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The dynamics of an introduced pathogen in a native Monterey pine (*Pinus radiata*) forest

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Abstract

The plant pathogenic fungus, *Fusarium circinatum*, is the cause of a major epidemic of pitch canker in urban forests of Monterey pine (*Pinus radiata*) in California. This pathogen is now also well established in all three mainland, native populations of Monterey pine where it causes conspicuous branch die-back and, frequently in association with native bark beetles, increased tree mortality. In the present study, permanent plots were established on the Monterey peninsula to characterize the severity and progress of pitch canker in the largest of the native *P. radiata* populations. The results indicate that the disease is significantly more severe, and is progressing more rapidly, in managed stands than in the wildland areas. Furthermore, the disease is progressing significantly faster in the coastal zone than in more inland locations.

Keywords: Urban forest; Forest pathology; Plant epidemiology; Fungal pathogen; Exotic microbe; Pitch canker; *Fusarium circinatum*

1. Introduction

Pitch canker disease is a plantation and nursery problem affecting pines in many parts of the world (Dwinell et al., 1985; Viljoen et al., 1994). In 1986, the causal pathogen, *Fusarium circinatum* Nirenberg and O'Donnell [=*F. subglutinans* (Wollenw and Reinking) Nelson et al. f.sp. *pini* (Correll et al.)], was discovered in California, where it was associated with mortality in planted Monterey pines (*Pinus radiata* D. Don) along roadsides and in other landscaped settings (McCain et al., 1987). The apparent absence of the disease in nearby native Monterey pine forests suggested that natural stands might escape significant damage. This view was consistent with the behavior of the disease in the southeastern US where pitch canker was problematic in plantations and seed orchards, but not in wildland situations (Dwinell et al., 1985). However, by 1994, pitch canker had been observed in all three native populations of Monterey pine in California (Storer et al., 1994; Gordon et al., 1996, 1997).

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The fungus causes girdling lesions on branches, exposed roots, and the main stems of pine trees. The tips of girdled branches wilt as a result of obstructed water flow, and the needles distal to the girdled branches turn yellow, and then red. The fascicles eventually fall off the tree, leaving bare branch ends. Multiple branch infections can cause extensive die-back in the crown of the tree, and may lead to tree mortality. The tree produces copious amounts of resin (pitch) in response to an infection. Numerous insects, including engraver beetles (*Ips* spp.), twig beetles (*Pityophthorus* spp.), the cone beetle (*Conophthorus radiata*), the deathwatch beetle (*Ernobius punctulatus*), and the spittlebug (*Aphrophora canadensis*) are associated with, and in many cases are capable of vectoring, the pitch canker pathogen (Fox et al., 1991; Fox and Schultz, 1991; Hoover et al., 1996; McNee et al., 2002; Storer et al., 1998).

Native populations of Monterey pine are found in only five locations worldwide. Two of these populations are on islands off the coast of Baja California, and are morphologically distinct from those in the mainland populations, typically having two needles per fascicle, rather than three (Hickman, 1993; Ciesla, 1995). The mainland populations occur in three disjunct locations along the coast of central California. The approximate size of forests with natural understory in each of these locations is as follows: Cambria (930 ha), Monterey (3800 ha), and Año Nuevo (600 ha) (Huffman and Associates Inc., 1994; Jones and Stokes Associates Inc., 1994). While the smallest population of native Monterey pine, in Año Nuevo, remains fairly undeveloped, approximately 50% of the Monterey pine forest on the Monterey peninsula has been urbanized (Jones and Stokes Associates Inc., 1994). Trees left within developed areas constitute an urban forest. Some conspecifics, often from non-local seed sources, have been planted within the urban forest to supplement the remnant stands of native trees.

Pitch canker causes tree mortality directly, or indirectly by predisposing trees to infestations by bark beetles, and has the potential to significantly increase the rate of mortality in all age classes of Monterey pine within its natural range. These losses are important not only to the forests themselves but also for their effects on a critical source of genetic material for Monterey pine, which is the most widely planted pine in the world (McDonald and Laacke, 1990; Ciesla, 1995).

Exotic pathogens have had major impacts on the ecology of North American forests, and the recent occurrence of pitch canker in California offered the opportunity to assess the impact of an exotic pathogen in the early stages of an epidemic. The present study was undertaken to characterize the development of pitch canker in native trees within urbanized (managed) and wildland (unmanaged) native forests. The specific objective was to test for an effect of landscape type on disease severity and progression. For this purpose, landscapes were considered to be either wildland or managed and the latter were further sub-divided into golf course, heavy urban, and light urban categories. In addition, effects of geographic (inland versus coastal) location on disease severity and progression were also tested. The present report, based on 3 years of survey data, reveals strong trends in the distribution and development of pitch canker on the Monterey peninsula.

2. Materials and methods

In spring 1996, 44 plots were established on the Monterey peninsula west of Highway 1 in Monterey County, California, to monitor the development of pitch canker disease both in the wildland and urbanized

Fig. 1. Location of the study site for monitoring pitch canker disease progression in native Monterey pines on the Monterey peninsula in Monterey County, California.

Monterey pine forests (Fig. 1). The locations of 40 plots were chosen by overlaying a grid on an aerial photograph of the Monterey peninsula and randomly generating numbers for coordinates to mark each plot's center until 10 forested plots were selected in each of four different landscape types: wildland, golf, light urban, and heavy urban. If permission from the landowners could not be obtained to establish a plot in a particular location, an additional plot was randomly selected.

