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Forest Ecology and Management 200 (2004) 67–76
Forest Ecology and Management
www.elsevier.com/locate/foreco

Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions

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Received 3 December 2003; received in revised form 29 May 2004; accepted 8 June 2004

Abstract

Four years of severe drought from 1999 through 2003 led to unprecedented bark beetle activity in ponderosa and Jeffrey pine in the San Bernardino and San Jacinto Mountains of southern California. Pines in the San Bernardino Mountains also were heavily impacted by ozone and nitrogenous pollutants originating from urban and agricultural areas in the Los Angeles basin. We studied bark beetle activity and bark beetle associated tree mortality in pines at two drought-impacted sites in the San Bernardino Mountains, one receiving high levels of atmospheric pollutants, and one with more moderate atmospheric input. We also investigated the effects of nitrogen addition treatments of 0, 50 and 150 kg N ha^{-1} $year^{-1}$ at each site. Tree mortality and beetle activity were significantly higher at the high pollution site. Differences in beetle activity between sites were significantly associated with ozone injury to pines, while differences in tree mortality between sites were significantly associated with both ozone injury and fertilization level. Tree mortality was 9% higher and beetle activity 50% higher for unfertilized trees at the high pollution site compared to the low pollution site. Tree mortality increased 8% and beetle activity increased 20% under the highest rates of nitrogen additions at the low pollution site. The strong response in beetle activity to nitrogen additions at the low pollution site suggests that atmospheric nitrogen deposition increased tree susceptibility to beetle attack at the high deposition site. While drought conditions throughout the region were a major factor in decreased tree resistance, it appears that both ozone exposure and atmospheric nitrogen deposition further increased pine susceptibility to beetle attack.

Keywords: Nitrogen deposition; Ozone; Ponderosa pine; Jeffrey pine; Western pine beetle; Mountain pine beetle; San Bernardino Mountains; Mixed conifer forest

1. Introduction

In a healthy forest, the distribution of bark beetles and pathogenic fungi is typically limited to a few stressed trees. Bark beetle activity on weakened trees results in scattered tree death which can increase habitat complexity for wildlife, reduce tree crowding, create canopy openings and promote plant diversity. However, stresses such as drought and air pollution can contribute to reduced tree resistance to beetle attack, and many trees in a stand could be affected. Consequently, many trees may become susceptible to beetle colonization and large-scale tree mortality could be an outcome. Such outbreaks can increase

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2004.06.003

fire severity and erosion, potentially threatening human communities and development, as well as affecting timber production in forests. Drought stress has frequently been reported as a major factor that contributes to susceptibility to beetle attack (Vité, 1961; Ferrell, 1978; Page, 1981; Paine and Baker, 1993). Drought stress may predispose trees to bark beetles by decreasing resin production or changing resin content (Vité, 1961; Lorio and Hodges, 1968, 1977; Hodges and Lorio, 1975).

Air pollution has been implicated in beetle outbreaks in forests exposed to emissions high in sulfur dioxide (Scheffer and Hedgcock, 1955; Führer, 1985; Skuhravy and Srot, 1991; Kula, 1992; Grodzki, 1997), and also for heavy metal deposition (Heliövaara and Väisänen, 1991; Soltes, 1996). Photochemical air pollution was first recognized as a possible factor for increasing beetle susceptibility in the 1960s in the San Bernardino Mountains of southern California. Ponderosa pine (*Pinus ponderosa* Laws.) trees showing greater oxidant injury were more frequently infested by western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*D. ponderosae* Hopkins) (Stark et al., 1968). Ozone damaged trees had several characteristics that were associated with increased bark beetle susceptibility, including lower resin flow rates, lower resin exudation pressure and an increased rate of resin crystallization (Stark and Cobb, 1969). Ozone and nitrogen deposition are considered the most important pollutants affecting North American forests (Taylor et al., 1994). Both ozone exposure and nitrogen deposition may potentially alter the susceptibility of trees to bark beetles. Currently, however, the effects of ozone on bark beetle success are better studied than the effects of nitrogen pollution.

Ozone exposure changes patterns of carbohydrate allocation in many plants, including conifers, in ways that may make plants more suitable for insect herbivores. Shoot growth is favored over root growth and carbohydrates allocated to storage decrease, while soluble sugars and free amino acids increase aboveground (Cooley and Manning, 1987; Andersen et al., 1991; Gorissen et al., 1991; Kainulainen et al., 1994). Ozone may affect not only tree susceptibility to beetle attack, but also beetle performance. Dahlsten et al. (1997) found higher fecundity in western pine beetle attacking oxidant-damaged trees compared to healthy ponderosa pine, especially for the first generation of beetles. Beetle predators and parasitoids also occurred in higher densities on healthy trees.

