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ScienceDirect
Forest Ecology and Management xxx (2007) xxx–xxx
Forest Ecology and Management
www.elsevier.com/locate/foreco

Overstory and shrub effects on natural regeneration processes in native *Pinus radiata* stands

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Received 16 October 2006; received in revised form 29 December 2006; accepted 29 December 2006

Abstract

Native Monterey pine (*Pinus radiata* D. Don) stands on the Monterey peninsula have been significantly modified by natural and anthropogenic disturbances. The exclusion of fire and the introduction of pitch canker (caused by *Fusarium circinatum* Nirenberg & O'Donnell) created a need for the examination of these changing ecosystems with respect to regeneration, especially as these stands reach mature ages. We established 210 plots on 35 transects distributed throughout five stands in order to describe the current stand structure and quantify the extent and condition of regeneration. The results indicated that Monterey pine seedling establishment varies throughout the peninsula depending on percent canopy cover, duff and litter depth, and percent shrub cover while seedling growth is influenced by percent shrub cover. Canopy cover was also found to inversely influence shrub cover. Our study highlights the importance of understory removal to increase Monterey pine regeneration and seedling growth as canopy cover decreases, especially in areas where coast live oak (*Quercus agrifolia* Nee) and poison-oak (*Toxicodendron diversilobum* E. Greene) are abundant.

Keywords: Monterey pine; Gap dynamics; Seedling regeneration; Natural disturbances

1. Introduction

Monterey pine (*Pinus radiata* D. Don) is one of the most widely planted pine species in the world, with extensive plantations in Chile, New Zealand, and Australia (Rogers, 2002). Native populations are found in only five locations worldwide (Rogers, 2002). Two of these populations are on islands off the coast of Baja California (Guadalupe and Cedros) and are morphologically distinct from those on the mainland (Rogers, 2002). Mainland populations occur in three disjunct locations along the coast of central California (Año Nuevo, Monterey, Cambria). These native populations occupy a total of approximately 5530 ha (McDonald and Laacke, 1990).

The current Monterey pine stands on the Monterey peninsula predominately regenerated following logging in the late 19th and early 20th century and by invading land cleared for pasture (Storer et al., 2001). Monterey pine has thrived in these native stands in part due to its adaptation to fire; it has been identified as having adapted to both stand replacing fires and low to moderate intensity surface fires (Fonda, 2001; Stephens et al., 2004). Serotinous cones, thick basal bark, and historical episodic regeneration provide further evidence that fire has been an important factor for seedling initiation (McDonald and Laacke, 1990; Storer et al., 2001; Stephens et al., 2004). Currently fire exclusion, which has become the dominant management practice and is necessary given the urbanization of these native stands, is influencing natural Monterey pine regeneration. Fire suppression also facilitates a transition to oak woodlands with a few sparsely distributed pines (McDonald and Laacke, 1990; Storer et al., 2001).

Furthermore, Monterey pine is a short-lived species with a life expectancy range from 80 to 120 years (McDonald and Laacke, 1990). Many of the standing Monterey pine stems are exhibiting dieback and mortality due to senescence (Storer et al., 2001). This dieback is further accelerated by the introduction of the exotic pitch canker disease (caused by *Fusarium circinatum* Nirenberg & O'Donnell), which has been evident in these pine stands since the early 1990s (Storer et al., 2001). The disease causes multiple stem and branch infections

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doi:10.1016/j.foreco.2006.12.025

that lead to extensive dieback in the crown leaving the tree susceptible to attack by bark beetles (*Ips* spp.) and mortality (Owens and Adams, 1999; Storer et al., 2001, 2002). Although pitch canker has been found throughout the California Monterey pine populations, resistance has been observed in many Monterey pine individuals. Storer et al. (2001) suggests that up to 30% of the trees in native stands are resistant to the pathogen. The removal of fire and the introduction of pitch canker are changing the dynamics of these pine stands and risking the sustainability of native populations (Gordon et al., 2001).

International concern has risen over the conservation of these stands as genetic resources for native populations and international plantation culture (Rogers, 2002; Piirto and Valkonen, 2005). Yet, little is known about the regeneration conditions of native Monterey pine stands (Vogl et al., 1977; White, 1999). Monterey pine research in the US has emphasized the epidemiology of pitch canker, with very little focus on Monterey pine ecology and native stand dynamics (Roy, 1966; Storer et al., 2002; Stephens et al., 2004; Piirto and Valkonen, 2005).