The Monterey peninsula is extensively developed, and as a result none of the plots was more than 1 km from an urban interface. We distinguished the landscape types in the following manner. Wildland plots were established in relatively undisturbed stands larger than 16 acres (6.5 ha), where management was limited to removal of invasive, non-native plants in the understory, such as broom (*Genista* spp.) and pampas grass (*Cortaderia jubata*), and fire was excluded. Light urban plots were established in semi-natural, non-irrigated forested areas designated as small open spaces (generally no larger than four acres (1.6 ha)). Unlike the wildland plots, light urban plots bordered paved roads and/or landscaped properties, and their understory was actively managed for fire suppression and/or aesthetics. Many of the light urban plots were in small easements separating house lots. Golf course plots were adjacent to fairways, and were impacted by turfgrass maintenance, including irrigation, fertilization, pesticide application, and other vegetation management applied to the courses. Heavy urban plots were located on landscaped homesites with managed understories of mostly non-native plants. Thirty-nine of the 40 plots were composed solely of *P. radiata*; but a single wildland plot had only Bishop pines (*Pinus muricata* D. Don); data from this plot were excluded from the analyses and the figures.

In addition to the 40 randomly selected plots described above, 4 additional plots were established, each on one of four different Del Monte Forest Foundation properties (hereafter referred to as ‘‘Foundation’’ plots), by randomly selecting a plot center within each preserve. These properties are dedicated as permanent open space, and have qualities similar to the ‘‘wildland’’ landscape type, but because they were not randomly selected, they were analyzed separately from the other 39 plots.

The plots were circular in outline, with a radius of 5.6 m (1/100 ha), 8 m (1/50 ha), 11.3 m (1/25 ha), 12.6 m (1/20 ha), or 17.8 m (1/10 ha), depending on the density of the trees in the location. If there were not at least 10 trees over 125 cm tall within the largest (1/10 ha) plots, the next closest trees over 125 cm were included, until the plot had a total of 10 trees. The only exception to this was a single urban plot that was established with only nine trees, because the neighboring trees were inaccessible. If there were more than 15 trees in a plot, 15 were randomly selected for data collection, and the same 15 trees were followed in each survey. If there were fewer than 15 trees in a plot, any juvenile trees that reached a height of 125 cm tall during the 3-year period were included in the survey, to a maximum of 15 trees.

Tree size was recorded annually as the diameter at breast height (DBH) of each tree, and the DBH of each tree was categorized as 1–4.9, 5–14.9, 15–39.9, 40–74.9 cm, or greater than 75 cm. For some of the statistical analyses, the two smallest DBH categories were grouped into a ‘‘small diameter’’ category, and the three largest DBH categories were grouped into a ‘‘large diameter’’ category.

Data on the severity of pitch canker in each tree were collected on seven occasions over a period of 3 years: twice in 1996, 1997, and 1998, and once in 1999. For each tree, the number of tips symptomatic of pitch canker was counted, and the tree was then categorized as having 0, 1–10, or >10 symptomatic tips. Stem cankers on each tree were also counted, and then categorized as 0, 1–3, or >3. Data on tip and stem symptoms were combined to give each tree a disease severity rating, such that 1–10 tips counted as 1 point; over 10 tip infections counted as 2 points; 1–3 stem cankers counted as 1 point; and over 3 stem cankers counted as 2 points. Thus, the minimum ‘‘tree disease severity rating’’ was 0, and the maximum was 4. Trees that died due to pitch canker were given a severity rating of 4. Disease severity in each plot was calculated as a percentage of the maximum severity possible in the plot:

$$\text{plot severity}\ (\%) = \left(\frac{\sum_{i=0}^{n} R_i}{n \times 4}\right) 100$$

where R_i is the tree disease severity rating of the ith tree within the plot, and n is the total number of trees rated in each plot.

The percentage of canopy infected, as measured by estimating the percentage of branch tips that were symptomatic, was recorded during the spring 1999 survey. The categories were: 0, 1–10, 11–50%, or over 50% of the canopy infected. These data were used for comparison with the severity measurements detailed above.

The trees were also grouped into 1 of 4 crown height categories depending on how many quadrants contained foliage. Crown height (the distance from ground level to the base of the live crown) was expressed as a percentage of the total height of the tree. Trees with a crown height of 75% or more had foliage only in the top quarter (a mushroom-shaped tree) and were assigned to category 1, while a tree with a crown height of less than 25% had foliage in the lower quarter of its height (a Christmas tree shape) and was assigned to category 4.

In July 1998, precise plot locations were mapped with a global positioning system (GPS) with sub-meter accuracy (Trimble TDC-1). Because the unit was unable to locate the satellites under thick canopy cover, an optical laser unit (Laser Atlanta) was employed to give the GPS a computable offset from the closest trackable location. After 100% correction, data were exported as an ASCII file, amended, and imported as a vector layer into a geographic information systems (GIS) software package (Microimages TNTMips). Vector data layers and raster images were exported into Arcview GIS software for simple graphic layouts. The distribution of the plots on the Monterey peninsula is shown in Fig. 2.

Data from the plots divided into the landscape types are presented graphically. Hierarchical log–linear analyses (Zar, 1984) were used to test for associations between various site and disease factors on each survey date. Contrasts among levels within factors were carried out using *G*-tests (Sokal and Rohlf, 1981). For the "geographic" analyses, trees in the 20 coastal plots (as determined by their distribution and distance from the coast) were grouped separately from the trees in the 19 inland plots (Fig. 2). For many of the statistical analyses and graphical presentations, three urbanized landscape types (golf course, heavy urban, and light urban) were combined together as a "managed" category.

