types. In South Africa, the invasion of forest species into the fynbos in the absence of fire is thought to be related to summer drought and soil moisture availability (Van Daalen 1981; Masson and Moll 1987; Manders and Richardson 1992). In central coastal California, limited regeneration of *Quercus* species in grasslands and oak woodlands is often attributed to Mediterranean summer drought conditions (Borchert et al. 1989; Gordon et al. 1989; Gordon and Rice 1993). Expansion of *P. menziesii* into grasslands has been noted to coincide with favorable moisture conditions (Arno and Gruell 1986). Although *P. menziesii* seedlings are considered relatively drought tolerant compared to other conifer seedlings (Livingston and Black 1987), xeric conditions and resulting desiccation of seedlings have been noted as an important source of mortality in efforts to restock clearcuts in the Pacific northwest. In some cases, drought caused more overall death to *P. menziesii* seedlings than predation even in the absence of seed and seedling protection (Isaac 1938; Maguire 1989), although we found the opposite result here.

With regard to soil microclimate, *P. menziesii* seedlings in this study exhibited lower drought mortality and higher survival in chaparral stands that had higher soil water potential during the summer drought. The seedlings underwent almost all of their first-year mortality during the period of the 4-month summer drought, with seedling survival stabilizing once autumn rains rehydrated the soil. Seedling mortality, mostly attributable to desiccation, accelerated towards the end of the summer drought, as soil at 20 cm reached its lowest water potential. Our data suggest that the seedlings were dependent on moisture availability in subsurface soil during the second half of the summer drought when surface soil has little or no available soil moisture.

The strong correlated trends in soil water potential at 20 cm and seedling drought mortality and survival are apparent in interspecies, intersite, and interannual comparisons. Species comparisons show that in both field seasons, summer soil water potential and seedling survival were much greater under stands of *A. glandulosa* than under *A. fasciculatum*. Results among three species at Rock Springs in 1994 provide even clearer evidence for the connection between seedling survival and summer soil water potential, since the seedling survival, seedling drought mortality, and soil water potential trends under *A. montana* were intermediate to trends under the other two species. Intersite comparisons show that chaparral stands at East Peak experienced higher soil water potential and greater seedling survival than at Bolinas Ridge (1993) or Rock Springs (1994). Interannual comparisons suggest that no survival of seedlings under *A. fasciculatum* in 1994 compared to some survival in 1993 is consonant with higher soil water potential at 20 cm and a wetter preceding winter in 1993. Results from stands of *A. glandulosa* are more ambivalent, since soil water potential was generally higher at 20 cm in 1993 when survival was lower. However, the lowest average soil water potential at 20 cm under *A. glandulosa* was also reached in 1993, which suggests that extreme lows in soil water potential are more important in driving seedling mortality than overall trends.

The dramatic differences in summer soil water potential under stands of *A. glandulosa* versus *A. fasciculatum* are surprising considering that the stands within each site shared a common microclimate, soil type, and topography. In some cases, sensors buried in adjacent stands were as little as 5 m apart, yet registered differences in 20-cm soil water potential of up to 3 MPa at the end of the summer drought. We suggest four hypotheses for future investigation that could explain strong species-mediated soil moisture resource patchiness. (1) Soil moisture may be retained better under *A. glandulosa* than under *A. fasciculatum* due to reduced evaporation of moisture from the soil surface as a result of a thicker litter layer (e.g., Page-Dumroese et al. 1990). *A. glandulosa*, with leaves of about 2–3 cm width and 2–5 cm length, produces a litter layer that can be many centimeters deep, unlike *A. fasciculatum*, a shrub with tiny needle-like leaves that produces little or no litter (personal observation). (2) *A. fasciculatum* may more thoroughly outcompete *P. menziesii* seedlings for soil water resources at key depths, due to factors such as patterns of root activity and water use during drought periods, than does *A. glandulosa*. This type of inhibition of tree seedling establishment and growth by shrubs has been suggested in other systems (Niering and Goodwin 1974; Petersen et al. 1988; Berkowitz et al. 1995; Callaway et al. 1996). (3) *A. glandulosa* may be a strong hydraulic lifter of soil moisture from deep soil layers to shallower layers as has been shown for other woody species in arid and semi-arid environments (Dawson 1993; Caldwell et al. 1998; Horton and Hart 1998), while *A. fasciculatum* may have less or no hydraulic lift activity. (4) Long-term biotic effects may result in soil under *A. fasciculatum* having lower levels of organic matter and higher percent rockiness (personal observation) than soil under *A. glandulosa*, thus lowering soil water-holding capacity and increasing drainage.

The intermediacy of soil water potential under *A. montana* may be related to a combination of species-mediated factors (e.g., intermediate leaf size and litter depth, different root activity) and site factors (e.g., water-holding capacity of serpentine versus Franciscan soils, depth to water table). However, the fact that *A. montana* on serpentine soil is associated with a 20-cm soil-drying trend intermediate to the two other species on continuous Franciscan soil suggests that site factors are not as important as species-mediated factors for driving the observed distinctive patterns of summer soil water availability. It is unlikely that adjacent areas of Franciscan soil, selected specifically to maximize microsite similarity, would have greater inherent differences in soil water potential to one another compared to a non-neighboring area of serpentine soil.