A need for a greater understanding of the changing regeneration processes in order to promote establishment of healthy seedlings is evident (Waring and O'Hara, 2005). Further, the favored strategy for managing mature Monterey pine forests impacted by pitch canker is to encourage regeneration so that pitch canker will kill susceptible seedlings and thus promote a more resistant forest in the future (Storer et al., 2001). The objective of this study is to assess the state and occurrence of Monterey pine regeneration in relation to stand structure and microsite conditions, including canopy cover, abundance of understory vegetation, and duff characteristics, on the Monterey peninsula. By improving the understanding of current regeneration processes in the absence of fire and with the influence of pitch canker, informative and sound ecological management can proceed to create an environment that allows Monterey pine to adapt by providing an opportunity for future generations to develop in the current environmental conditions.

2. Methods

In January 2005, a total of 35 transects were established throughout the Monterey peninsula (36°36′N, 121°54′W) in Monterey Co., California, to examine the extent and growth of natural Monterey pine regeneration in relation to forest structure and microsites. Transects were divided between five stands of at least 20 ha. Four of the five stands – PQR, Huckleberry Hill, Navajo, and Spyglass – are privately owned and are between 1 and 4 km east of the Pacific coast, while the fifth stand is further inland at Jack's Peak County Park, approximately 10 km east of the coast. The average distance between stands is 5.62 km with a standard deviation of 2.5 km.

All stands had a canopy composed of Monterey pine, with the Navajo stand containing a second canopy layer of coast live oak (*Quercus agrifolia* Nee). Spyglass and Jack's Peak also had intermittent areas containing a second canopy layer of coast live oak. The five sites had a similar understory composition. The most commonly occurring shrub species were coyotebrush (*Baccharis pilularis* D.C.), poison-oak (*Toxicodendron diversilobum* E. Greene), California huckleberry (*Vaccinium ovatum* Pursh), bush monkey-flower (*Mimulus aurantiacus* Curtis), and California blackberry (*Rubus ursinus* Cham. & Schldl.). Although not measured, these species were approximately 1–2 m in height at most sites. There was also a regular herbaceous layer consisting of *Sanicula* spp., *Galium* spp., and a variety of grasses.

Transect starting points were generated using digital topographic layers and a random number generator to select random GPS points and cardinal directions within each stand. Each transect was 100 m in length with plot centers established at 0, 20, 40, 60, 80, and 100 m along the transect. At each plot center, sampling consisted of three parts: stand structure, microsite, and Monterey pine seedling conditions.

Stand structure analysis was undertaken to determine stand age, average dominant tree size, and canopy closure. The closest (within 10 m) apparently healthy (i.e. crown with limited to no die-back and no pitch cankers on the stem) dominant overstory tree was measured for height, diameter at breast height (DBH) (1.37 m), and cored for age at breast height (the annual rings were counted in the lab). Because local site index relationships do not exist for Monterey pine, curves for unmanaged ponderosa pine (*Pinus ponderosa* P. & C. Lawson) in California were used for the tallest tree in each stand (Dunning and Reineke, 1933). In addition, a basal area prism sweep and convex spherical densiometer measurements, centered over the plot center, were taken to assess density and canopy cover. Finally, number of canopy strata and overstory species present within the immediate surroundings were recorded.

Analysis of microsite factors (including duff depth, percent shrub cover, and percent herbaceous cover) was undertaken within a 1 m radius (1/3183 m^2/ha area) from the plot center. This plot size was chosen to ensure that measurements deviated no more than 1 m from the plot center where environmental conditions were assessed. Ocular estimates of percent cover of all competing shrub and herbaceous understory species within this circle were recorded. Duff depth (litter layer was included in the measurement of depth) was also taken at the plot center.

Seedling analysis was undertaken only when Monterey pine seedlings were growing within the plot. Seedlings were all Monterey pines under 1 cm at DBH. The seedling closest to the plot center was measured for height, diameter at base, age, and length of past year's terminal extension (called 1-year height growth). In addition, the convex spherical densiometer reading to estimate canopy cover was taken directly above the sampled seedling (i.e. moved from plot center when a seedling was present). Duff depth was measured beneath the seedling instead of at the plot center. The seedling was then removed to determine age in the lab. All other Monterey pine seedlings within a 1 m radius were counted and placed in three height classes: <0.10, 0.10–2, and >2 m. Exact height was also recorded for all seedlings between 0.10 and 2 m.

