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Management strategies for pitch canker infected Año Nuevo stands of Monterey pine

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ABSTRACT

The future resilience of *Pinus radiata* D. Don (Monterey pine) is dependent upon the development of a silviculture program inclusive of either preventative or management techniques for the potentially fatal pitch canker disease (*Fusarium circinatum* Nirenberg and O'Donnell (=*F.subglutinans* (Wollenw and Reinking) Nelson et al. f. sp. *Pini*). As an ecologically and commercially valued species of limited natural range, a number of factors threaten to reduce the Monterey pine gene pool potentially impacting its long-term resilience. This study evaluated the effectiveness of uneven-aged forest management for regeneration success applied in the native, pitch canker infested Año Nuevo stands at Swanton Pacific Ranch in Davenport, California. The impact of gap size (0.20-ha (0.50 acre), 0.10-ha (0.25 acre), and 0.05-ha (0.125 acre)), site-preparation treatment (pile and burn, lop and scatter), and parent tree (13 local seed sources) on seedling survival and growth response (height, diameter) were addressed. Pitch canker symptoms were quantified to conclude if there is indeed a range of expressed resistance according to parent tree. The above independent variables were also examined for being correlated with branch tip incidence of pitch canker and western gall rust disease.

A generalized linear mixed model estimated that the odds of seedling survival varied by site treatment and parent, but not by gap size. Pile and burn sites were estimated to have higher survival rates than lop and scatter sites. Linear mixed models estimated that gap size was associated with average seedling growth, both in terms of height and diameter. Parent and site treatment were not found to be significantly associated with the growth outcome measures. The 0.05-ha sites had smaller average height and diameter than the 0.20-ha sites. The 0.10-ha site also had smaller average diameter than the 0.20-ha sites. The presence of pitch canker disease on branch tips was found to be correlated only with gap size, with 0.10-ha sites having higher pitch canker incidence than the 0.05- and 0.20-ha sites. Though gall rust presence on branch tips was not associated with any of the hypothesized independent variables, there was an association between gall rust presence and pitch canker presence on branch tips. Site treatment and parent tree were associated with seedling survival, while gap size was found to be associated with seedling growth and disease resistance.

1. Introduction

Monterey pine (*Pinus radiata* D. Don) is one of the most widely exported and planted trees in the world. Its international populations have reached an estimated 4.1 million hectares, dwarfing the native range, which covers less than 0.2% of that area (Rogers et al., 2002). Yet, little is known about management techniques to sustain forest health and reproduction in the limited native stands that occur in California (Cope, 1993; Smith et al., 1997). The remaining five native stands represent only a small portion of the historical range and are considered to be a critical genetic resource (Rogers, 2004). A variety of ecological (e.g., pitch canker disease) and anthropogenic factors (e.g., urban development, fragmentation, non-native weed invasion) are affecting these native stands.

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Three of the native stands are found along California's coast with the northernmost Año Nuevo stand reaching 37°8′N, the southernmost Cambria population at 35°34′N, and the Monterey Peninsula population at 36°35′N in between (Moulds, 1950; Forde, 1964). The other two stands are found on the Cedros and Guadalupe islands off the coast of Baja, Mexico (Libby et al., 1968). Due to the geographic division, these stands are genetically distinct from each other and comprise variability vital for the future of the species in the face of threatening factors (Deghi et al., 1995; Stuart and Sawyer, 2001).

The native stands have not spread partly due to climatic and topographic (e.g., aspect) limitations (Roy, 1966; McDonald and Laacke, 1990). Monterey pines do best in soils that are described as medium to coarse textured and medium fertility with a pH range of 4.5–5.2. As soils become finer in texture, as with Diablo clay adobe soils, the species' development becomes poor or entirely gives way to grasslands as has occurred in parts of the Cambria stand (Moulds, 1950).

Monterey pine is one of the species included in the closed-cone pine ecological group, which regenerate most successfully after a fire has exposed the mineral soil, reduced vegetation density, and opened cones to release seeds (Smith et al., 1997; Stephens et al., 2004). However this process has been interrupted and dramatically reduced by fire suppression policy in the native stands (Stuart and Sawyer, 2001). Additionally, at Año Nuevo, proliferation of broadleaf species and other common associates increasingly hamper regeneration (Piirto and Valkonen, 2005). A cutting or fire treatment is necessary to counterbalance the aforementioned conditions, restoring an environment favorable for a sustained Monterey pine population (Piirto and Valkonen, 2005).

Other challenges caused by urbanization additionally threaten the three native California stands. Urban development has impacted the native stands through fragmentation, increased stress, introduction of invasive weeds, and genetic contamination from exotically propagated landscape plantings of Monterey pine (White, 1999; Storer et al., 2001; Rogers, 2004; Piirto and Valkonen, 2005).

One of the most notable consequences of urbanization was the introduction of the non-native pathogen *Fusarium circinatum* Nirenberg & O'Donnell (=*F. subglutinans f. sp. Pini* J.C. Correll), commonly known as pitch canker (Dwinell, 1999). The exotic pitch canker infection of Monterey pine was first discovered in California's Santa Cruz County in 1986 and has since been a topic of discussion and research (McCain et al., 1987). In addition to Monterey pine, this pathogen is known to affect a variety of species inclusive of *Pinus muricata* D. Don, *P. coulteri* D. Don, *P. ponderosa* Laws,*P. canariensis* C. Smith, *P. pinea* Linnaeus, *P. halepensis* Mill, and *P. attenuata* Lemm. By 1992 the disease had been identified in each of the three native California stands (Storer et al., 1994). Along California, Monterey pines closer to the coast (within 1.5 km) are at higher risk for infection and are prone to quick progression of symptom advancement (Wikler et al., 2003; Ganley et al., 2009). Insight into which factors impact the progression of incidence and subsequent disease symptoms is key to understanding the pathogen's behavior and ultimately developing management guidelines (Dallara et al., 1995).

Pitch canker is caused by the fungus *Gibberella circinata* Nirenberg & O'Donnell, which is more commonly known by its conidial condition, *F. circinatum* Nirenberg & O'Donnell. Tissue damage and exposure resulting from natural growth, weather, pruning, and insects can all provide sites for infection (Harrington and Wingfield, 1998). Dissemination is also possible through infested seed (Dwinell, 1999). Pitch canker is characterized in pines by stem death and necrosis of the interior woody tissue of shoots, branches, cones, and exposed roots (Dallara et al., 1995; Dwinell, 1999).

Currently the intricacies of the disease remain unclear. For example, it is speculated that infected individuals that do not experience more severe symptoms or do not die as a result of an advanced infection are expressing a genetic resistance to the disease (Aegerter and Gordon, 2006; Matheson et al., 2006). Another belief that insect vectors affect infection is supported by: (1) successful isolations of the *F. circinatum* fungus from several species of bark and cone beetles and (2) appearance of pitch canker disease symptoms during periods of increased insect activity (Storer et al., 1994, 2004; Gordon et al., 2001). Theories and hypotheses are being tested to gain the scientific understanding necessary to manage the disease (Gordon et al., 2001).

Another major disease affecting Monterey pines in California is western gall rust caused by a fungal pathogen (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka) that affects two- and three-needled *Pinus* ssp. (European and Mediterranean Plant Protection Organization and CAB International, 2010). Detection of this 'pine–pine rust' (i.e., only a pine host is needed for disease's full life-cycle) has been identified in each of the three native California stands (Adams, 1997; Offord, 1964). Infecting the cambium, the disease can severely degrade growth and overall tree health, potentially proving fatal (Adams, 1997; Oregon State University Extension, 2010). Young trees are most susceptible to infection, easily succumbing to main stem infections (Oregon State University Extension, 2010). More mature trees experience branch infections that stunt growth and weaken structural integrity at infection site (Adams, 1997; Oregon State University Extension, 2010). Considering the ease of rapid intensification of this 'pine–pine' disease within a population, low proportions of western gall rust infection in native stands may indicate that either Monterey pines exhibit more resistance than other *Pinus* ssp. or the environment is not optimal for the fungus (Henry, 2005).

The silvical, genetic, and forest health factors outlined above present concern for the long-term resilience of the species. Conserving the native stands of Monterey pines and their genetic resources could prove critical for protecting the future of international industry and for safeguarding processes of the native ecosystem against changing global demands (Deghi et al., 1995). This study addresses potential elements of an appropriate and effective science-based forest management program. Features associated with uneven-aged forest management were investigated to evaluate how silvicultural methods affect survival, growth, and pitch canker infection. This study was designed to test the following hypotheses: Monterey pine seedling survival, height and diameter growth, and severity of pitch canker incidence are influenced by: gap-size, site preparation treatment, and parent tree.

2. Materials and methods

2.1. Study site

The study site is located at the southern end of the native Año Nuevo Monterey pine forest within the Scotts Creek Management Unit at Swanton Pacific Ranch (property of California Polytechnic State University, San Luis Obispo [Cal Poly]). Differentiating it from the other two native stands in California, the Año Nuevo is the smallest with an estimated 400–600 ha of forestland (Roy, 1966; Deghi et al., 1995). These stands provide an invaluable research opportunity to study Monterey pine in its native environment.

Uneven-aged forest management is being implemented and evaluated at Swanton Pacific Ranch in response to a number of factors including very strict California Practice Rules (Piirto et al., 1997; Big Creek and Cal Poly, 2008; CDF, 2012). Containing 106 ha, the Scott's Creek Management Unit is comprised of two distinct aggregations including a Monterey pine concentration (22 ha) (Wise, 2004). At the western end of the unit where the ground is fairly level with only a few gentle slopes, Monterey pine grows in domination, and in some cases comprises 100% of the overstory (Piirto and Valkonen, 2005). Elsewhere in the unit Monterey pines grow among coast redwood (*Sequoia sempervirens* (D. Don) Endlicher), Douglas-fir (*Pseudostuga menziesii* (Mirbel) Franco), California nutmeg (*Torreya californica* Torrey), and a variety of broadleaf species, most notably coast live oak (*Quercus agrifolia* Nee) and Shreve oak (*Quercus parvula* var *shrevei* (C.H. Muller)) (Piirto and Valkonen, 2005; Auten, pers. comm., 2010).

Santa Cruz County is considered Mediterranean in climate with a mean annual precipitation of 77.9 cm (30.7 in.) and a mean annual temperature of 13.9 °C (57°F). The mean daytime high is 20 °C (68°F) and the mean nighttime low is 7.8 °C (46°F) (U.S. Dept. of Commerce et al., 2004; California Polytechnic State University, San Luis Obispo, 2007). A combination of summer fogs, an average humidity between 70% and 80% in winter, and overcast skies accounting for 30–40% of daylight hours annually, translates into reduced solar energy received by vegetation (California Polytechnic State University, San Luis Obispo, 2007).