3. Results

When the survey plots were established (spring 1996), 10 plots had no pitch canker-infected trees,

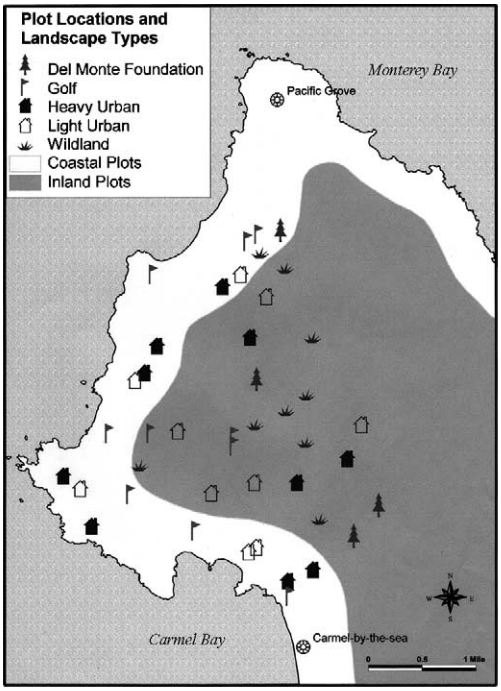

Fig. 2. Distribution of the plots for monitoring pitch canker disease progression in native Monterey pines on the Monterey peninsula, California, with reference to their landscape types and geographical locations.

but by the final survey (spring 1999) only 5 plots were free of pitch canker. Likewise, 29.9% ($n = 485$) of the trees had disease in the first survey, and 48.9% ($n = 438$) had disease by the spring 1999 survey. Overall, pitch canker severity in each plot increased during the 3 years of the survey (Fig. 3).

Three-way interactions between tree disease severity, geographical location, and either landscape type or management type, were not significant (log–linear analysis, $P > 0.05$). Two-way interactions between disease severity and each of the other variables were either significant throughout the study, or were significant in the later rounds of the survey (Table 1).

3.1. Trends with respect to landscape type and management

Disease severity increased in light urban, heavy urban and golf course plots during the 3 years of this study, but did not appear to increase in wildland plots (Fig. 4a). Four managed plots in spring 1996 did not

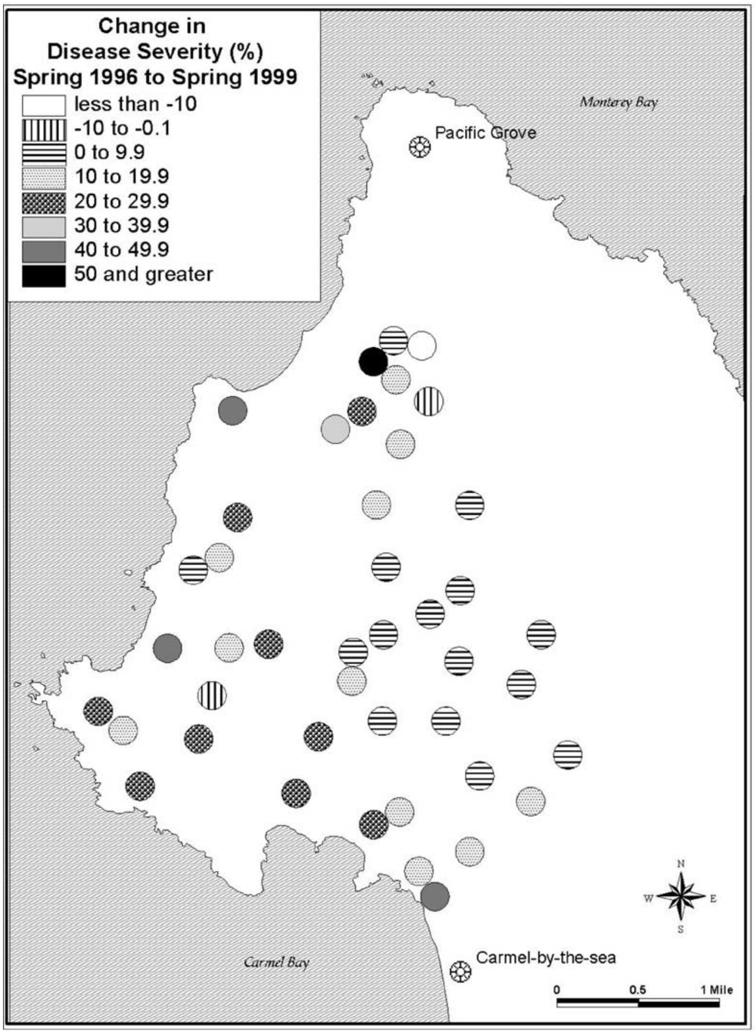

Fig. 3. Change in pitch canker disease severity in native Monterey pines in monitoring plots on the Monterey peninsula, California, from the first survey in spring 1996 to the last survey in spring 1999.

have any pitch canker symptomatic trees, but by spring 1999, all managed plots had at least one tree with pitch canker symptoms. In contrast, six wildland plots did not have any pitch canker-infected trees in the spring 1996 survey, and five were still pitch canker-free in the spring 1999 survey.