Seedlings were aged in the laboratory by either counting annual rings at the base, if diameter was of sufficient size, or by

Table 1
Mean and standard deviation (mean ± S.D.) of height, DBH, age of dominant trees, basal area (BA), and percent canopy cover for the overstory of each stand

Sites	Height (m)	DBH (cm)	Age at BH	BA (m^2/ha)	Percent canopy
PQR	24.8 ± 6.0	49.2 ± 11.6	45 ± 9.2	26.3 ± 11.3	82.2 ± 13.7
Huckleberry Hill	24.9 ± 5.8	55.4 ± 14.0	62 ± 19.8	29.6 ± 11.1	92.8 ± 7.1
Spyglass	30.0 ± 8.1	64.1 ± 13.0	80 ± 20.3	15.4 ± 9.8	88.8 ± 12.9
Jack's Peak	26.0 ± 5.9	57.7 ± 18.9	53 ± 15.8	19.5 ± 7.7	74.6 ± 25.4
Navajo	29.5 ± 2.6	67.5 ± 12.3	57 ± 9.3	36.3 ± 12.9	77.6 ± 13.7
Average	27.0 ± 2.5	58.8 ± 7.2	59 ± 5.4	25.4 ± 1.9	83.2 ± 7.6

Height, DBH, age at BH, and BA were calculated using 40 samples for PQR and Jack's Peak and 20 samples for Huckleberry Hill, Spyglass, and Navajo. Percent canopy was calculated using 60 samples for PQR and Jack's Peak and 30 samples for Huckleberry Hill, Spyglass, and Navajo.

counting bud scars. Bud scars were also used to distinguish 1-year growth intervals on small seedlings. Alternatively, seedlings that had overgrown bud scars were measured for 1-year growth using the length of internodes between yearly branch whorls. The number of internodes was referenced with the seedling's age at base and yearly diameter growth, which prevented errors in missing possible multiple whorl years. For example, if a seedling was 5 years old but had six whorls then two whorls were produced in 1 year. This was assumed to be the year with the greatest diameter growth.

SPSS 11.5 was used to examine statistical correlations among variables measured. Multiple linear regressions were used to examine the relative influence of stand characteristics (basal area, age, and canopy cover) and understory variables (shrub cover and duff depth) on seedling density and growth. Several independent variables (percent canopy cover, basal area, age, percent shrub cover, and duff depth) were regressed on two dependent variables (1-year growth and number of seedlings/ha). Factors contributing to the occurrence of pine seedling regeneration were examined with logistic regression. This is used when the dependent variable is dichotomous. Logistic regression is useful in ranking the relative importance of independent variables, assessing interaction effects, and when the primary concern is the occurrence of the dependent variable, which in this study is Monterey pine seedlings (Welsh et al., 1996).

3. Results

3.1. Stand characteristics

Of the 210 plots sampled, 30.5% contained Monterey pine seedlings, and 93.8% of those plots had two or more seedlings. The five stands showed variation in many structural characteristics among the stands (Table 1). Mean height (ranged from 24.8 ± 6.0 to 30.0 ± 8.1 m), DBH (ranged from 49.2 ± 11.6 to 67.5 ± 12.3 cm), age at BH (ranged from 45 ± 9.2 to 80.0 ± 20.3 years), basal area (ranged from 15.4 ± 9.8 to 36.3 ± 12.9 m^2/ha), and canopy cover (ranged from 74.6 ± 25.4 to 92.8 ± 7.1%) varied among stands. Average basal area was highest in Navajo followed by Huckleberry Hill, PQR, Jack's Peak, and Spyglass, while average age at breast height was highest at Spyglass. The Huckleberry Hill stand also had a distinct second stratum of Monterey pine with an average height of 14.3 m, an average DBH of 20.3 cm, and ages at breast height ranging from 15 to 38 years. Site index averaged 33.5 m (50 years base age) at all sites indicating minimal variation in site qualities.

3.2. Microsite characteristics

Microsite characteristics were relatively similar across the sites in terms of duff depth, percent shrub cover, and percent herbaceous cover (Table 2). However, shrub cover was much lower at the PQR site than the other sites. Linear regressions comparing stand characteristics and microsite conditions did not statistically explain duff depth, percent shrub cover, and percent herbaceous cover, but correlations were found between the understory conditions and overstory cover (Table 3). Percent canopy cover was positively related to duff depth and negatively related to percent understory cover (with 1-tailed significance of 0.001 and <0.001, respectively).