Nitrogen inputs often increases the susceptibility of vegetation to attack by insects or pathogens (Skeffington and Wilson, 1988; Waring and Cobb, 1992). Increased deposition of atmospheric nitrogen can act as a fertilizer, stimulating forest growth and increasing plant nitrogen content (Skeffington and Wilson, 1988; Powers and Reynolds, 1999; Canary et al., 2000). Alternatively, fertilization may increase resin content in pines (Kyto et al., 1996), which may be detrimental to bark beetles.

The San Bernardino Mountains are located northeast of Los Angeles, approximately 90 km from the Pacific Ocean (34°15′N, 117°W). Atmospheric pollutants, particularly nitrogen pollutants and ozone are transported inland from urban and agricultural areas, along the western slopes of the San Bernardino Mountains by prevailing weather patterns (Miller, 1992). The mixed conifer forest of the San Bernardino Mountains has been impacted by air pollution arising from the Los Angeles basin for more than five decades (Takemoto et al., 2001).

In the San Bernardino Mountains, ponderosa pine have been strongly affected by both ozone exposure and nitrogen deposition. Ponderosa pine is among the most susceptible plant species to ozone injury in the San Bernardino Mountains, and many have already died due to a combination of stresses, including oxidant injury, bark beetle attacks and disease (Pronos et al., 1999). Pine trees from highly polluted western areas of the mountain range had greater symptoms associated with ozone injury, including decreased radial growth (Miller, 1992), reduced fine root mass and belowground allocation of carbohydrates (Grulke et al., 1998), chlorotic mottling of needles and reduced needle retention (Miller, 1973; Miller and Rechel, 1999). Both ozone and nitrogen deposition decreased needle retention in pines (Grulke and Balduman, 1999). High nitrogen deposition has increased needle nitrogen content (Fenn et al., 1996) and offset some growth reductions and foliar injury associated with ozone exposure (Grulke and Balduman, 1999).

Decades of fire suppression have increased stand density in the San Bernardino Mountains (Minnich et al., 1995) and exacerbated the effects of drought stress on pines (Savage, 1994). In 2003, several years of drought left pines throughout the San Bernardino

Mountains susceptible to bark beetle attack, including pines that were part of a long-term nitrogen addition study. Annual precipitation was below half-normal for 4 years beginning in the winter of 1999–2000. Rainfall for 2001–2002 was the lowest ever recorded for the San Bernardino Mountains (California Department of Water Resources, public information). Drought conditions continued through winter 2002–2003, although precipitation in April 2003 brought annual rainfall for 2002–2003 to 75% of normal. Consequently, bark beetle populations have increased dramatically, with some areas experiencing between 30 and 100% tree mortality. Ponderosa pine killed by western pine beetle were observed throughout the San Bernardino Mountains (personal observation). Background levels of tree mortality due to scolytid beetle activity are less than 1% throughout western forests (Keen, 1952). The goal of this study was to use this unprecedented level of bark beetle activity to revisit the interaction of stress and bark beetle activity in the same areas evaluated in pioneering studies 40 years ago. We examined the interactions of ozone injury and nitrogen additions with drought stress on tree susceptibility to bark beetle attack. Previous research has shown that oxidant injury was associated with increased beetle activity in pine in the San Bernardino Mountains (Stark et al., 1968), but the role nitrogen pollutants may play has not been examined previously.

2. Methods

Long-term fertilization plots were established by the USDA Forest Service Pacific Southwest Research Station Forest Fire Laboratory in 1996 at two locations in the mixed conifer zone of the San Bernardino Mountains (San Bernarindo County, CA) along a west/east gradient for ozone and nitrogen deposition (Fenn and Poth, 2001). One site, Camp Paivika (CP), is near the town of Crestline and the other site, Camp Osceola (CAO), is in the Barton Flats area. The western-most site at CP has been impacted by high concentrations of ozone and high levels of nitrogen deposition while the more eastern site at CAO has received relatively low input from atmospheric ozone and nitrogen (Table 1). Historically, ozone concentrations decreased by 50% between CP and CAO. In the late 1970s 24 h average ozone concentrations were 235 μg m^{-3} at the high pollution site and 118 μg m^{-3} at the low pollution site (Miller et al., 1986). Although differences in atmospheric ozone exposure between the two sites have decreased in recent years, the difference in exposure still produced significant differences in ozone impact to pines (Fig. 1). Compared to the high pollution site, the site at low pollution site is 300 m higher in elevation and winter temperatures at the low pollution site are slightly lower resulting in a slower snow melt so that a greater proportion of precipitation at the low pollution site may come from snow. However, both sites were strongly affected by drought (California Department of Water Resources, public information).