In Spring 1996, the percentage of disease-free trees in managed plots was significantly lower than in wildland plots (Table 2). Of the diseased trees, no significant differences were evident in the contrasts among disease severities. In Spring 1999, the percentage of disease-free trees in managed plots remained significantly lower than in wildland plots. Furthermore, in Spring 1999, of diseased trees, the percentage of trees in disease severity levels 2–4, was significantly higher in the managed plots compared with the wildland plots (Table 2).

The percentage of disease-free trees in wildland plots changed very little from the first survey (88.4%) to the last (86.7%); likewise the number of highly diseased trees remained nearly identical (Table 2). However, in the managed plots the percentage of trees

Table 1
Probability of interaction between pitch canker tree disease severity in native Monterey pine monitoring plots on the Monterey peninsula, California, geographical location[a], landscape type[b], and management type[c]

	P-value						
	Spring 1996	Fall 1996	Winter 1997	Summer 1997	Winter 1998	Summer 1998	Spring 1999
Landscape type × disease severity	n.s.	0.0303	n.s.	n.s.	0.0012	<0.0001	<0.0001
Geographical location × disease severity	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Management type × disease severity[d]	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Management type × disease severity[d]	n.s.	n.s.	n.s.	0.0047	<0.0001	<0.0001	<0.0001

n.s.: not significant; $P > 0.05$.
[a] Coastal vs. inland locations.
[b] Wildland, light urban, heavy urban, and golf.
[c] In this analysis, golf, heavy urban, and light urban plots were grouped together as managed plots, and compared to wildland plots.
[d] Inland plots only.

that were disease-free declined from 63.5 to 37.7% between the first and last surveys.

The percentage of trees that progressed from disease-free to diseased between 1996 and 1999 was 8.8% (10/114) in wildland plots, and this was significantly lower than the 46.9% (106/226) of trees in managed plots that made this progression ($G = 55.9$, $P < 0.001$). Furthermore, in wildland plots, only 7.7% of trees with low disease severity in the first survey had more severe disease in the final survey; this was significantly less than the 56.9% of trees in the managed plots that made this progression ($G = 12.98$, $P < 0.01$).

3.2. Trends with respect to geographical location

Throughout the study period, disease severity was greater in coastal locations compared with more inland locations (Fig. 5). Disease severity increased in both coastal and inland plots between 1996 and 1999 whether or not wildland plots are included in the data (Fig. 5a and b). Throughout the study, disease severity was dependent on geographical location (Table 1).

In both the first and last surveys, a significantly greater percentage of inland trees than coastal trees were disease-free (Fig. 6) (Table 3). In addition, of trees that had pitch canker, a significantly higher

Table 2
Contrasts among the percentages of trees in each pitch canker disease severity level during the first (spring 1996) and last (spring 1999) surveys of native Monterey pine monitoring plots on the Monterey peninsula, California, with respect to management type

Tree disease severity level	Spring 1996		Spring 1999	
	Wildland ($n = 129$) (%)	Managed[a] ($n = 356$) (%)	Wildland ($n = 120$) (%)	Managed[a] ($n = 318$) (%)
0	88.4	63.5	86.7	37.7
1	10.0	28.7	10.8	28.3
2	1.6	7.3	1.7	15.4
3	0.0	0.0	0.8	11.0
4	0.0	0.6	0.0	7.5
	Wildland/managed contrast			
0 vs. 1–4	$G = 31.47$ ($P < 0.01$)		$G = 90.8$ ($P < 0.001$)	
1 vs. 2–4	$G < 1$ (n.s.)		$G = 7.83$ ($P < 0.01$)	
2 vs. 3–4	$G < 1$ (n.s.)		$G < 1$ (n.s.)	
3 vs. 4	$G < 1$ (n.s.)		$G < 1$ (n.s.)	

n.s.: not significant; $P > 0.05$.
[a] Managed plots include the golf, heavy urban, and light urban landscape types.