3.3. Probability of regeneration

Average seedling density varied from 0 seedlings/ha at the Navajo stand to 11,035 seedlings/ha in the Huckleberry Hill stand. No relationships between seedlings/ha and stand and microsite characteristics were found, but the data displayed distinct tendencies between stand and microsite conditions and seedling presence. For example, Fig. 1A shows that 95% of all seedlings occur with less than 30% shrub cover, and Fig. 1B shows 92% of all seedlings were present in less than 10 cm duff. Also, Fig. 1C shows that seedling presence only occurred with canopy cover greater than 40%, and 95% of all seedlings were

Table 2
Mean and standard deviation (mean ± S.D.) of duff depth, percent shrub cover, and percent herbaceous cover for each stand

Sites	Duff depth (cm)	Percent shrub	Percent herbaceous
PQR	5.8 ± 3.6	10.8 ± 15.1	25.7 ± 24.6
Huckleberry Hill	5.1 ± 4.3	24.1 ± 29.7	22.4 ± 26.9
Spyglass	6.0 ± 5.1	23.6 ± 29.6	32.4 ± 33.6
Jack's Peak	8.8 ± 6.2	40.4 ± 39.0	19.5 ± 26.5
Navajo	8.4 ± 6.5	41.8 ± 37.5	36.0 ± 42.1
Average	6.8 ± 1.7	28.1 ± 13.0	27.2 ± 6.9

PQR and Jack's Peak values were calculated with 60 samples each while Huckleberry Hill, Spyglass, and Navajo were only calculated with 30 samples each.

Table 3
Correlation coefficients between microsite characteristics (canopy cover, duff depth, and understory cover) and seedling characteristics (seedling/ha, seedling height, 1-year height growth, and seedling age) with 1-tailed significance

	Canopy (%)	Duff depth (cm)	Understory (%)	Seedling/ha	Seedling height (cm)	One-year height growth (cm)	Seedling age
Canopy cover (%)	–	**0.221***	**−0.262***	0.06	0.03	0.05	0.078
Duff depth (cm)	**0.221***	–	0.104	**−0.188****	−0.106	**−0.149*****	**−0.172****
Understory cover (%)	**−0.262***	0.104	–	**−0.274***	**−0.189****	**−0.255***	**−0.229***
Seedling/ha	0.06	**−0.188****	**−0.274***	–	0.106	**0.259***	**0.283***
Seedling height (cm)	0.03	−0.106	**−0.189****	0.106	–	**0.845***	**0.847***
One-year height growth (cm)	0.05	**−0.149*****	**−0.255***	**0.259***	**0.845***	–	**0.921***
Seedling age	0.078	**−0.172****	**−0.229***	**0.283***	**0.847***	**0.921***	–

Significant values are in bold and asterisked. ($^{*}\leq 0.001$, $^{**}\leq 0.01$, and $^{***}\leq 0.05$).

found with greater than 60% canopy cover. Therefore, the probability of regeneration being present (probability of a single seedling establishing) was evaluated using logistic regression. A logistic model indicated that the probability of regeneration occurring (P_i) in a given environment is dependent on the percent canopy cover, depth of duff, and the percent shrub cover.