The pitch canker incidence rate in 2005 within the Scott Creek Management unit was 35.3% (SE 3.5), making it one of the highest of the native stands evaluated (Henry, 2005). Yet these numbers indicate a decrease in disease incidence from several years earlier (1999) when an estimated 90% of trees ($d > 2.54$ cm) were symptomatic (Piirto and Valkonen, 2005). Death of infected trees may account for this drop in recorded incidence. Moreover, this decrease in occurrence may lend support that a range of susceptibility exists where trees previously recorded as infected were able to resist disease advancement and eliminate symptoms (e.g., overgrowth of branch tips, dropping of infected branches) (Gordon et al., 2001; Storer et al., 2002). Needless to say, pitch canker has heavily impacted the Scott's Creek Management Unit in the 10 or so years since original confirmation of the disease in Año Nuevo in 1992 and warrants scientific study (Storer et al., 1994).

2.2. Experimental design

The field-design entails nine experimental conditions comprised of three gap sizes and three site treatments which were randomly assigned to 27 plots available to the study, yielding three plots per experimental condition. The circular plots are 0.20-, 0.10-, or 0.05-ha in size ($r = 25.37$ m (83.23 ft.), 19.94 m (65.42 ft.) or 12.68 m (41.60 ft.), respectively) (Wise, 2004). Plots chosen for group-selection harvesting were treated with one of two preparation-methods: lop and scatter or pile and burn. As such, a total of 18 treated circular gaps and nine control plots

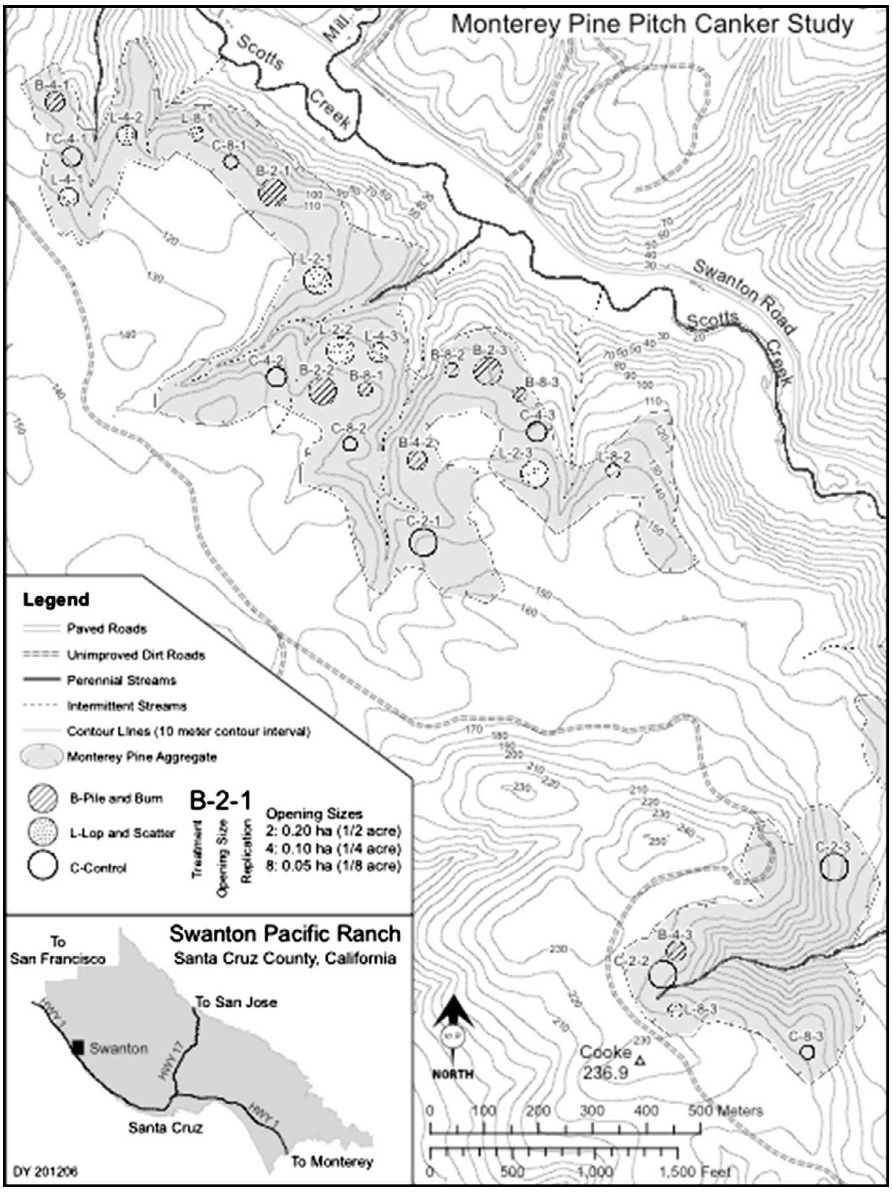

Fig. 1. Map of Group Selection Openings, illustrating plot placement, study site details and location.

were produced. Control plots remained untreated; no trees were cut, no preparation method was performed, and no seedlings were planted. Note that *gap* will refer to only the treated openings whereas *plot* refers to all 27 plots. Likewise the term *study area* refers to all plots, treated and control. The plot location and designation of treatment were chosen in a random and unbiased fashion. All plots are located within aggregations that are predominantly Monterey pine at Swanton Pacific Ranch (Fig. 1). For further information please refer to Wise (2004) for illustrations of the experimental design and information regarding soil composition within each plot.

2.3. Field procedures

2.3.1. Plot location

The following is a summary of the procedures utilized in this long-term study. For a more thorough description please refer to Wise (2004), Pinkerton (2006), Loe (2010), and Yun (2011). Geographic Information Systems (GIS) software was used to randomly locate plots and designate site-treatment and gap-size within the study area. Each plot was subsequently ground-truthed to ensure the following requirements were satisfied:

- Adhere to California regulations (CDF, 2012) for watercourse and lake protection zones.
- 30.48 m (100 ft.) minimum slope distance from class II watercourse;
- No inclusion of class II ponds.
- No less than 15.24 m (50 ft.) slope distance from class III watercourse;
- Slope less than 35% (tractor accessible).
- Located *within* the Monterey pine aggregation (suitable MP habitat).
- Minimum 30.48 m (100 ft.) buffer between adjacent plots; and
- Consideration of residual stand features and forest components (i.e., avoid wildlife trees, archaeological sites, areas with known concentration of root rot and areas of problematic erosion).

2.3.2. Gap creation and site preparation

During the late summer and early fall of 2001, trees within the 18 group-selection plots were felled, bucked, and tractor yarded to a nearby landing. Following the opening of the gaps, one of the two site preparation methods was applied. Remaining biomass in the lop and scatter plots was cut into less than 1.1 m sections and distributed throughout the unit to create a layer of slash no more than 45.7 cm deep. Remaining biomass in the pile and burn plots was gathered into a central pile and burned (January 2002). Burn remnants were distributed throughout the unit before planting (Wise, 2004).

2.3.3. Reforestation

After creation of the gaps, each was reforested with seedlings generated from seeds collected from 13 mother (parent) trees from the Año Nuevo stand. In October 2000, seeds from the 1998 crop of Monterey pine were gathered from trees already existing in the study area as well as trees on the Big Creek Lumber Company's portion of the native stand. Mother trees were tested for resistance to pitch canker using methods outlined by Gordon et al. (1998). Parents BC6, BC11, BC12, and SP2 were ranked as resistant, BC3, BC13, SP3, SP5, and SP6 as intermediate, and BC4, SP15, SP1, and SP4 as susceptible. SP# signifies a tree sourced from Swanton Pacific Ranch whereas BC# signifies a tree sourced from Big Creek Lumber. In an attempt to provide a variety of expressed resistance, the 13 parents chosen for use in the study were selected based on the results of the screening process. Please note that mother tree is the only control for the "parent" variable since the seeds used in the study were a product of open pollination.

Table 1
Number of seedlings planted per gap and parent (Wise, 2004).

Gap size (ha)	Total # of seedlings	Seedlings/parent/gap
0.05	52	4
0.10	112	8 or 9[a]
0.20	216	16 or 17[a]

[a] Differed due to total number of trees/plot not evenly divisible by number of parent trees (13).

After screening, seeds were sown at Cal Poly in May 2001 and transported to a shade-house at Swanton Pacific Ranch in August 2001. In February 2002 the seedlings were out-planted into treated plots in accordance with the systemized random pattern outlined by Wise (2004). Each of the 13 parents constituted roughly 7% of the seedlings in each gap (Table 1). A total of 2280 trees were planted at 3 m by 3 m spacing, resulting in 1074 trees per hectare. Several hundred additional trees were saved in a shade-house for future reforestation needs (Pinkerton, 2006).

2.3.4. Interplanting

It was determined during the 12 month data collection period that 673 (29.5%) of the 2280 original trees were missing. The consequent empty tree spaces were considered detrimental to the outcome of the original experimental design and thus trees saved for reforestation from the original 2002 planting were used to fill in (Pinkerton, 2006). Due to limited reserves, seedlings from only eight parent trees were used for interplanting resulting in two sub-categories of planted seedlings: original (trees sustained from the 2002 planting) and interplanted (trees planted in February 2003) (Table 2).

2.4. Data collection and analyses

To describe the general condition of the study site prior to treatment, an inventory was conducted to determine tree size, density, and degree of damage and disease infestation of all plots. Inventory data included: diameter at breast height (1.37 m), damage (e.g., crooks, bends, forked tops, etc.), and presence of disease signs/symptoms for all existing trees with a diameter greater than 2.54 cm. Evidence and severity of pitch canker infection was the main concern; however, detection of other pathogens (e.g., western gall rust (*E. harknessii* (J.P. Moore) Y. Hiratsuka [=*Peridermium harknesii* J.P. Moore] and *Armillaria mellea* ([Vahl.:Fr.] Karst)) were also noted. Understory vegetation and natural regeneration surveys were conducted to determine a baseline for ongoing studies and shed further light on subsequent post-treatment development (Wise, 2004).