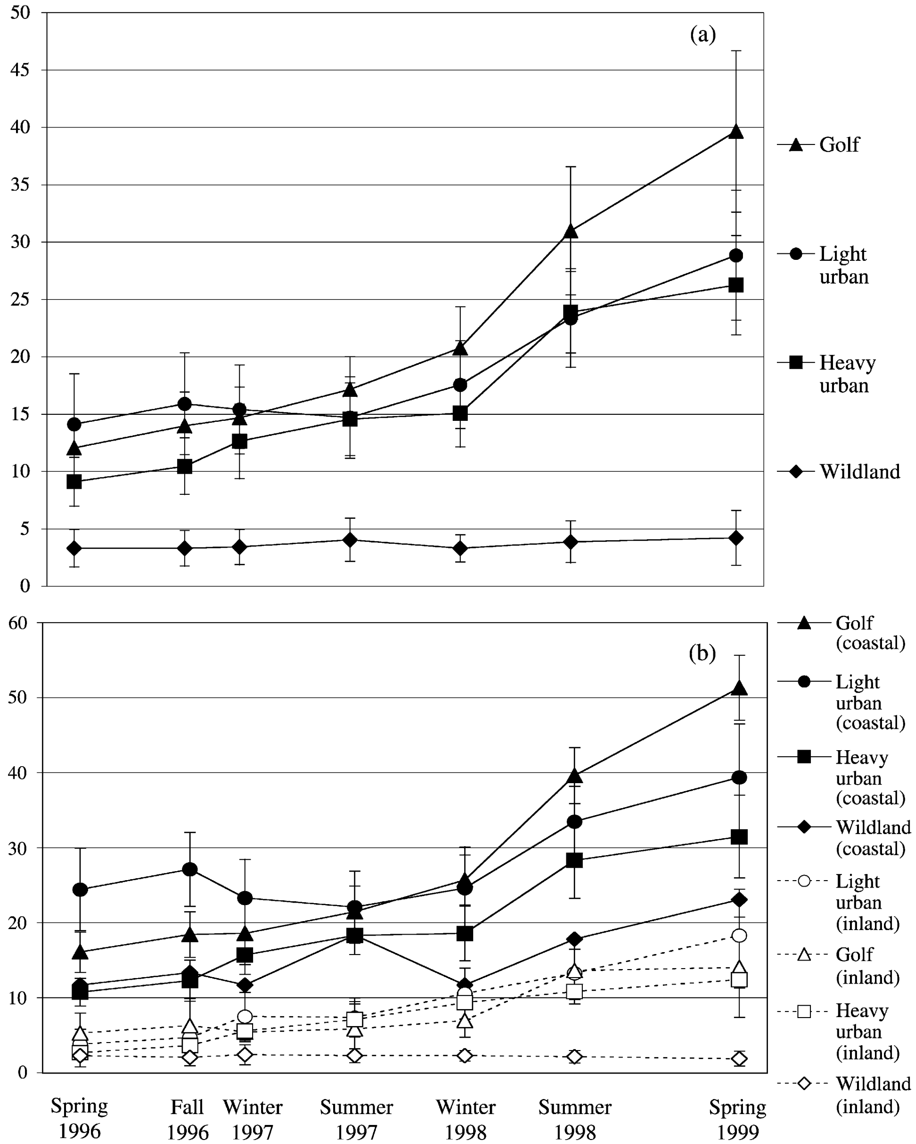

Fig. 4. Disease progress of pitch canker in native Monterey pines on the Monterey peninsula, California, over a 3-year period (a) with respect to landscape type (b) with respect to landscape type and geographic location. Error bars ± S.E.

percentage of coastal trees had high levels of disease severity, compared with inland trees on both survey dates (Table 3).

To ensure that the observed effect of higher disease severity in coastal plots compared to inland plots was not an artifact resulting from the fact that most wildland plots were inland and had less disease, and despite the fact that the three-way interaction between landscape type, geographical location and disease severity was not significant, a further analysis was carried out that excluded the wildland plots. This analysis showed that inland "managed" plots had lower levels of disease than coastal "managed" plots throughout the study (Table 4).

Furthermore, trees in all plots with a low level of disease at the first survey were more likely to increase