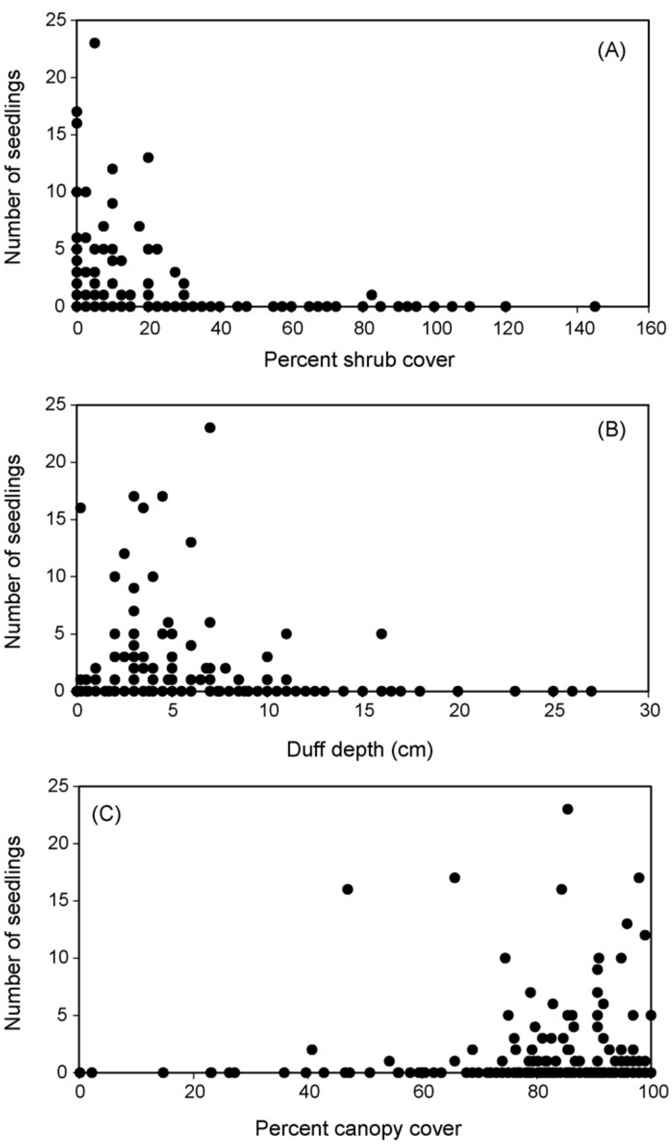

Fig. 1. Number of seedlings sampled at a plot graphed against: (A) shrub cover (%) (percent greater than 100% are due to layers of shrubs); (B) duff depth (cm); (C) canopy cover (%). There are a total of 210 points plotted.

$$P_i = \frac{e^{V_i}}{1 + e^{V_i}} \quad (1)$$

where

$$V_i = -1.650 + 0.029(\%\,\text{canopy}) - 0.125(\text{duffdepth}) - 0.048(\%\,\text{shrub})$$

The standard error of the coefficients for canopy cover, duff depth, and shrub cover were 0.011, 0.046, and 0.012, respectively, and the p-values for the coefficients were found to be 0.012, 0.007, and <0.001, respectively. The significance (<0.001) and larger equation coefficient (-0.048) of percent shrub cover indicates it has greater importance than percent canopy cover in predicting the probability of regeneration. The Wald statistic also shows increasing significance of the independent variables from percent canopy cover to duff depth to shrub cover (6.36, 7.40, 14.96). Using Eq. (1), probability of regeneration was graphed against percent canopy cover and percent shrub cover with a mean duff depth of 6.8 cm (Fig. 2). Using mean values for canopy cover (83.2%), duff depth (6.8 cm), and shrub cover (28.1%), Eq. (1) produces a probability of occurrence of 0.192 or 19.2%.

3.4. Seedling growth

Seedling height growth varied among sites (Table 4). Seedlings were generally suppressed with height:diameter ratios of 74:1 and ages ranging from 1 to 17 (Table 4). Multiple linear regression was used to identify stand and microsite factors significantly influencing seedling height growth (cm/year). The following equation was developed:

$$G = 3.380 + 0.109(\text{SH}) - 0.046(S) \quad (2)$$

where G is the 1-year growth, SH the seedling height (cm), and S is the shrub cover (%).

The adjusted R^2 for the regression was 0.89, and the standard error of the estimate was 1.7 cm. The standard error and p-values of seedling height and shrub cover are (0.005 and 0.018) and (<0.001 and 0.012), respectively. Fig. 3 shows the relationship between 1-year growth and shrub cover and

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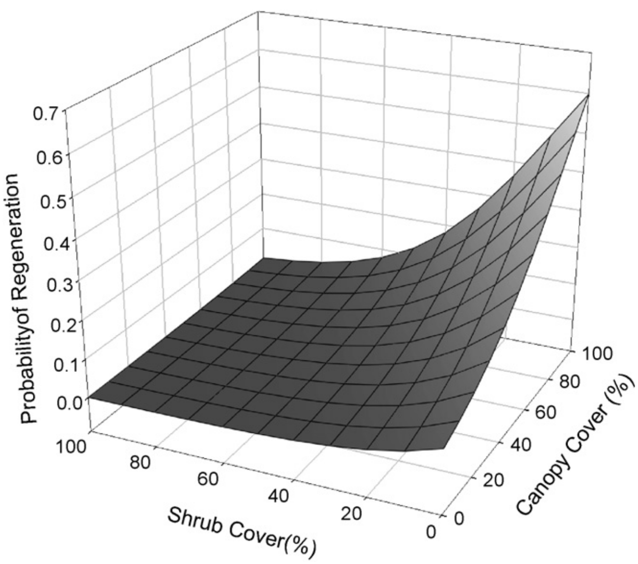

Fig. 2. Probability of regeneration graphed against percent canopy cover and percent shrub cover. The graph was generated using Eq. (1) with a mean duff depth of 6.8 cm.