Although soil water potential during the summer drought appears to be linked closely to different rates of *P. menziesii* seedling mortality and survival under three chaparral species, other factors could contribute to the patterns of establishment we have documented. Potential abiotic factors include temperature, light availability, and soil nutrient status, and biotic factors include herbivory, allelopathy, competition, and mutualism. While this study and a related study (Horton et al., in press) did not investigate the concurrent effect of multiple factors and their interactions on tree seedling establishment (e.g., Borchert et al. 1989; DeSteven 1991a, 1991b; Callaway 1992), we have examined several other factors besides soil moisture for their potential role in increased seedling establishment under *Arctostaphylos* stands, particularly *A. glandulosa*, in our research area.

Integrated light measurements at all three sites (Dunne 1994; Horton et al. in press) suggest that there is slightly, but not significantly, less light penetrating the canopies of *A. glandulosa* than *A. fasciculatum*. Horton et al. (in press) also found that soil surface temperatures were not significantly different between stands of the two species. Jones (1995) suggests that increased shade under particular shrub species does facilitate establishment of first-year *P. menziesii* seedlings. However, too much shading can inhibit germination, photosynthetic activity, and growth of seedlings. The negligible species differences observed for light and temperature at our sites do not allow us to distinguish between relative facilitative versus inhibitive effects of shading by chaparral, but do suggest that shading does not drive the strong seedling establishment patterns we observed.

In the uncaged seed experiment, which demonstrates that vertebrate seed and seedling predation may be a significant factor in driving temporal patterns of *P. menziesii* seedling establishment in this ecosystem, too few seedlings emerged to determine whether there were differential rates of vertebrate predation within chaparral that correspond with spatial patterns of seedling establishment. However, differences in rates of tree seedling predation by vertebrates tend to be associated with changes in plant architecture (e.g., shrubs vs grassland; Callaway 1992) and associated herbivore refuges and habitat (Gill and Marks 1991; Ostfeld and Canham 1993). Species differences within an architecture type, in this case chaparral, are less likely to give rise to significant differences in those factors. The observed rates of non-drought mortality, which consisted mostly of pathogen effects and invertebrate herbivory, followed no consistent patterns with species, seedling survival, or soil water potential, which suggests that non-vertebrate predation also does not account for differential rates of first-year *P. menziesii* seedling establishment.

Allelopathy and nutrient differences between shrub species do not appear to explain the differential seedling establishment observed. Both *A. glandulosa* (Chou and Muller 1972) and *A. fasciculatum* (McPherson and Muller 1969; Kaminsky 1981) have been noted to have allelopathic effects on other plant species. Horton et al. (in press) found no significant difference in allelopathic inhibition of *P. menziesii* seed germination and seedling growth by leachates collected from *A. glandulosa* and *A. fasciculatum* foliage. Soil nutrient analyses in this system (Horton et al., in press) suggest that *A. fasciculatum* soils generally have similar or higher nutrient levels than *Arctostaphylos* soils (see also Fenn et al. 1993). This nutrient profile could act to promote seedling establishment under *A. fasciculatum*, but such an effect would be inconsistent with our results.

The most promising alternative, or complementary, hypothesis to summer soil moisture availability is that differential *P. menziesii* seedling establishment may be facilitated by provision of mycorrhizal mycelia by *Arctostaphylos* species and other members of the Ericaceae (Amaranthus and Perry 1989; Horton et al., in press). While *A. fasciculatum* is currently recognized as a vesicular-arbuscular mycorrhizal plant (Allen 1991), *A. glandulosa* forms arbutoid mycorrhizae with fungal species that have also been demonstrated through genetic techniques to form ectomycorrhizae with *P. menziesii* in the current study area (Horton et al., in press). Ectomycorrhizae may have a strong impact on the ability of *P. menziesii* seedlings to withstand summer drought conditions, particularly through maintenance of higher photosynthetic activity (Dosskey et al. 1991) and increased uptake of soil moisture (Duddridge et al. 1980; Brownlee et al. 1983). Mycorrhizae can also form direct linkages between plants that facilitate resource flows among species (e.g., Francis and Read 1984). The types of plants involved in the current study have shown the potential for such direct interspecies flows. Carbon transfer, apparently via shared mycorrhizal mycelia, has been documented in the field between *Betula papyrifera* (paper birch) and *P. menziesii* seedlings (Simard et al. 1997). Initial greenhouse isotopic data suggest that mycorrhizal water transfer can occur between *Acer saccharum* (sugar maple) and *Vaccinium vacillans* (blueberry), a member of the Ericaceae (T.E. Dawson, personal communication). The potential for indirect and direct mycorrhizal benefits to *P. menziesii* seedlings from *Arctostaphylos* species may help to explain why there is any tree establishment in chaparral at all given the very low soil water potentials induced by the seasonal drought (Parke 1983).

In conclusion, we have shown that stands of *Arctostaphylos* species, but not *A. fasciculatum*, appear to ameliorate the harsh xeric conditions of Mediterranean summer droughts to a degree that can facilitate establishment of *P. menziesii* seedlings in otherwise inhospitable chaparral habitat. This first-year establishment success, and more specifically patterns of subsurface soil water potential and seedling mortality and survival during the last 2 months of the summer drought, appear to underlie a historical pattern of invasion of mixed evergreen forest into chaparral in the absence of fire. In this ecosystem, small-scale, species-mediated patchiness of a single limiting resource, soil moisture, may strongly constrain early conifer life history dynamics that lead to distinctive spatial patterns of vegetation distribution.

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