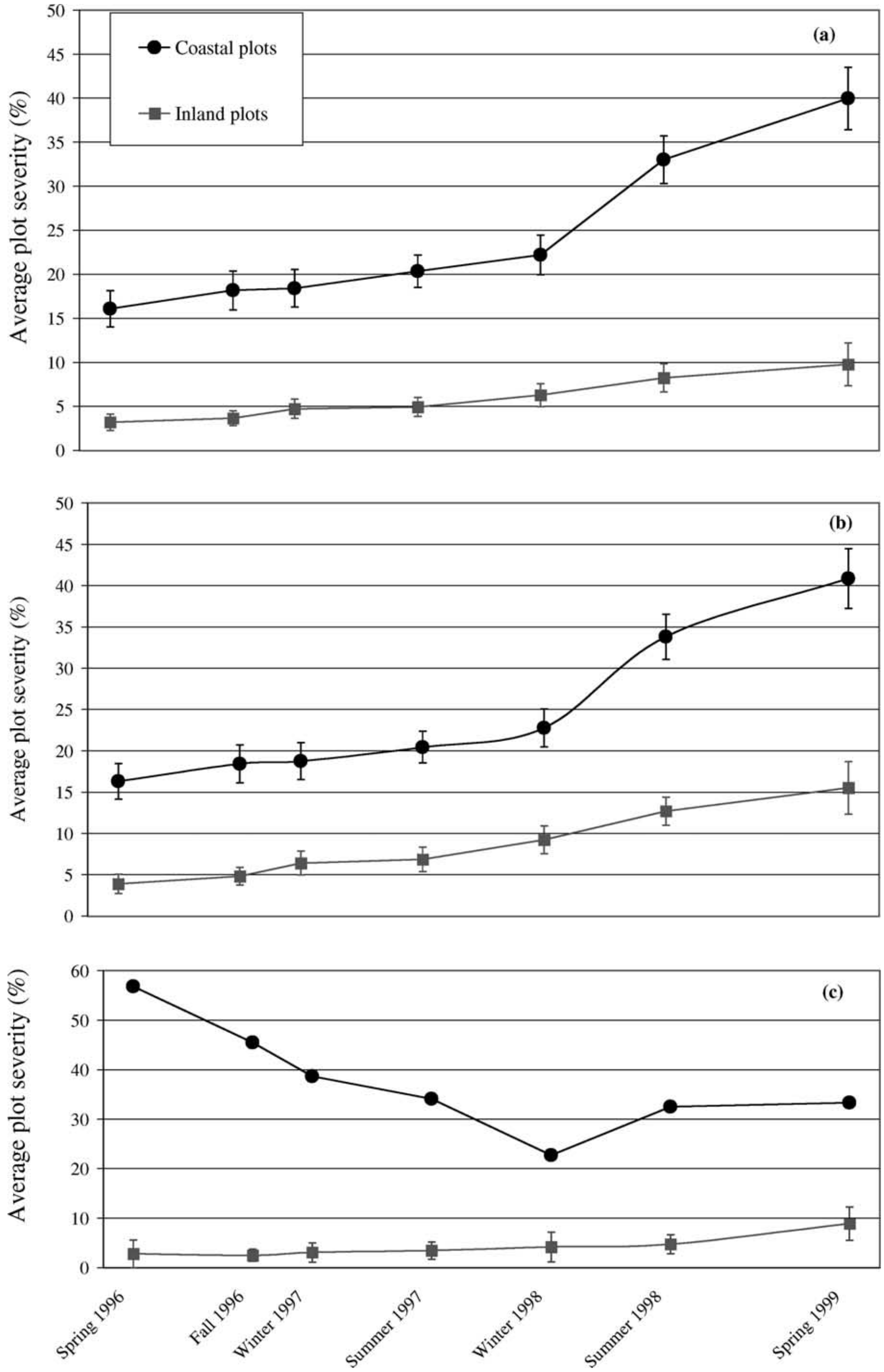

Fig. 5. Progress of pitch canker in native Monterey pines on the Monterey peninsula, California, with respect to geographic location (a) in all randomly selected plots (b) in managed plots only (c) in Del Monte Forest Foundation plots only. Error bars ± S.E.

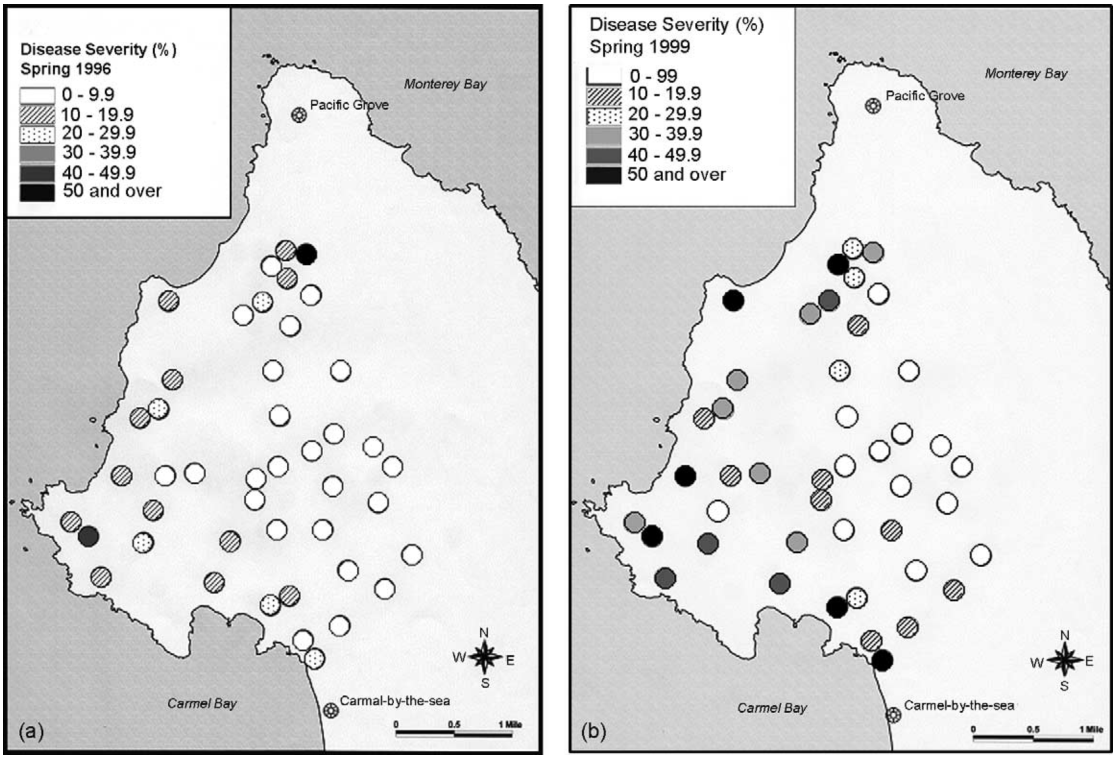

Fig. 6. Pitch canker disease severity in native Monterey pine monitoring plots on the Monterey peninsula, California (a) in the spring 1996 survey and (b) in the spring 1999 survey.

in severity by the final survey if they were in coastal plots, than if they were in inland plots. Of trees that were in the low disease category in spring 1996, 57.5% ($n = 87$) of those in coastal plots and 32.1% ($n = 28$) of those in inland plots had higher disease severities by the spring 1999 survey (G = 5.41, $P < 0.05$).

Table 3
Contrasts among the percentages of trees in each pitch canker disease severity level during the first (spring 1996) and last (spring 1999) surveys of the native Monterey pine monitoring plots on the Monterey peninsula, California, with respect to geographical location

Tree disease severity level	Spring 1996		Spring 1999	
	Inland ($n = 261$) (%)	Coastal ($n = 224$) (%)	Inland ($n = 249$) (%)	Coastal ($n = 189$) (%)
0	88.1	49.1	71.5	24.3
1	11.1	38.4	20.9	27.0
2	0.8	11.6	4.4	21.2
3	0.0	0.0	2.8	15.3
4	0.0	0.9	0.4	12.2
	Inland/coastal contrast			
0 vs. 1–4	$G = 90.6$ ($P < 0.01$)		$G = 99.2$ ($P < 0.001$)	
1 vs. 2–4	$G = 90.6$ ($P < 0.01$)		$G = 27.3$ ($P < 0.01$)	
2 vs. 3–4	$G < 1$ (n.s.)		$G = 1.3$ (n.s.)	
3 vs. 4	$G < 1$ (n.s.)		$G = 3.1$ (n.s.)	

n.s.: not significant; $P > 0.05$.