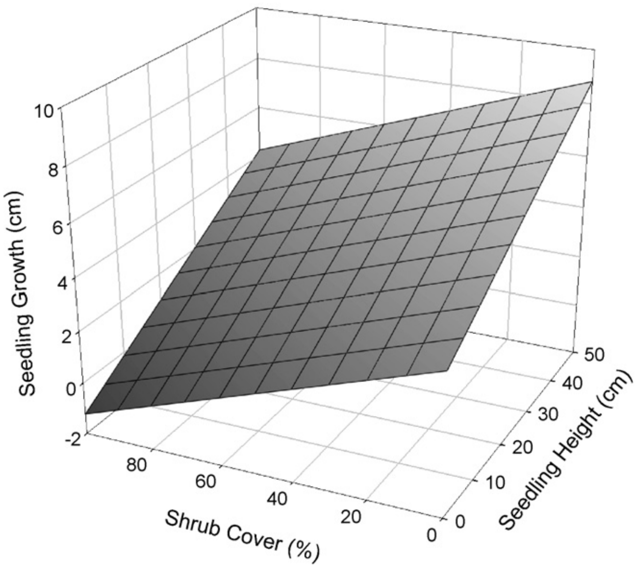

Fig. 3. One-year growth graphed against percent shrub cover and seedling height using Eq. (2).

seedling height. The model indicated that 1-year growth was most strongly correlated with seedling height. It also indicated an inverse relationship between 1-year growth and shrub cover, when keeping seedling height constant.

In a separate analysis, a multiple linear regression was produced with natural log of 1-year growth as the dependent variable and canopy cover and seedling height as the two independent variables. The resulting equation showed a negative correlation between 1-year growth and percent canopy cover. The R^2 for the regression was 0.64, and the standard error of the estimate was 0.4 cm (not shown). The p-values for canopy cover and seedling height were 0.045 and <0.001, respectively; while the B coefficients were -0.008 and 0.010 with standard errors equaling 0.004 and 0.001, respectively This suggests an inverse relationship between 1-year growth and percent canopy cover, when controlling for seedling height (i.e. holding the seedling height constant).

A third analysis examined the combined effects of shrub cover, canopy cover, and seedling height. The adjusted R^2 of this regression was 0.90, and the standard error of the estimate was 1.7 cm. The B values, standard error, and p-values of shrub cover, canopy cover, and seedling height were (-0.046, -0.03, and 0.109), (0.018, 0.018, and 0.005), and (0.011, 0.095, and <0.001), respectively. This shows a negative influence of shrub cover and canopy cover on seedling growth; however, canopy cover had an insignificant influence on seedling growth when examined with shrub cover.

4. Discussion

Monterey pine regeneration occurred in aggregations throughout the area sampled. MacLaren (1993) suggested certain site conditions, such as well drained soils, bare mineral soil, and limited understory competition, were superior for natural seedling establishment and survival of Monterey pine in New Zealand. In the current study, we found significant variations on the duff depths, percent shrub cover, and the number of seedlings/ha among sites. Huckleberry Hill, PQR, and Spyglass have the lowest mean duff depths (5.1, 5.8, and 6.0 cm, respectively) and percent shrub covers (24.1, 10.8, and

Table 4
Mean and standard deviation of seedling height, diameter at base, 1-year height growth, age, and number per hectare are presented for each stand

Sites	Height[a] (cm)	Diameter base[a] (cm)	One-year height[a] (cm)	Seedling age[a]	Age range (min.–max.)	Seedlings/ha[a]
PQR	20.3 ± 47.6	0.3 ± 0.6	5.8 ± 5.5	3.0 ± 3.4	1–17	8117 ± 14131
Huckleberry Hill	24.0 ± 10.5	0.4 ± 0.2	4.5 ± 3.1	5.0 ± 4.0	1–5	11035 ± 16460
Spyglass	17.6 ± 8.5	0.2 ± 0.2	4.9 ± 2.0	4.0 ± 2.1	2–8	2440 ± 6565
Jack's Peak	56.4 ± 63.8	0.8 ± 0.5	12.0 ± 6.7	7.0 ± 2.6	1–9	531 ± 1455
Navajo	N/A	N/A	N/A	N/A	N/A	N/A
Average	29.6 ± 18.1	0.4 ± 0.3	6.8 ± 3.5	4.0 ± 1.7	1–10	5531 ± 4883

Maximum and minimum seedling ages are also given. Height, diameter at base, 1-year height growth, seedling age, and age range were calculated using 32 samples for PQR, 17 samples for Huckleberry Hill, 7 samples for Spyglass, and 8 samples for Jack's Peak. Seedlings/ha was calculated using 60 samples for PQR and Jack's Peak and 30 samples for Huckleberry Hill and Spyglass. No seedlings were found at the Navajo site.
[a] Mean ± standard deviation (S.D.).

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23.6, respectively) (Table 2). The same three sites also have the highest mean seedlings/ha (11,035, 8117, and 2440) (Table 4). However, the number of seedlings/ha was also highly variable throughout the stands. This was attributed to the heterogeneity (the high standard deviation) of duff depth, herbaceous cover, and shrub cover (Table 2). Though heterogeneity existed, correlations were found between stand and microsite characteristics throughout the stands.