In treated gaps, artificially regenerated seedlings were assessed for several factors: (1) survival (both original and interplanted seed-

Table 2
Number of interplanted seedlings by parent. *Source:* Pinkerton, 2006

Parent ID	Number planted
2BC3	34
2BC6	151
2BC11	139
2BC12	48
2BC13	43
2SP2	150
2SP5	54
2SP6	54
Total	673

lings), (2) height (cm), (3) diameter (mm), (4) pitch canker symptoms, and (5) western gall rust symptoms. All plots were assessed for: (1) ocular estimate of understory density and composition, (2) natural regeneration, and (3) vegetation change. Photo points were used to observe the latter feature and make visual record of gap development. The three survey periods, approximately 12 (February 2003), 24 (February 2004), and 68 (October 2007) months post-reforestation treatment (hereinafter referred to as post-treatment), followed uniform collection methods where possible to ensure consistency. Any deviations or dissimilar methods will be noted in the following text. This paper publishes for the first time the long-term data and analysis record reported in Master's theses prepared by Wise (2004), Pinkerton (2006), Loe (2010), and Yun (2011).

Understory vegetation data was collected and analyzed with descriptive statistics for all study plots. Each plot was visually divided into quadrants with division lines determined by hand compass at the four cardinal directions. Vegetation cover was ocularly estimated (to a sum of 100%) for each of the four subplots. The data from the four subplots were averaged to estimate vegetation cover (to 100%) for the whole plot. Major species were recorded as well as areas of no vegetation (bare ground or leaf/needle litter). Most vegetation types detected were identified to species level; however, for ease of subsequent analysis, some were only identified to family level (e.g., grasses, rushes, sedges, and ferns).

At pre-treatment, post-treatment 12 and 24 month collection periods, micro-site plots were created to estimate the number of naturally occurring seedlings (both residual pre-treatment seedlings and newly recruited post-treatment seedlings) in the understory. The micro-site sample method entailed subplots (two square meters in dimension) systematically laid out along lines radiating from plot center. The number of lines increases as gap-size enlarges. The 0.05-ha plots have four lines (at each cardinal direction), 0.10-ha plots have lines every 45°, and 0.20-ha plots, every 22°. Three subplots were evenly spaced along each line, translating to a total of 13 subplots in 0.05-, 25 subplots in 0.10-, and 52 subplots in 0.20-ha plots, resulting in a 10% sample. Furthermore, the seedlings were categorized as being located in inner, middle or outer rings of the circular gap to observe spatial relationship to natural regeneration success. At 68 months post-treatment, a 100% survey was conducted in all gaps to accurately count naturally occurring regeneration Monterey pines.

For survival assessment, all artificially regenerated tagged trees were identified and recorded as surviving or dead. Dead trees were defined as having no living needles. If a tree death was observed, a red "X" was placed in the field records. This field data was transferred into a digital database using a "0" for dead trees and "1" for surviving trees. Missing trees (i.e., no tree found at planting location) were considered dead. All surviving trees were assessed for pitch canker and western gall rust symptoms. Each tree was observed from all angles to accurately tally the number of symptomatic branch tips, stem or branch cankers, and stem or branch galls.

Growth data (height and diameter) were collected for a random 25% sample of original trees ($n = 546$). The same trees were measured for each of the three data collection periods. Height measurements were taken at the tip of the apical meristem or the top of the living tissue if the tree's top growth was dead or dying. Diameter measurements were taken at soil level. At 68 months post-treatment, a 100% growth survey was conducted for all surviving artificially regenerated seedlings.

The primary outcome variables of the study were seedling height (cm), diameter (mm), and survival, all at 68 months post-treatment post-planting. Survival of artificially regenerated seedlings was analyzed for all 2280 trees. Growth of artificially regenerated seedlings was analyzed for the 271 surviving seedlings of the original 546 sampled trees. Descriptive statistics for interplanted seedlings are excluded in this paper, but were analyzed by Loe (2010). Some descriptive statistics and graphs for survival and growth will be presented for intermediate time periods (12 and 24 months post-treatment) as well as for the end point.

The inferential statistics regarding survival and growth was done for 68 months post-treatment. Mixed-effects models were used to account for a random parent effect as well as potential correlation between trees within the same gap. For seedling survival a generalized linear mixed model was used to model the binary response of survival. A binomial distribution with a logit link function was used to predict the log-odds of survival as a function of the fixed effects for site treatment and gap size, and a random effect for parent tree. Several possible correlation structures were explored for modeling the dependency of trees within the same gap. A compound symmetry correlation structure was found to be adequate. For the continuous response variables, height and diameter at 68 months post-planting, a mixed linear model assuming normally distributed sources of variation was used; again, with fixed effects for site treatment and gap size, a random effect for parent tree, and a compound symmetry correlation structure for trees within the same gap. We also controlled for baseline seedling height and diameter at the time of planting, respectively, in the two models. For more details about mixed effects models, the reader is referred to McCulloch and Searle (2001) and Littell et al. (2006).

A secondary analysis was conducted to investigate relationships between the silivicultural variables and pitch canker and western gall rust incidence. We fit several additional generalized linear mixed models similar to the model used to predict seedling survival, but predicting either the log-odds of being infected by pitch canker or by western gall rust. In particular, three models were estimated to assess correlates of pitch canker infection of branch tips, pitch canker infection of the main stem, and western gall rust infection of branch tips. Lastly, a model was fit to examine the association between pitch canker infection and western gall rust infection. In all of the models predicting disease incidence we also controlled for tree height.

The mixed effects models were estimated with PROC MIXED and PROC GLIMMIX using SAS/STAT software, Version 9.1 of SAS System for Windows. All other analyses, descriptive statistics and figures were produced using SPSS, Version 18 for Macintosh. A 10% significance level will be used for the results that follow.

3. Results

3.1. Pre-treatment conditions

The study area's overstory was composed of 54% (709 trees) conifer species and 46% (604 trees) hardwoods. Dominating were Monterey pine (44% of the overstory), and a combination of coast live and Shreve's oak (collectively 34% of the overstory) (Wise, 2004). Species represented in lesser amounts include Douglas-fir, big-leaf maple (*Acer macrophyllum* Pursh), California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), California buckeye (*Aesculus californica* (Spach) Nutt.) and Pacific madrone (*Arbutus menziesii* Pursh) (Wise, 2004).

Of the 575 living Monterey pines surveyed pre-treatment, 75% of the sampled trees had a diameter less than 51 cm. This indicates the study area was dominated by a large number of pole-sized trees and included only several dozen larger individuals. Tree diameter measures ranged from 2.54 cm to 190.54 cm with an average of 30.5 cm (SD = 33 cm). Density measures ranged from 148 to 1165 trees per hectare and averaged 411 trees per hectare. Basal area for all tree species was approximately 49 m^2/ha, of which 27.5 m^2/ha was Monterey pine. The remainder was chiefly occupied by Douglas-fir and live oak species (Wise, 2004).

Damage appraisal of all 709 surveyed conifer trees showed that 16.8% (119) had some degree of damage, inclusive of such traits as dead tops (not associated with pitch canker), crooks, bends, suppression, bole or branch damage (mechanical, animal, or unknown). Disease appraisal showed that the two most frequently occurring diseases were pitch canker and western gall rust. Of the 575 Monterey pines surveyed pre-treatment, 34.6% were symptom free, 65.4% appeared to have some level of pitch canker infection, and 10% showed signs of western gall rust. Pitch canker symptoms ranged from branch flags to resinous cankers and top kill. Fourteen percent of the infected individuals had multiple symptoms such as branch flags and stem cankers (Wise, 2004).

3.2. Understory vegetation

Prior to treatment, the study site based on percent cover had a fairly homogenized mix of species (refer to Table 3 for predominant species detected and scientific names), comprised of poison oak (24%), California blackberry (21%), and 'other species' (15%), leaving 40% unvegetated (bare ground or leaf/needle litter). Please note the 'other species' are those that represent less than 5% of the total area at the size or treatment level (Wise, 2004). By 24 months post-treatment, the two most significant changes were the appearance of annual weedy species (e.g., grasses and thistles that were not found in the study site prior to treatment), and an increase in overall species diversity (Pinkerton, 2006).

Table 3
Predominant under- and overstory species observed within the study site (Wise, 2004; Hickman, 1993; UCB, 2010).

Sp code	Botanical name	Common name
Conifer species		
PiRa	*Pinus radiata* D. Don	Monterey pine
PsMe	*Pseudostuga menziesii* (Mirbel) Franco var. *menziesii*	Douglas-fir
ToCa	*Torreya californica* Torrey	California nutmeg
Hardwood species		
AcMa	*Acer macrophyllum* Pursh	Big-leaf maple
AeCa	*Aesculus californica* (Spach) Nutt.	California buckeye
ArMe	*Arbutus menziesii* Pursh	Pacific madrone
QuAg	*Quercus agrifolia* Nee	Coast live oak
QuSh	*Quercus parvula* var. *shrevei* (C.H. Muller) K. Nixon	Shreve's oak
UmCa	*Umbellularia californica* (Hook & Arn.) Nutt.	California bay
Understory species		
BaPi	*Baccharis pilularis* DC.	Coyote bush
CeTh	*Ceonothus thyrsiflorus* Eschsch.	Blue blossom
CiVu	*Cirsium vulgare* (Savi) Ten.	Bull thistle
ClPe	*Claytonia perfoliata* Willd.	Miner's lettuce
CoCo	*Corylus cornuta* Marsh var. *californica* (A. DC.) W. Sharp	California hazelnut
CoMa	*Conium maculatum* L.	Poison hemlock
DrAr	*Dryopteris arguta* (Kaulf.) Maxon	Coastal wood fern
ErMi	*Erechtites minima* (Poiret) DC.	Burnweed
FrCa	*Fragaria vesca* L. ssp. *californica* (Cham. & Schldl.) Staudt	Wood strawberry
Ga sp.	*Galium* sp.	Bedstraw
GnLu	*Gnaphalium luteo-album* L.	Cudweed
IrDo	*Iris douglasiana* Herbert	Mountain iris
LoHi	*Lonicera hispidula* Douglas var. *vacillans* A. Gray	California honeysuckle
MaOr	*Marah oreganus* (Torrey & A. Gray) Howell	Coast manroot
MiAu	*Mimulus aurantiacus* Curtis	Sticky monkey flower
NaSq	*Navarretia squarrosa* (Eschsch.) Hook & Arn.	Skunkweed
PoMu	*Polystichum munitum* (Kaulf.) C. Presl	Sword fern
PtAq	*Pteridium aquilinum* (L.) Kuhn var. *pubescens* L. Underw.	Bracken
RhCa	*Frangula californica* (Eschsch.) A. Gray	Coffee berry
RiSp	*Ribes speciosum* Pursh	Fuschia flowering gooseberry
RuUr	*Rubus ursinus* Cham. & Schldl.	California blackberry
SaMe	*Sambucus nigra L. subsp. caerulea (Raf.) Bolli*	Blue elderberry
SiMa	*Silybum marianum* (L.) Gaertner	Milk thistle
SmRa	*Smilacina racemosa* (L.) Link	False soloman's seal
StBu	*Stachys bullata* Benth.	Hedge nettle
SyAl	*Symphoricarpos ablus* (L.) S.F. Blake var. *laevigatus* (Fernald) S.F. Blake	Common snowberry
ToAr	*Torilis arvensis* (Hudson) Link	Hedge parsley
ToDi	*Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene	Western poison oak
UrDi	*Urtica dioica* (L.) ssp. *holsericea* (Nutt.) Thorne	Stinging nettle

By 68 months post-treatment, the cover of grass and thistle diminished from the peak values seen in previous surveys. Similarly, there was a drop in unvegetated areas and California blackberry occurrence. The decrease in these categories was counterbalanced by an increase of poison oak and 'other species'. The increase Wise (2004) and Pinkerton (2006) observed in species diversity was more dramatically expressed in all plots by 68 months. The understory vegetation trends for the overall study site (inclusive of all 27 plots: pile and burn, lop and scatter, and control) are presented in Fig. 2.