Table 4
Probability of association between pitch canker disease severity, geographical location[a], and landscape type[b] in native Monterey pine monitoring plots on the Monterey peninsula, California: managed plots only

	P-value						
	Spring 1996	Fall 1996	Winter 1997	Summer 1997	Winter 1998	Summer 1998	Spring 1999
Landscape × geography × disease severity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Landscape × disease severity	n.s.	0.0415	n.s.	n.s.	n.s.	n.s.	n.s.
Geography × disease severity	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

n.s.: not significant; $P > 0.05$.
[a] Inland versus coastal locations.
[b] Light urban, heavy urban, and golf.

Disease severity in the coastal Foundation plot appeared to decrease during this study, while disease severity remained fairly constant in the three inland Foundation plots (Fig. 5c). Tree disease severities in the coastal plot were significantly higher than in the three inland plots, at all survey dates except winter 1998 (log–linear analysis, $P = 0.003$).

3.3. Size factors

The three-way interaction between DBH category, management type, and tree disease severity was not significant (log–linear analysis). There was a significant interaction between DBH and tree disease severity ($P < 0.01$), and, with the exception of spring 1996, DBH was not significantly associated with management type. A greater percentage of trees in the smaller size class (<15 cm DBH) were free of pitch canker (69.8%) compared with trees in the larger (>15 cm DBH) size class (45.6%) (Table 5). Of trees in the two most severe disease categories, trees in the large size class were significantly more likely to be in the most severe disease severity category than were trees in the small size class.

Table 5
Percentage of trees in each pitch canker disease severity category with respect to DBH class in native Monterey pine monitoring plots on the Monterey peninsula, California (spring 1999)

Tree disease severity level	1–14.9 cm ($n = 106$) (%)	15 cm and over ($n = 329$) (%)
0	69.8	45.6
1	15.1	26.1
2	6.6	13.4
3	8.5	8.2
4	0.0	6.7
	DBH contrast	
0 vs. 1–4	$G = 19.2$ ($P < 0.01$)	
1 vs. 2–4	$G \leq 1$ (n.s.)	
2 vs. 3–4	$G \leq 1$ (n.s.)	
3 vs. 4	$G = 6.7$ ($P < 0.01$)	

n.s.: not significant; $P > 0.05$.

There was no significant difference in the percentage of trees in the small (<15 cm) size class between coastal (35.8%) and inland (45.1%) plots ($G = 2.8$, $P > 0.05$). Within the larger (>15 cm) size class, a significantly greater percentage of the trees were over 40 cm diameter in the coastal (67.8%) than in the inland (41.3%) plots ($G = 27.0$, $P < 0.001$).

3.4. Crown height

There was a significant interaction between tree disease severity and crown height ($P < 0.0001$). Trees with smaller crown heights had higher ratings of disease severity (Fig. 7), and contrasts between tree disease severity level and crown height confirm that trees with larger crown heights (categories 1 and 2) were less likely to have disease (59.1%; $n = 237$) than trees with smaller crown heights (categories 3 and 4) (42.2%; $n = 199$), ($G = 12.30$; $P < 0.0005$). Furthermore, trees with small crown heights were significantly more likely to have severe levels of disease (21.61%; $n = 199$) than trees with larger crown heights (6.33%; $n = 237$) ($G = 22.17$; $P < 0.0005$). A significant three-way interaction between crown height category, landscape type (or management type), and geographical location indicates that trends

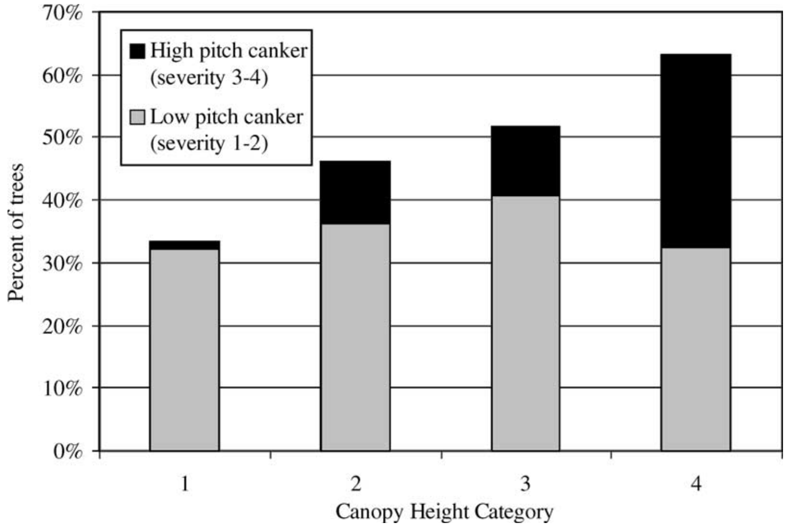

Fig. 7. Pitch canker disease severity in native Monterey pine monitoring plots on the Monterey peninsula, California, with respect to canopy height.

between the pair-wise grouping of these factors are not consistent enough to confirm their significance.