Canopy cover was positively correlated with duff depth and negatively correlated with understory cover (Table 3). There are also unmeasured factors such as crown dieback and loss that may contribute to duff and litter production. As these stands reach mature ages (>80 years), productivity slows causing foliage and branch dieback (Oliver and Larson, 1996). Also, gradual foliage dieback, topkill, and tree mortality associated with pitch canker contributes more dead foliage and woody debris to the forest floor (Owens and Adams, 1999; Storer et al., 2002; Wikler et al., 2003).

Seedlings were found at sites with less understory competition, which provided more available growing space. Eq. (1) indicates the most important factors in determining the presence or absence of seedlings are percent canopy cover, duff depth, and shrub cover. For example, using the overall mean values of 83.2%, 6.8 cm, and 28.1% for canopy cover, duff depth, and shrub cover, the probability of regeneration occurring is 0.192 or 19.2% (Eq. (1)). A 1% increase in shrub cover, while holding all other independent variables constant, will decrease the probability to 0.185 or 18.5% (Eq. (1)). Therefore, an increase of 13% in shrub cover, the standard deviation, will decrease the probability of regeneration by 7.9–11.3%. This is likely due to the increased competition for light and moisture (Facelli and Pickett, 1991; Schupp, 1995; Aussenac, 2000), as Monterey pine is an intermediate shade tolerance species (Baker, 1949) and requires moist soil for successful natural regeneration (McDonald and Laacke, 1990).

Duff depth had less influence on pine regeneration than percent shrub cover in our study sites. Monterey pine prefers bare mineral soil but is capable of germinating in areas with duff over mineral soil (McDonald and Laacke, 1990). Incorporating the overall mean values of the independent variables into Eq. (1), the probability of occurrence was 0.192 or 19.2. Increasing duff depth by 1–7.8 cm decreased the probability to 0.174 or 17.4%, and an increase of 1.7 cm, the standard deviation, reduced the probability to 0.161 or 16.1%. Although duff depth appeared to have a greater influence on the probability of seedling regeneration, it had a smaller range, from a mean of 5.1 to 8.8 cm (Table 2), a lower Wald statistic, and a higher p-value than percent shrub cover indicating that it actually had less impact on seedling establishment. This is further supported by the fact that 21.9% of all seedlings were found in duff depths greater than or equal to the mean 6.8 cm, while only 4.7% of seedlings were found in percent shrub cover greater than or equal to the mean 28.1%.

The increase in seedling occurrence with increasing canopy cover is apparently due to the interaction between canopy cover and shrub cover. Eq. (1) indicates shrub cover has a greater affect on seedling occurrence than canopy cover, and high percentages of shrub cover reduce the probability of seedling presence (Fig. 2). The negative correlation coefficient between canopy cover and shrub cover (Table 3) suggests an inhibitory effect. Denser canopies intercept more light, decreasing growing space availability to competing species (Facelli and Pickett, 1991; Schupp, 1995; Oliver and Larson, 1996). By preventing the establishment and growth of shrubs, an increase in canopy cover indirectly improves the probability of Monterey pine regeneration. Canopy cover also indirectly favors Monterey pine regeneration by apparently altering basic microsite characteristics such as moisture regimes and soil and air temperature (Facelli and Pickett, 1991; Schupp, 1995). Monterey pine is known to have greater seedling regeneration in cooler soils with best root growth in soil temperatures of 15 °C (59 °F) (Kaufmann, 1977; McDonald and Laacke, 1990). The species is also considered drought-hardy, but performs better in moist soils (Roy, 1966; Kaufmann, 1977; McDonald and Laacke, 1990). Greater canopy cover may provide more favorable temperatures and retain soil moisture for seed germination while still providing sufficient light penetration for seedling growth (Facelli and Pickett, 1991; Schupp, 1995). Aussenac (2000) suggests that shaded areas improve the establishment and juvenile development of trees by reducing wind speed and temperatures as well as improving the water status of seedlings by reducing potential evapotranspiration. Therefore, denser canopy cover increases the probability of regeneration by restricting the development of shrubs and other competing species and improving site conditions (Table 3).

The positive relationship between canopy cover and seedling presence (Eq. (1)) may also be due to higher seed production. Monterey pine is a prolific yearly cone producer and has semi-serotinous to serotinous cones that are persistent in the canopy, an adaptation to historical stand replacement fires. As cones age they will open after their moisture content drops below 20%, which occurs regularly from August to October on the Monterey peninsula (Roy, 1966; McDonald and Laacke, 1990). Following this initial opening, cones will continue to open and close as temperature and humidity change, yet not all seeds are released. Also, seeds can remain viable for many years (Roy, 1966; McDonald and Laacke, 1990). More extensive canopies may therefore have more extensive seed banks, both on the ground and in the canopy.