In control plots 68 months post-treatment, understory vegetation was dominated by poison oak and 'other species', staying fairly consistent with surveys from 12 and 24 months post-treatment. California blackberry maintained presence but decreased by about half in all plot sizes.

In pile and burn plots 68 months post-treatment, poison oak and 'other species' dominated. Both categories showed increased cover since 12 and 24 month surveys. California blackberry and grasses accounted for substantial amounts of cover, coming back from a lull seen at 24 months yet not reaching the peak percentages seen at 12 months.

Much like the other plots in the study, lop and scatter gaps 68 months post-treatment were predominately vegetated by poison oak, 'other species', California blackberry, and grasses. Understory in 0.10-ha gaps were most strongly dominated by poison oak whereas both 0.20- and 0.05-ha gaps have a more even distribution of above-named species/categories.

3.3. Natural regeneration

Pre-treatment natural regeneration seedlings were comprised of 79% hardwood and 21% conifer species (57% Monterey pine, 43% Douglas-fir). Similarly, at post-treatment 12 months, 78% were hardwoods and 22% conifers (Wise, 2004). Yet by post-treatment 24 months, hardwood seedlings only accounted for 58% of naturally regenerated seedlings, resulting in a growing percentage of conifer species (42%). Of the 42% softwoods seedlings, 91% were Monterey pine and 9% were Douglas-fir, indicating a dramatic change from the proportions recorded during pre-treatment survey (Pinkerton, 2006).

Vegetation sampling, used for all but the post-treatment 68 month survey, allowed for observation of spatial relationship to natural regeneration success. The post-treatment 24 month survey concluded that the Monterey pine natural regeneration was spatially distributed as follows: 13% (inner), 23% (middle), and 64% (outer). The highest percentage of the 69 new recruitments was produced in the 0.05-ha pile and burn gaps (42%) (Pinkerton, 2006).

At 68 months post-treatment, the count of naturally regenerated Monterey pine seedlings had reached 159 (Table 4). The 'pile and burn' and 'lop and scatter' treatments had substantially higher per-hectare averages than the control. The 0.10 ha plots had the highest per-hectare averages of the three gap-sizes.

3.4. Survival of artificially regenerated seedlings

The progression and comparison of the survival rates for all 2280 seedlings over the study period is illustrated in Fig. 3, and

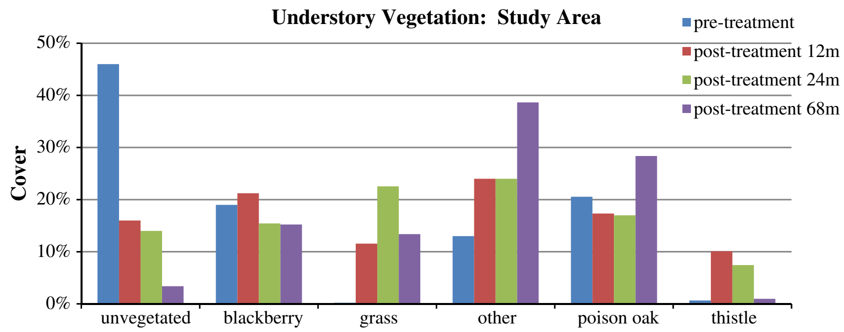

Fig. 2. Summary of understory vegetation cover (%) for study site at pre-, post-treatment 12, 24 and 68 month (*Source:* 12 month data: Wise, 2004; 24 month data: Pinkerton, 2006; 68 month data: Loe, 2010).

Table 4
Summary of natural regeneration trees of Monterey pine by treatment and gap-size at 68 months post-treatment.

	# Seedlings	% of total	Trees/(ha)
Treatment			
Pile and burn	75	47.2	71.6
Lop and scatter	69	43.4	65.9
Control	15	9.4	14.3
Size (ha)			
0.05	19	12.0	42.2
0.10	74	46.5	82.2
0.20	66	41.5	36.7
Total	159		50.5

in the descriptive statistics of Tables 5 and 6. At 3 months post-treatment nearly all the planted seedlings were alive, eliminating the concern that poor planting technique was accountable for seedling mortality. At 68 months, the pile and burn plots had a higher survival rate (54.6%) than lop and scatter (43.7%). Survival rate differences between gap sizes were negligible (range 48.1%–50.4%). Though survival rates were higher for pile and burn gaps vs. lop and scatter gaps regardless of gap size, we did find that the differences between treatments was larger for 0.05-ha and 0.20-ha gaps than for the 0.10-ha gaps (Table 6).

The generalized linear mixed model predicting log-odds of seedling survival at 68 months post-treatment estimated a significant association between survival and site treatment (p-value = 0.0660; Table 7). The model estimated that seedlings in pile and burn sites have a 51.7% higher odds of survival than seedlings in lop and scatter sites. Gap size was not found to be significantly associated with the odds of seedling survival (p-value = 0.9456).

The variance/covariance parameter estimates for the random effect of tree parent and the compound symmetry parameter indicate that both of these elements are helpful in explaining the variability in the odds of seedling survival.

Interactions between the independent variables were explored but not found to be statistically significant, nor did they change the substantive results of the analyses. Thus, we have presented the results of this more parsimonious model.

3.5. Growth

The height and diameter development of the surviving sample trees at each of the data collection periods (384 sample trees at 12 month post-treatment: 315 at 24 months post-treatment; 271 at 68 months post-treatment) are illustrated in Figs. 4 and 5. Descriptive statistics for the growth variables for 271 surviving sample trees at 68 months post-treatment are shown in Tables 8 and 9, and reflect the trends seen in Figs. 4 and 5. Overall, seedlings at 68 months post-treatment had grown an average of 397.2 cm (SD = 165.3 cm) in height and 66.8 mm (SD = 36.8 mm) in diameter. These averages account for a height range of 30.5–792.5 cm and a diameter range of 7.0–182.9 mm. Seedlings in the pile and burn gaps had slightly larger height and diameter averages than seedlings in lop and scatter gaps for all three collection periods. Between gap sizes, the 0.20-ha gaps have the largest growth (height and diameter) averages, followed closely by 0.10-ha gaps, with a dramatic drop in averages for 0.05-ha gaps. Similar to the trend seen for survival to parent tree, there was an increasingly divergent variability among parent-tree growth averages at 68 months post-treatment. Note that growth performance averages for all surviving original seedlings are nearly identical to those calculated by treatment, gap-size, and parent, thus validating the sample-set's results.

The results of the estimated linear mixed models predicting average height and diameter of the surviving seedlings at 68 months post-treatment are given in Tables 10 and 11. Both the model for height and the model for diameter controlled for initial height and initial diameter (respectively). However, these covariates were not found to be significantly associated with 68 months average height and diameter, and have been excluded from the output in Tables 10 and 11.

Contrary to what was estimated for seedling survival, site treatment was not found to be significantly associated with average seedling height (p-value = 0.3550) nor with diameter (p-value = 0.5365). On the other hand, gap size which was not significantly associated with survival, was found to be associated with average seedling height (p-value = 0.0688) and diameter (p-value = 0.0199). Tukey adjusted pairwise comparisons indicated that the growth differences between gap sizes were primarily due to the 0.20-ha vs. 0.05-ha comparisons.

When looking at the ratios of the variance estimates to their standard errors (the approximate z-statistics), we find that parent tree is less of a factor in growth than it was in survival. Among the three outcome variables, parent tree was estimated to contribute least to the variability in seedling height.

Again, interactions were explored in the mixed models for height and diameter, but not found to improve model fit. The more parsimonious models were retained and presented here.

3.6. Disease symptom occurrence

Pitch canker infection rates of branch tips for seedlings from the 13 parent trees (Table 12) range from 18.5% to 34.6%. Of the infected trees, the highest number of symptomatic branch tips and stem cankers on any one tree were 18 and 2 respectively. Both maximum values were found on seedlings from the same parent tree (SP15), the parent that also showed the second highest infec-