3.5. Tree mortality

Though many trees died over the course of the survey, most were lost during winter storms or to removal of trees in the urbanized landscapes. Only three trees appeared to have died as a direct result of pitch canker infection. Each of these three trees died between the last two surveys: one in a light urban plot and the other two in golf course plots.

4. Discussion

Pitch canker is an epidemic in the native population of Monterey pine where this survey was conducted. As illustrated by the disease progress graphs, the disease increased rapidly in many locations over the 3-year period of this study. Though many trees had very high levels of disease, including multiple stem cankers, only three trees died during the survey as a result of pitch canker. To better assess the ultimate impact of pitch canker on the viability of the species, it will be necessary to follow the course of the severely infected trees into the future, to determine the impact on their longevity. Based on a survey of the progress of pitch canker in coastal and inland, urban Monterey pines in California we expect that severely infected trees are more likely to die, or be removed, than trees that are disease-free (Storer et al., 2002).

The data presented here indicate that the severity of pitch canker is associated with both landscape type and geographic factors. The three managed landscapes (golf, urban, and heavy urban) had higher levels of disease than the wildland plots, independently of geographical location. And the coastal locations had higher levels of disease than the inland locations, independently of landscape type. However, a long-term study will be necessary to determine if the incidence of pitch canker in the low disease locations remained low simply due to an initially lower inoculum load.

In this study, only a single wildland plot fell into the coastal category. However, when only inland plots were compared, wildland plots still had less disease than managed plots in the final four surveys, indicating that the difference in disease level between landscape types was not solely attributable to geographic location. Given the high incidence of pitch canker in plantation settings, including nurseries around the world, and its comparatively rare occurrence in natural landscapes, it is not surprising that the disease was less severe in the wildland locations than the urbanized (managed) forests. The trend of disease progression appeared similar in the light urban and the more intensely managed plots (heavy urban and golf). Therefore, fertilization and irrigation in close proximity to the trees appear unlikely to explain the observed pattern. Furthermore, the majority of the trees in the urbanized forest arose from natural regeneration of the native population. Thus, a chance association of susceptibility with a restricted gene pool in the urbanized forest probably does not explain the difference. It is possible that higher levels of disease in managed landscape types compared to the wildland stands are due to human activities that intensify the movement of inoculum into and within the managed forest. Additionally, the apparent resilience of the wildland forest to the progression of pitch canker, when compared to the urban forest, may be related to biotic interactions in the natural stands that are altered in the managed stands.

Many differences between the coastal and inland locations may influence disease severity and rate of spread. Though the maximum distance between coastal and inland plots is only 4.8 km (Fig. 2), micro-climate variation on this scale could influence the success of the fungus in colonizing its host. For example, the reduced evaporative demand associated with longer periods of intense fog in the coastal zone may increase the efficiency of the infection process. The difference in disease between inland and coastal locations may also be due to geographic differences in the abundance of insects that vector the disease. Thus, the rate at which pitch canker develops could be directly related to the distribution of the most efficient vectors and/or wounding agents. For example, the spittlebug, *A. canadensis*, appears to be more common in coastal areas than farther inland (unpublished observations, 1996–1999). Thus, the association of spittlebug induced wounds with shoot tip infections (Storer et al., 1998), may contribute to greater disease severity near the coast.

In assessing the effects of various factors on pitch canker, tree disease severity was used in order to include the occurrence of stem cankers, which are associated with tree mortality (Storer et al., 2002). Because smaller trees tend to have fewer total branches, the rating system may have created a slight bias for smaller trees to have lower infection ratings. However, the "percent canopy infected" categorization, a less size-biased indicator, was highly associated to tree severity rating ($P < 0.0001$). Furthermore, though DBH category was significantly associated with tree disease severity rating, a large portion of the association arose from the higher proportion of small diameter versus large diameter uninfected trees. However, a bias was detected in the percentage of small diameter trees versus large diameter trees in the highest severity level. When tree disease severity rating was used for the comparison, a significantly larger percentage of large diameter trees were in the highest category, but when percent canopy infected was analyzed against DBH category, there was no significant difference. But, this was only a small difference among a few trees, and it is unlikely that it influenced our analyses. In addition, because there were no significant trends in DBH category with respect to management type or geographic location, this finding does not influence the interpretation of the results with respect to those factors.

5. Conclusion

The most significant finding of this survey was the influence of landscape type and location on the severity of pitch canker on the Monterey peninsula. The location effect may be due to weather differences. Greater insight into this possibility could be gained by collecting data on temperature extremes and duration of fog cover, to determine if disease severity is greater in areas where trees are exposed to conditions that are more conducive to infection. If such data are consistent with a limiting effect of the ambient environment, studies under controlled conditions could be conducted to confirm this correlation. Additionally, a survey of the distribution and abundance of the insect vectors in areas of differential disease development would be a useful complement to the present study.

The factors responsible for the effect of landscape type on disease severity may prove to be more elusive. However, if the trend remains in place, it should receive consideration in the context of disease management, even in the absence of a mechanistic explanation. In particular, the open spaces that serve to preserve remnants of the native forest (corresponding to plots in the light urban category) may not offer the same degree of refuge from pitch canker as wildland forests. Therefore, it may be more productive to maintain fewer large, contiguous tracks of native forest, rather than the equivalent area divided among numerous fragmented parcels of 16 acres or less.

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