A factor contributing to error in the canopy cover measurements was the use of the densiometer. Densiometers allow estimates of canopy cover but do not account for variations in foliage density. Therefore, the densiometer may not be effective in quantifying the extent of openings due to senescence and dieback from pitch canker and other agents. Many of the overstory trees in these stands are showing senescent traits such as flat irregular tops (McDonald and Laacke, 1990), and strong coastal winds may be causing extensive abrasion between tree canopies (Oliver and Larson, 1996). Foliage reductions would allow more diffuse light penetration. All of these factors may account for increased light penetration to the forest floor. Although measurements may have shown high percent cover, more light may penetrate the canopy in these mature stands than in younger Monterey pine stands. In a healthy forest with dense canopies, the probability of regeneration would likely be much lower.

One-year height growth, like seedling establishment, was influenced by shrub cover and canopy cover. The second and third linear regressions analyzing 1-year growth show the negative influence of canopy cover, but the high p-values and low B coefficients for canopy cover emphasize shrub cover as the most influential factor in seedling growth. Our study shows a negative relationship between shrub cover and seedling growth while controlling for seedling height (Eq. (2)). For example, holding the seedling height constant at the mean of 29.6 cm, an increase in shrub cover from the minimum mean of 10.8% to the maximum mean of 41.8% will reduce predicted 1-year height growth from 6.1 to 4.7 cm (Table 4). This implies Monterey pine seedlings grow slowly after establishment, with increased growth as they gain a competitive advantage against shrubs. Aussenac (2000) suggests that understory competition encourages water stress and the understory layer may account for up to 50% water loss through evapotranspiration in Monterey pine stands. Shrubs compete with establishing pine seedlings for soil nutrients as well (Aussenac, 2000). Therefore, greater seedling growth is achieved with less competition from understory shrub species. The reduction of shrub establishment due to canopy cover has positive impacts on seedling growth. However, canopy cover and shrub cover interact to affect seedling survival and growth. If the effects of shrub cover could be removed, canopy cover would likely demonstrate negative effects on seedling survival, growth and vigor.

This concept has many implications for management of Monterey pine in natural stands. It may indicate that as senescence continues and growing space is made available the number of seedlings present, or the number of potential establishment sites, will increase. This process is likely to have a threshold. At some point, increasing overstory mortality will allow more growing space for other species such as coast live oak and shrubs (Waring and O'Hara, 2005). This process has begun in Navajo, Spyglass, and small areas of Huckleberry Hill and PQR. In stands with high percentages of shrub cover, understory removal should create better regeneration sites (MacLaren, 1993). Shrub removal could also coincide with reductions in duff depth to further increase the likelihood of regeneration. This could be achieved with a mechanical treatment using tracked machinery (McDonald and Laacke, 1990). Alternatively, as trees die in these stands, a level of resistance in remaining trees may be passed to future seedlings, thus enhancing development of resistant natural populations (Storer et al., 2001). Furthermore, as canopies die, planting may become necessary because seed banks on the forest floor only stay viable for a few years (McDonald and Laacke, 1990).

5. Conclusions

The establishment of Monterey pine natural regeneration is negatively affected by shrub cover and positively affected by canopy cover. These results are probably due to the confounding effects of these two variables: shrub cover negatively affects the probability of regeneration but canopy cover negatively affects shrub cover. Shrub cover appears to be a more significant factor in adversely affecting Monterey pine regeneration. This complex interaction probably conceals the negative interactions of canopy cover on seedling survival and growth.

Management to encourage Monterey pine in declining natural stands should focus on reducing shrub cover while providing seed sources and overstory light penetration. Reductions of duff levels will also assist seedling germination and early development. Planted seedlings may be successful because of a potential head start in height growth that may allow them to grow above shrub competitors.

Acknowledgements

The authors would like to thank the University of California, Berkeley and the Pebble Beach Co., for providing funding for this project, and also thanks to the Pebble Beach Co. and Jack's Peak County Park, for providing access to study sites. We would also like to thank Andrew Storer and Brian Henry at the Michigan Technological University, for their contributions to the fieldwork, and Pascal Berrill at the University of California, Berkeley, for his suggestions regarding statistical analysis and interpretation.

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Please cite this article in press as: O'Brien, M.J. et al., Overstory and shrub effects on natural regeneration processes in native *Pinus radiata* stands, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2006.12.025