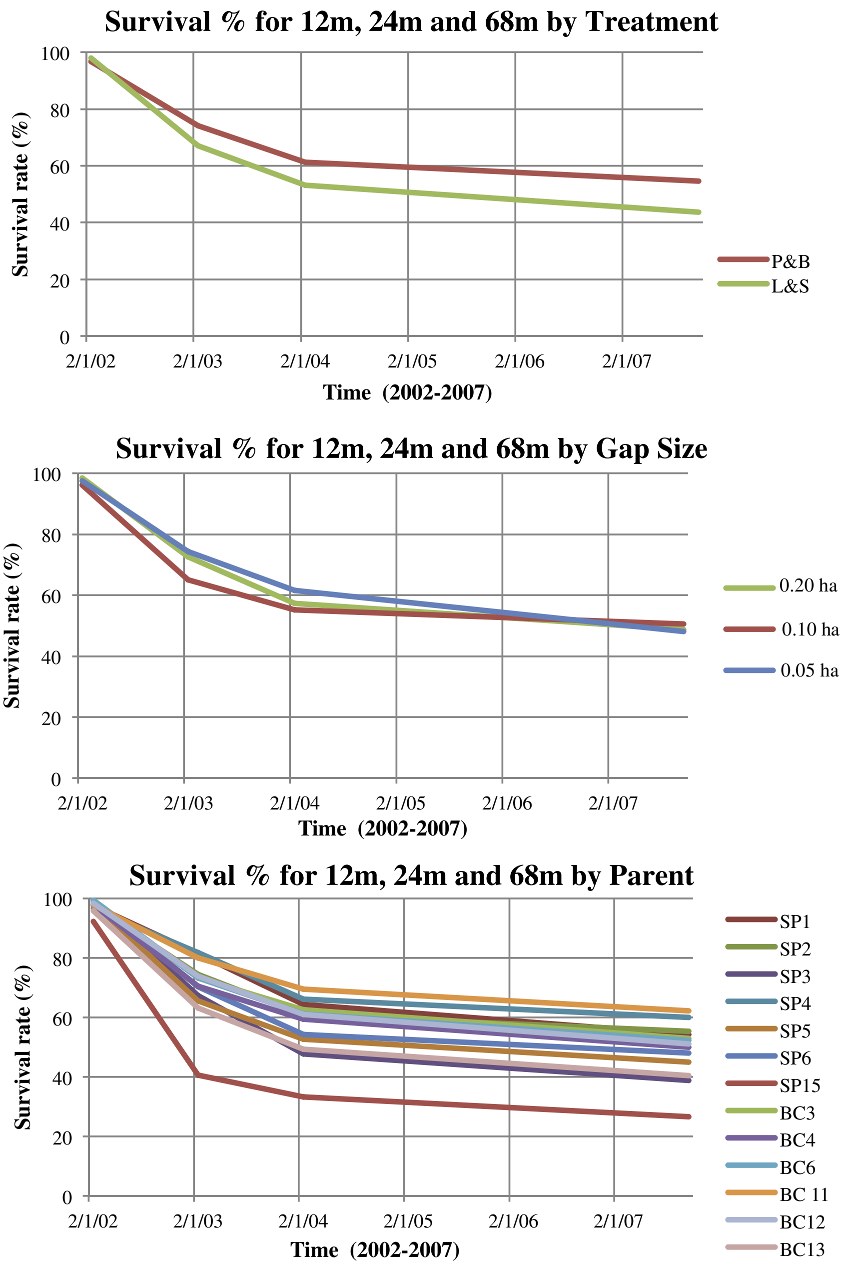

Fig. 3. Illustration of survival rates (%) of all original seedlings overtime by treatment, gap size, and parent (*Source:* 12 month data: Wise, 2004; 24 month data: Pinkerton, 2006; 68 month data: Loe, 2010).

tion rate for pitch canker. Pile and burn gaps had a similar branch infection rate (29.0%) compared to lop and scatter gaps (28.5%). The 0.10-ha plots had the highest rate of branch infection (36.7%) over 0.20- and 0.05-ha plots (27.6% and 16.1% respectively). Overall, 28.8% (322 out of 1118) of the individual trees were infected, of which 91.6% had less than five branch flag symptoms.

Western gall rust infection rates for seedlings from the 13 parent trees range from 2.1% to 13.2% (Table 12), with 15 being the highest number of symptomatic stem galls on any one tree (SP3). Pile and burn gaps had a slightly higher western gall rust seedling infection rate (7.6%) than lop and scatter gaps (6.4%). The 0.05-ha gaps had the highest western gall rust infection rate (9.4%) over 0.20- and 0.10-ha gaps, (7.5% and 5.3% respectively). Overall, only 7.1% (79 out of 1118) individuals were infected, almost all of which had two or less galls (97.3%).

The three mixed effects models estimated that, after controlling for seedling height, pitch canker and gall rust disease presence was only associated with gap size (p-value = 0.0245), and this was found only for pitch canker presence on branch tips (Table 13). The seedlings in the 0.10-ha gaps were estimated to have significantly greater odds of having pitch canker symptoms on branch tips than seedlings in 0.05- and 0.20-ha gaps. None of the hypothesized independent variables were significantly associated with the presence of pitch canker on the main stem or with gall rust (p-values for all effects > 0.15). The association between pitch canker and gall rust presence was tested by adding gall rust presence as an independent variable to the model summarized in Table 13. After controlling for seedling height, gap size, site treatment and parent tree, there was a significant association between gall rust presence and pitch canker on branch tips (p-value = 0.0562; not shown in Table 13).

Table 5
Survival rate by parent, gap size and treatment at 68 months post-treatment (Loe, 2010).

Group	*n*	68 Month survival rate
All	2280	49.1
Parent		
SP1	168	53.6
SP2	168	55.4
SP3	168	41.1
SP4	180	60.0
SP5	180	45.0
SP6	180	47.8
SP15	180	26.7
BC4	180	50.0
BC6	180	52.2
BC11	180	62.2
BC12	180	51.1
BC13	168	40.5
Gap size (ha)		
0.05	312	48.1
0.10	672	50.4
0.20	1296	48.7
Treatment		
Pile and Burn	1140	54.6
Lop and Scatter	1140	43.7

Table 7
Mixed model results for survival: Overall tests of significance for fixed effects, and variance/covariance parameter estimates for random components of models.

Source of variation			
Fixed effects	*F*-stat	*P*-value	
Treatment	3.83	0.0660	
Gap size	0.06	0.9456	
Random effects	Cov param. estimate	SE	Approx. *z*-stat.
Parent	0.1219	0.0578	2.11
Gap (Comp Sym)	0.0394	0.0162	2.43
Residual	0.9570	0.0285	

4. Discussion

4.1. Pre-treatment conditions

The Scott's Creek Management Unit is diverse in structure and composition, containing a mix of both conifer and broadleaf species with a wide range of diameter and density measures. Similar results were reported by Piirto and Valkonen (2005). Disease appraisal indicates that infection rates have risen since the 2005 survey from 35.3% to 65.4%, climbing towards the 90% recorded in 1999 (Henry, 2005; Piirto and Valkonen, 2005).

4.2. Understory vegetation

Through the 68 months since treatment, understory cover can be characterized by sustained growth, consistent presence of a few specific species, and changes in cover proportion. The most notable changes were an increase in cover percentage of weedy and grass species, a dramatic decrease of unvegetated areas, and the continued increase of species diversity and poison oak. The abundance of weedy species seen (for example thistle) at 12 months and the increase of grass seen at 24 months were both reduced by 68 months post-treatment.

Overall, poison oak in the study-site gradually increased over the 68 months post-treatment from 21% to 28%. Although abundant in the pre-treatment study site, poison oak dominates the understory at 68-months post-treatment. This may be due to a variety of factors such as: (1) a positive reaction to the disturbance caused by site-treatment, (2) the species' ability to survive in a variety of moisture and sun intensities, and/or (3) the species' suppression capability. In full sun these plants can develop into a dense shrub 0.30– 1.82 m (1–6 ft.) high with a widespread root system (DiTomaso and Lanini, 2009).

Species diversity, encompassing the 'other species' category and the introduction of new species (species not recorded in previous survey-summaries) increased across the study site, including control plots. Appearances of species such as blue blossom in pile and burn gaps, mountain iris in the 0.05-ha lop and scatter gaps, and poison hemlock in 0.20- and 0.10-ha lop and scatter gaps could be the result of several factors: (1) increased human, animal and treatment activity within the study site, (2) random or episodic seed (residual or from adjacent stands) germination and establishment as light, moisture, and competition levels change within the plot, and (3) close proximity to grazed rangeland. The species that have increased or maintained presence in the understory vegetation appear to be the ones that can survive on very little unvegetated space and withstand the domination of the Monterey pine seedlings, poison oak, and other well established individuals. Collectively, these understory changes are indicative of a secondary succession process that occurred within the study site.

4.3. Natural regeneration

In hopes of sustaining a population, reproduction for any tree species is paramount. With pre-treatment regeneration proportion favoring hardwoods (79%) rather than softwoods (21%), the outlook seemed dismal for Monterey pine within the Scott's Creek Management Unit. Without fire or small-scale disturbances, studies indicate that this Año Nuevo stand could transition from a Monterey pine to a Coast Live/Shreve oak forest type (Piirto and Valkonen, 2005).

In the treatment area the chances for natural regeneration of pines appeared to be increasing as a result of site treatment. Survey of the naturally occurring seedlings showed softwood species composition within the study-area had risen from 21% to 42% of total seedlings present. Pre-treatment, Monterey pine seedlings comprised only 8% of softwood species composition, yet by 24 months

Table 6
Survival number and rate by gap-size and treatment in unison at 12, 24, and 68 months post-treatment. *Source:* 12 month data: Wise, 2004; 24 month data: Pinkerton, 2006; 68 month data: Loe, 2010.

Gap size (ha)	Treatment	12 months		24 months		68 months	
		# Seedlings	% Surv.	# Seedlings	% Surv.	# Seedlings	% Surv.
0.05	Lop & Scatter	107	68.6	88	56.4	65	42.0
	Pile & Burn	122	76.9	103	66.0	85	54.0
0.10	Lop & Scatter	215	63.7	178	52.0	165	49.0
	Pile & Burn	220	65.5	190	56.6	174	52.0
0.20	Lop & Scatter	437	67.6	334	51.7	268	41.0
	Pile & Burn	502	76.9	399	61.6	363	56.0
Total		1603		1292		1119	

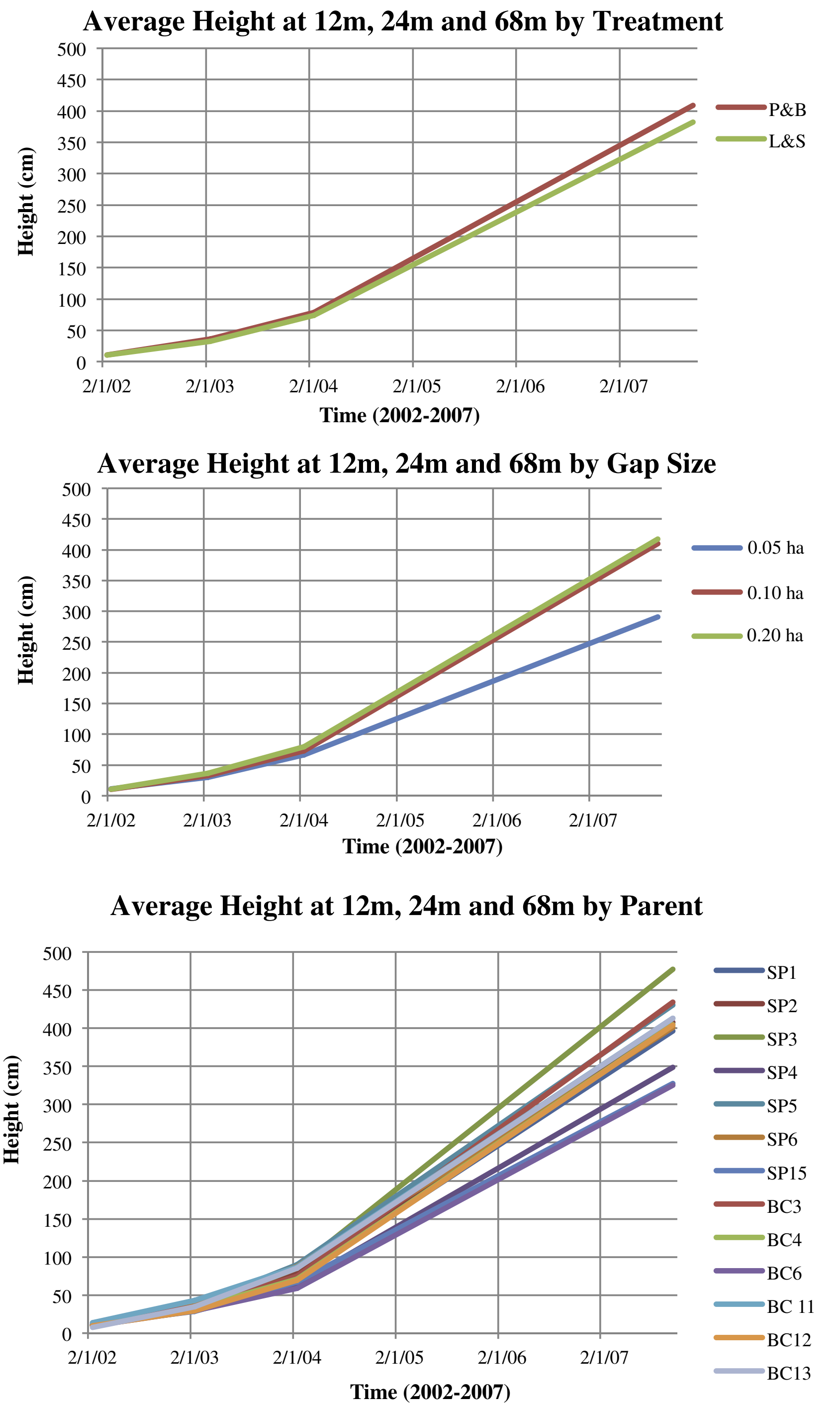

Fig. 4. Average height (cm) over time by treatment, gap-size and parent for surviving seedlings (*Source:* 12 month data: Wise, 2004; 24 month data: Pinkerton, 2006; 68 month data: Loe, 2010).

post-treatment, that percentage had more than quadrupled (38%). These results are not conclusive yet encourage further research and offer hope for restoration of this native stand.

The number of naturally occurring Monterey pine seedlings within treated gaps at 68 months post-treatment show a significant difference compared to the control plots (47.2-, 43.4- and 9.4%, respectively). This result is expected given that the literature reports Monterey pines seedling establishment and survival rates are higher on disturbed sites (e.g., bare soil, cleared competition) (McDonald and Laacke, 1990; Smith et al., 1997). Gap size did not seem to have influenced the rate of natural regeneration significantly.

4.4. Survival of artificially regenerated seedlings

With the goal of restoring a strong population of Monterey pine in native stands there is an advantage to preparing planting sites with a pile and burn treatment. The bare soil, elimination of competition, increased availability to nutrients and sun exposure in these sites has given seedlings in this study a 51.7% greater odds of survival than seedlings in the lop and scatter plots (p-value = 0.0660) (Wise, 2004; Pinkerton, 2006; Loe, 2010).

The lower survival odds of seedlings in lop and scatter plots as compared to the pile and burn plots can be attributed to several

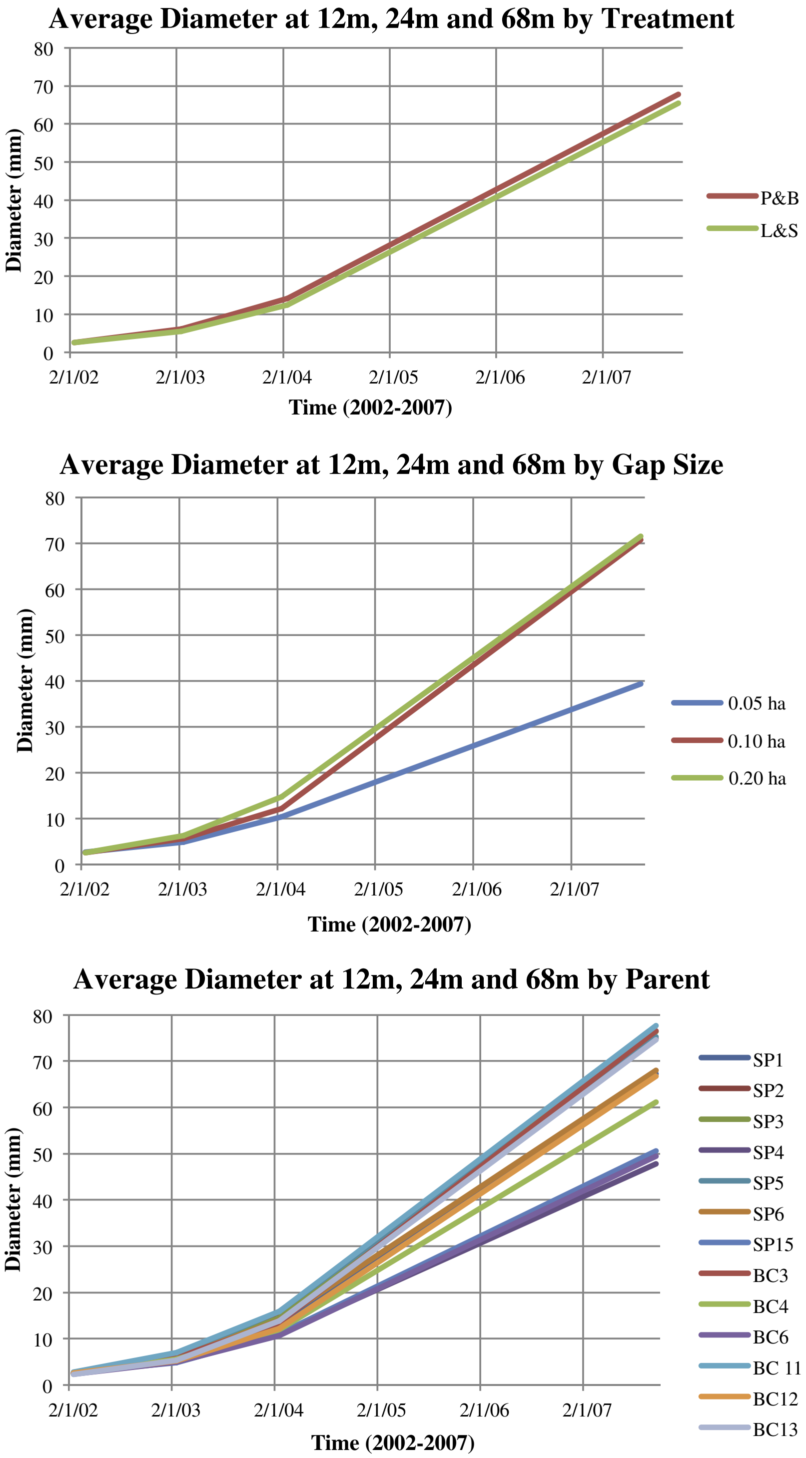

Fig. 5. Average diameter (mm) over time by treatment, gap-size and parent for surviving seedlings (*Source:* 12 month data: Wise, 2004; 24 month data: Pinkerton, 2006; 68 month data: Loe, 2010).

factors, most of which involve the remaining slash layer: (1) remnant fungal inocula (e.g., pitch canker) in slash; (2) competition for nutrients; (3) altered moisture and temperature of soil due to blanket of slash; (4) decreased sun exposure to seedlings, and lastly; (5) the lesser degree of site-disturbance in comparison to pile and burn plots (Wise, 2004; Pinkerton, 2006; Loe, 2010; McDonald and Laacke, 1990). Although a layer of slash may slow the growth of weedy or shade intolerant competition-species, the thicker layer of biomass effectively acts against the seedlings' growth preferences (e.g., full sun, bare soil, and minimal competition) to discourage establishment and ultimately survival (Gotou and Nishimura, 2003; McDonald and Laacke, 1990).

The three gap-sizes used in this study do not conclusively suggest that any one gap-size improves survival odds of artificially regenerated seedlings. The California Forest Practice Rules limit group selection openings to 0.20 ha and smaller. Previous studies for coniferous species have demonstrated that larger gap-sizes (e.g., 0.40 or 0.80 ha) have significant beneficial effects on survival

Table 8
Descriptive statistics for height (cm) at 68 months post-treatment.

Group	Height (cm) at 68 months					
	n	Min	Max	Mean	SD	SE
All	271	30.5	792.5	397.2	165.3	10.0
Parent						
SP1	27	121.9	701.0	396.2	176.6	34.0
SP2	25	152.4	762.0	407.8	174.9	35.0
SP3	13	213.4	762.0	477.1	160.0	44.4
SP4	22	30.5	792.5	348.4	188.2	40.1
SP5	16	61.0	716.3	430.5	184.4	46.1
SP6	19	76.2	624.8	401.1	164.7	37.8
SP15	12	152.4	533.4	327.7	121.7	35.1
BC3	23	182.9	777.2	434.0	168.2	35.1
BC4	20	167.6	762.0	404.5	148.7	33.3
BC6	26	76.2	731.5	325.3	166.0	32.6
BC11	28	137.2	701.0	413.1	147.8	27.9
BC12	21	152.4	792.5	404.2	160.0	34.9
BC13	19	45.7	670.6	413.1	148.5	34.1
Gap size (ha)						
0.05	38	61.0	624.8	290.8	149.7	24.3
0.10	77	137.2	792.5	409.7	184.5	21.0
0.20	156	30.5	792.5	416.9	149.4	12.0
Treatment						
Pile and burn	150	91.4	792.5	409.3	147.0	12.0
Lop and scatter	121	30.5	792.5	382.1	185.1	16.8

Table 9
Descriptive statistics for diameter (mm) at 68 months post-treatment.

Group	Diameter (mm) at 68 Months					
	n	Min	Max	Mean	SD	SE
All	271	7.0	182.9	66.8	36.8	2.2
Parent						
SP1	27	12.7	142.2	67.2	37.3	7.2
SP2	25	15.2	160.2	74.9	42.9	8.6
SP3	13	20.3	147.3	76.4	34.8	9.7
SP4	22	15.2	107.7	47.8	26.0	5.5
SP5	16	10.2	152.4	75.3	39.2	9.8
SP6	19	7.6	142.2	68.0	38.0	8.7
SP15	12	21.6	94.0	50.6	23.0	6.6
BC3	23	17.8	182.9	76.5	43.2	9.0
BC4	20	7.0	137.2	61.2	32.9	7.4
BC6	26	10.2	134.6	49.5	33.5	6.6
BC11	28	15.2	166.0	77.7	37.9	7.2
BC12	21	12.7	152.4	66.8	35.1	7.7
BC13	19	20.3	134.6	74.6	32.2	7.4
Gap size (ha)						
0.05	38	10.2	109.2	39.4	26.2	4.3
0.10	77	12.7	182.9	70.7	38.8	4.4
0.20	156	7.0	166.0	71.5	35.3	2.8
Treatment						
Pile and burn	150	7.0	182.9	67.8	34.8	2.8
Lop and scatter	121	7.6	166.0	65.5	39.3	3.6

and growth of seedlings (Smith et al., 1997). Further research on the relationship of gap-size to survival of Monterey pine seedlings is recommended.

Survival analysis of seedlings from the 13 parent-trees shows a fairly wide range of rates. Offspring from parent SP15 (screened 'highly susceptible' to pitch canker) have consistently been the least likely to survive since project inception. Similarly, seedlings from parent trees BC11 and SP2 (screened 'resistant' to pitch canker) represent two of the top three survival rates. These results could indicate either a relationship between screening-results and seedling survival or marks overall phenotypic hardiness of an individual. However, this trend is not consistent among comparisons for all parent tree results. Further studies may conclusively decipher whether or not a relationship exists between survival rates and pitch canker resistance. Survival rates also show no observable pattern between parents sourced from Swanton Pacific Ranch and Big Creek Lumber Company's portion of the Año Nuevo stand.

4.5. Growth of artificially regenerated seedlings

The 0.20-ha gaps yielded seedlings with a significantly larger average height and diameter over the seedlings in the 0.05-ha gaps. Seedlings in 0.20-ha gaps, once established, may have superior growth averages due to more abundant sunlight, creating an optimal balance of temperature, moisture, nutrient, and exposure

Table 10
Mixed model results for height at 68 months post-planting: Overall tests of significance for fixed effects, Tukey adjusted pairwise comparisons; and variance/covariance parameter estimates for random components of models.

Source of variation			
Fixed effects	*F*-stat	*P*-value	Turkey *P*-value
Treatment	0.90	0.3550	
Gap Size	3.08	0.0688	
0.05 vs. 0.10-ha			0.1574
0.05 vs. 0.20-ha			0.0680
0.10 vs. 0.20-ha			0.9058
	Cov Param		Approx.
Random effects	Estimate	SE	*Z*-Stat
Parent	216.7	485.9	0.45
Gap (Comp Sym)	5774.1	2424.4	2.38
Residual	19,269.0	1747.3	

Table 11
Mixed model results for diameter at 68 months post-planting: Overall tests of significance for fixed effects, Tukey adjusted pairwise comparisons; and variance/covariance parameter estimates for random components of models.

Source of variation			
Fixed effects	*F*-stat	*P*-value	Turkey *P*-value
Treatment	0.40	0.5365	
Gap Size	5.15	0.0199	
0.05 vs. 0.10-ha			0.0477
0.05 vs. 0.20-ha			0.0222
0.10 vs. 0.20-ha			0.9370
	Cov Param		Approx.
Random effects	Estimate	SE	*Z*-stat
Parent	65.01	46.07	1.41
Gap (Comp Sym)	270.69	132.11	2.05
Residual	973.68	88.50	

Table 12
Infection rates for pitch canker branch-tips symptoms, pitch canker stem symptoms and western gall rust by parent, gap-size, and treatment at 68 months post-treatment. Refer to Loe (2010) for further descriptive statistics.

	n	Branch symptom rate (%)	Stem symptom rate (%)	Western gall rust rate (%)
All	1118	28.8	5.2	7.1
Parent				
SP1	90	28.9	4.4	8.9
SP2	93	26.9	4.3	5.4
SP3	69	31.9	7.3	10.1
SP4	107	34.6	6.5	5.6
SP5	81	28.4	3.7	3.7
SP6	86	22.1	3.5	7.0
SP15	48	33.3	8.3	2.1
BC3	88	29.6	4.6	5.7
BC4	90	27.8	4.4	7.8
BC6	94	33.0	7.5	4.3
BC11	112	31.3	5.4	12.5
BC12	92	18.5	4.4	4.4
BC13	68	29.4	7.4	13.2
Gap size				
0.05 ha	149	16.1	1.3	9.4
0.10 ha	338	36.7	5.0	5.3
0.20 ha	631	27.6	6.5	7.5
Treatment				
Pile & Burn	620	29.0	6.1	7.6
Lop & Scatter	498	28.5	4.4	6.4

conditions. Additionally, there may be an element of decreased competition when considering the nominal differences in growth between seedlings in 0.20- and 0.10- ha gaps. Superior survival results in 0.10-ha gaps translate to a higher density of trees competing for water, nutrients and sunlight. Thus, trees in 0.20-ha gaps may have a better chance to flourish as a result of a mortality-induced decrease in seedling density (McDonald and Laacke, 1990).

The 13 parent trees produced a wide range of growth averages (both height and diameter). Consistently through the study (Wise, 2004; Pinkerton, 2006; Loe, 2010) the same parents hover at the top of the range and others at the bottom. Though not statistically significant, this information warrants attention and further research as choices are made for plantation plantings when yield is critical.

Table 13
Mixed model results for pitch canker on branch tips: Overall tests of significance for fixed effects, and variance/covariance parameter estimates for random components of models.

Source of variation			
Fixed effects	*F*-stat	*P*-value	Turkey *P*-value
Height	39.89	<0.0001	
Treatment	0.00	0.9698	
Gap size	4.91	0.0245	
0.05 vs. 0.10-Ha			0.0384
0.05 vs. 0.20-Ha			0.5457
0.10 vs. 0.20-Ha			0.0745
	Cov Param		Approx
Random effects	Estimate	SE	*Z*-stat
Parent	0.0007	0.0234	0.03
Gap (Comp Sym)	0.0164	0.0140	1.17
Residual	0.9885	0.0426	

4.6. Disease symptom occurrence

Our analysis found an association between pitch canker incidence (as represented by detection of symptomatic branch tips) and gap-size and tree height. The explanation for these two relationships may be one and the same. Considering the larger growth averages in 0.20- and 0.10- ha gaps, trees in these gaps may experience higher rates of infection due to the increased amount of surface area, translating to an increased opportunity for wounding and infection occurrence. The association between the odds of pitch canker infection and tree size was also detected by Piirto and Valkonen's models, where trees with a diameter smaller than 25.4 mm were less often infected than those over 25.4 mm (2005). It is also possible that the environmental conditions in these gaps (e.g., increased exposure to sun, rain, and wind) could exacerbate spore dispersion and/or wounding agents. Surprisingly, no relationship is detected between site treatment and pitch canker incidence, possibly suggesting that unsterilized biomass in lop and scatter plots does not put seedlings at greater risk of infection over those in pile and burn plots. However, it is more likely that a relationship exists yet was not detected due to low survival rates of trees in lop and scatter plots, where seedlings were fatally infected and therefore not accounted for by 68 month post-treatment disease survey.

Also notable in this study is the difference between rates of less severe infection (e.g., symptomatic branch tips; 28.8%) and more advanced infection (e.g., stem and branch canker; 5.2%). This dramatic contrast aligns with previous observations that pitch canker initially affects many trees in stands prior to advanced development in individual trees (Storer et al., 2002).

Western gall rust was less prevalent among the seedlings in the study site than pitch canker. However, there was a significant association between pitch canker and gall rust presence. This result may simply confirm that trees infected by one disease are predisposed for attack from other pests or pathogens. However, other studies on slash and loblolly pine found no relationship (Dwinell and Barrows-Broaddus, 1984). These different findings warrant further research between pitch canker and western gall rust with a focus on detection and management.

Some of the relationships that may have been expected to prove statistically significant based on descriptive statistics and figures did not bear out in the results of the mixed models. For example, Table 6 indicates a possible interaction between gap size and treatment in terms of survival, and Figs. 4 and 5 would lead one to guess that 0.10- and 0.20-ha gaps would both significantly differ in terms of height and diameter compared to 0.05-ha gaps. One thing to remember is that although there were 2280 seedlings planted, our effective sample size is based more on the number of plots randomized to experimental conditions and constraints: and we had three replicates for each gap size/site treatment combination. This did limit our statistical power and our ability to discern some associations that were more moderate in nature.

5. Summary and conclusions

The results of this study support the following conclusions for survival, growth, and pitch canker infection of Monterey pine seedlings within an uneven-aged silvicultural management strategy:

Seedling Survival:

1. Gaps prepared with pile and burn site treatment produce higher survival rates than gaps with lop and scatter treatment (68 months post-treatment). This site preparation technique abides by regulations mandated for the study site (CDF, 2012).
2. Gap size (i.e., 0.20-, 0.10-, and 0.05-ha) does not have a significant effect on Monterey pine survival (68-months post-treatment).
3. A range in parent survival rates for the 13 tested parents indicates a genotypic impact on survival success. Thus, seed source is an important consideration for reforestation.

Seedling Growth:

1. Seedling growth (i.e., height or diameter) was not significantly affected by site-treatment (68 months post-treatment).
2. Seedlings in 0.20-ha gaps had average heights significantly larger than those in 0.05-ha gaps (68 months post-treatment).
3. Seedlings in 0.20- and 0.10-ha gaps had average diameters significantly larger than those in 0.05-ha gaps (68 months post-treatment).
4. Seedling growth was not significantly affected by parent tree (68 months post-treatment).

Disease:

1. Pitch canker infection rates were not significantly associated with site treatment (68 months post-treatment).
2. Pitch canker branch infection rates were significantly higher in 0.10-ha gaps compared to 0.05- and 0.20-ha gaps (68 months post-treatment).
3. Pitch canker infection rates were not significantly associated with parent (68 months post-treatment).
4. Pitch canker branch infection is significantly associated with gall rust infection.

In hopes of developing management guidelines for Monterey pine, existing real-world restraints were considered in the experimental design. Conducting the experiment in-lab would have had some benefit; however, results obtained under actual conditions would be most applicable to the native stands. Most notable are the limitations presented by California Forest Practice Rules, environmental politics, project budget, ecological integrity, and operational environment (Wise, 2004).

Artificial gap-phase regeneration as explored by this study in synthesis with other techniques may provide a sound foundation for development of an effective management plan critical for restoring health in native Monterey pine stands. Namely, a combination of genetic conservation (*in situ* and *ex situ*) and discouraging use of exotically propagated Monterey pines will help to maintain invaluable genetic variability and integrity of each distinct population, protecting evolutionary adaptability (Rogers, 2004; Deghi et al., 1995). Furthermore, within the context of a broad gene pool, research is recommended to determine Monterey pine pitch canker resistant seed stock. This will be a critical component to a successful sustainability plan as it will allow for reforestation of native stands and will hopefully eliminate disease losses in international plantations. As our world evolves environmentally, ecologically, politically, legally, and socially, it is important that an appropriate, attentive variety of measures be taken to maintain the prized Monterey pine in the context of the 21st century and beyond.

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References

Adams, D., 1997. Western Pines and Western Gall Rust. Tree Notes #22. California Dept. of Forestry and Fire Protection.

Aegerter, B.J., Gordon, T.R., 2006. Rates of pitch canker induced seedling mortality among *Pinus radiata* families varying in levels of genetic resistance to *Gibberella circinata* (anamorph *Fusarium circinatum*). For. Ecol. Manage. 235, 14–17.

Big Creek Lumber Company; California Polytechnic State University (Big Creek and Cal Poly), 2008. Non-industrial timber management plan for Swanton Pacific Ranch. Davenport, CA. On file with California Department of Forestry and Fire Protection (CDF). Santa Rosa, CA.

California Polytechnic State University, San Luis Obispo, 2007. Nonindustrial timber management plan: Swanton Pacific Ranch. <ftp://thp.fire.ca.gov/THPLibrary/North_Coast_Region/NTMPs2007/1-07NTMP-020SCR/> (Ver. 29.05.10).

California Department of Forestry and Fire Protection (CDF), 2012. California forest practice rules. Title 14, California Code of Regulation. Resource Management, Forest Practice Program, Sacramento, CA. <http://www.fire.ca.gov/resource_mgt/resource_mgt_forestpractice.php> (Ver. 29.05.10, Chapters 4, 4.5, and 10).

Cope, A., 1993. *Pinus radiata.* In: Fire Effects Information System. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <http://www.fs.fed.us/database/feis/> (Ver. 08.10.08).

Dallara, P.D., Storer, A.J., Gordon, T.R., Wood, D.L., 1995. Current status of pitch canker disease in California. Dept. of Environmental Science, Policy and Management, Div. of Environmental/Biology, Berkeley, California, <http://frap.cdf.ca.gov/pitch%5Fcanker/prevention_management/treenotes.html> (Ver. 23.01.08).

Deghi, G.S., Huffman, T., Culver, J.W., 1995. California's native Monterey pine population: potential for sustainability. Fremontia 23, 14–23.

DiTomaso, J.M., Lanini, W.T., 2009. IPM Education and Publications, UC Statewide IPM Project, Univ. of California, Davis. <http://www.ipm.ucdavis.edu> (Ver. 26.04.10).

Dwinell, L.D., 1999. Contamination of *Pinus radiata* seeds in California by *Fusarium circinatum*. USDA Forest Service, Southern Research Station, Athens, Georgia.

Dwinell, L.D., Barrows-Broaddus, J., 1984. Infection of Fusiform Rust Galls on Slash and Loblolly Pines by Pitch Canker Fungus, *Fusarium moniliforme* var *subglutinans*. In: Proceedings IUFRO Rusts of Hard Pines. October 1–6, 1984, Athens, GA.

European and Mediterranean Plant Protection Organization and CAB International, 2010. Data sheets on quarantine pests: *Endocronartium harknessii*. <www.eppo.org/QUARANTINE/fungi/.../ENDCHA_ds.pdf> (Ver. 09.05.10).

Forde, M.B., 1964. *Pinus radiata* in California. Forest Research Institute, Rotorua.

Ganley, R.J., Watt, M.S., Manning, L., Iturritxa, E., 2009. A global climatic risk assessment of pitch canker disease. Can. J. For. Res. 39 (11), 2246–2256.

Gordon, T.R., Winkler, K.R., Clark, S.L., Okamota, D., Storer, A.J., Bonello, P., 1998. Resistance to pitch canker disease, caused by *Fusarium subglutinans* f. sp. *pini*, in Monterey pine (*Pinus radiata*). Plant Pathol. 47, 706–711.

Gordon, T.R., Storer, A.J., Wood, D.L., 2001. The pitch canker epidemic in California. Plant Dis. 85 (11), 1128–1139.

Gotou, J., Nishimura, T., 2003. Effects of slash chips placed around trees planted after whole-tree logging: movement and nutrient supply. J. For. Res. 8, 67–76.

Harrington, T.C., Wingfield, M.J., 1998. Diseases and the ecology of indigenious and exotic pines. In: Richardson, D.M. (Ed.), Ecology and Biogeography of *Pinus*. Cambridge Univ. Press, Cambridge, pp. 381–404.

Henry, B.P., 2005. Monterey pine (*Pinus radiata*) in California: Variation among native forests and health as a predictor of tree removal in an urban forest. M.S. thesis, Michigan Technological Univ., Houghton, MI.

Hickman, J. (Ed.), 1993. The Jepson Manual: Higher Plants of California. Univ. of California Press, Berkeley.

Libby, W.J., Bannister, M.H., Linhart, Y.B., 1968. The pines of Cedros and Guadalupe islands. J. For. 66 (11), 846–853.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS for Mixed Models, second ed. SAS Institute Inc., Cary, NC.

Loe, V., 2010. Management Strategies for Pitch Canker Infected Año Nuevo stands of Monterey pine. M.S. Thesis, California Polytechnic State Univ., San Luis Obispo, CA.

Matheson, A.C., DeJey, M.E., Gordon, T.L., Werner, W., Vogler, D.R., Balocchi, C., Carson, M.J., 2006. Heretability of response to inoculation by pine pitch canker of seedlings of radiata pine. Aust. Forest 69 (2), 101–106.

McCain, A.H., Koehler, C.S., Tjosvold, S.A., 1987. Pitch canker threatens California pines. Calif. Agric. 41, 22–23.

McCulloch, C.E., Searle, S.R., 2001. Generalized, Linear, and Mixed Models. John Wiley & Sons, Inc., New York.

McDonald, P.M., Laacke, R.J., 1990. *Pinus radiata* D. Don Monterey pine. In: Burns, R.M., Honkala, B.H. (Tech. Coord.) Silvics of North America, vol. 1. Conifers. Agric. Handbook 654. US Dept. of Agriculture, Forest Service, Washington, DC, pp. 433–441.

Moulds, F.R., 1950. Ecology and Silviculture of *Pinus radiata* (Don) in California and in Southern Australia. Doctoral Dissertation. Yale Univ.

Offord, H.R., 1964. Diseases of Monterey pine in native stands of California and in plantations of western North America. USDA Forest Service, Research Paper PSW-14. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, pp. 1–9.

Oregon State University Extension, 2010. An online guide to plant disease control. Western gall rust fact sheet. <http://plant-disease.ippc.orst.edu/disease.cfm?RecordID=858> (Ver. 09.05.10).

Piirto, D.D., Valkonen, S., 2005. Structure and development of pitch canker infected Monterey pine stands at Año Nuevo, California. For. Ecol. Manage. 213, 160–174.

Piirto, D.D., Thompson, R., Piper, K., 1997. Implementing Uneven-Aged Redwood Management at Cal Poly's School Forest. In: Proceedings of the Conference on Coast Redwood Forest Ecology and Management, June 18–20, 1996, pp. 78–82.

Pinkerton, J., 2006. Silvicultural management strategies for pitch canker infected Año Nuevo stands of Monterey pine: Second year gap regeneration results. M.S. Thesis, California Polytechnic State Univ., San Luis Obispo, CA.

Rogers, D.L., 2004. In situ genetic conservation of a naturally restricted and commercially widespread species, *Pinus radiata*. For. Ecol. Manage. 197, 311–322.

Rogers, D.L., Vargas Hernández, J.J., Matheson, A.C., Guerra Santos, J.J., 2002. The Mexican island populations of *Pinus radiata*: An international expedition and ongoing collaboration for genetic conservation. Food and Agricultural Organization of the United Nations. <http://www.fao.org/docrep/005/y4341e/y4341e07.htm#P947_91075> (Ver. 07.05.10).

Roy, D.F., 1966. Silvical characteristics of Monterey pine. USDA Forest Service Research Paper PSW-31. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, pp. 1–16.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.S., 1997. The Practice of Silviculture. Applied For. Ecol., ninth ed. John Wiley & Sons Inc., New York.

Stephens, S.L., Piirto, D.D., Caramagno, D., 2004. Fire regimes and resultant forest structure in native Año Nuevo Monterey pine forest, California. Am. Midl. Nat. 152, 25–36.

Storer, A.J., Gordon, T.R., Dallara, P.L., Wood, D.L., 1994. Pitch canker kills pines, spread to new species and regions. Calif. Agric. 48 (6), 9–13.

Storer, A.J., Wood, D.L., Gordon, T.R., Libby, W.J., 2001. Restoring native Monterey pine forests in the presence of an exotic pathogen. J. For. 99 (5), 14–18.

Storer, A.J., Wood, D.L., Gordon, T.R., 2002. The epidemiology of pitch canker of Monterey Pine in California. For. Sci. 48, 694–700.

Storer, A.J., Wood, D.L., Gordon, T.R., 2004. Twig beetles, Pityophthorus spp. (Coleoptera Scolytidae), as vectors of the pitch canker pathogen in California. Can. Entomol. 36 (5), 685–693.

Stuart, J.D., Sawyer, J.O., 2001. Trees and Shrubs of California. Univ. of California Press, Berkeley, pp. 89–90.

U.S. Department of Commerce, National Oceanic & Atmospheric Administration, National Environmental Satellite, Data, and Information Service, 2004. Climatography of the United States National Climatic Data Center. Asheville, NC. <http://ggweather.com/climate/santa_cruz.htm> (Ver. 09 May 2010).

University of California Berkeley (UCB), 2010. Jepson Flora Project: Jepson Exchange. Index to Treatments and Keys from *The Jepson Manual*. <http://ucjeps.berkeley.edu/interchange/I_treat_indexes.html> (Ver. 25.05.10).

White, K.L., 1999. Revisiting native *Pinus radiata* forests after twenty-nine years. Madroño 46 (2), 80–87.

Wikler, K., Storer, A.J., Newman, W., Gordon, T.R., Wood, D.L., 2003. The dynamics of an introduced pathogen in a native Monterey pine (*Pinus radiata*) forest. For. Ecol. Manage. 179, 209–221.

Wise, E., 2004. Silvicultural management strategies for pitch canker infected Año Nuevo stands of Monterey pine: First year gap regeneration results. M.S. Thesis, California Polytechnic State Univ., San Luis Obispo, CA.

Yun, D., 2011. Utilization of Geographic Information System for research, management, and education in the Natural Resources Management Dept. at California Polytechnic State Univ., San Luis Obispo. M.S. Thesis, California Polytechnic State Univ., San Luis Obispo, CA.