Table 1
Site comparison for CAO and CP

	CAO	CP
Atmospheric pollution exposure	High	Low
Elevation (m)	1900	1600
Average annual precipitation (mm)[a]	534	994
Average annual temperature (°C)[a]	10.6	12.9
Ozone (ppb)[b]		
Summertime 24 h hourly average	60.9	67.5
Summertime average peak values	91.3	101.6
Nitrogen deposition as throughfall (kg N ha^{-1} $year^{-1}$)[c]		
Under tree canopy	18.0	193.9
Integrated stand total	8.3	81.6

[a] Annual precipitation and temperature were calculated from data obtained from the San Bernardino County Water Resources Division. Additional precipitation data was obtained from Fenn and Poth (1999). Yearly precipitation was recorded from October of the year listed through September of the following year. Precipitation data covered 1956–1993 for CP and 1975, 1977–1979 and 1991–1998 for CAO. Temperature data spanned 1992–1997 for CAO and 1956–1991 for CP.

[b] Summer ozone concentrations were obtained from continuous ozone monitors at Crestline (California Air Resources Board, public information) and Barton Flats (Atmospheric Deposition Group, USDA PSW Research Station) for June–September 2002. Summertime average ozone concentrations were determined from daily 24 h averages while the summer peak concentration was the average of peak hourly concentrations for each day.

[c] Nitrogen deposition data were obtained from bulk ion exchange throughfall collectors under pines and in forest openings (Fenn et al., 2002). Tree canopy deposition was the rate of nitrogen deposition under pine canopies. Stand total deposition was integrated from data for canopy deposition and deposition to open areas. Yearly average deposition was determined from deposition rates from July 2000 to November 2002 (M.E. Fenn, unpublished data).

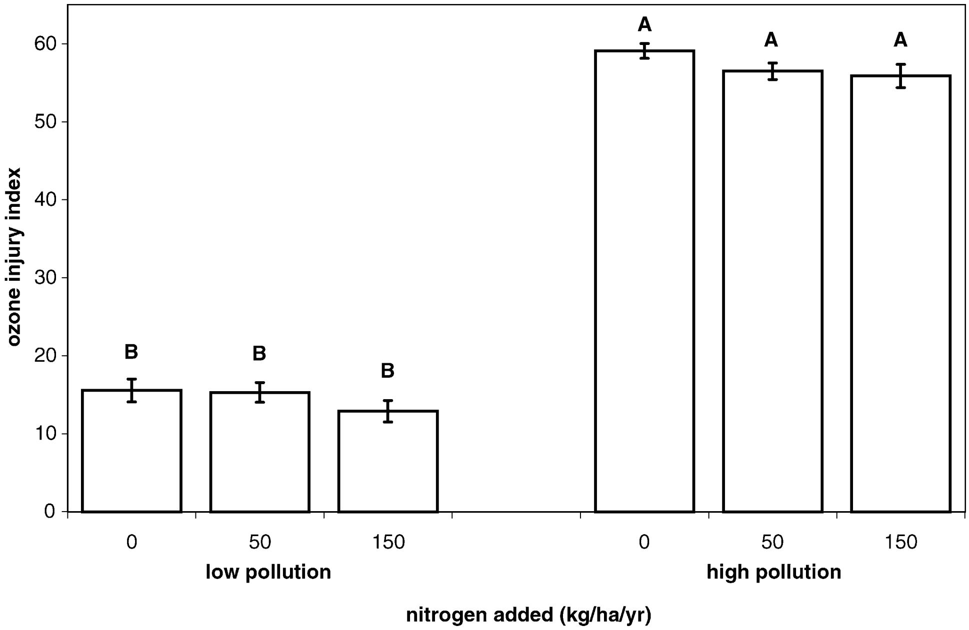

Fig. 1. Ozone injury index for pines at low and high pollution sites. Ozone injury was assessed in 1997, 7–9 months after the first nitrogen addition treatment. The ozone injury index incorporates an assessment of needle chlorotic mottle, the number of annual whorls retained, needle length and the percent live crown for each tree (Miller et al., 1996). The index ranges from 0 (no injury) to 100 (maximum injury). Bars with different letters are significantly different at $P = 0.05$.

The sites are located in the mixed conifer zone of the San Bernardino Mountains. The dominant overstory species at the high pollution site are ponderosa pine, California black oak (*Quercus kellogii* Newb.) and incense cedar (*Calocedrus decurrens* (Torr.) Florin.) with a minor component of sugar pine (*Pinus lambertiana* Dougl.). Bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) forms a dense understory in many locations. The overstory at the low pollution site is dominated by ponderosa pine and the closely related Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.), California black oak and white fir (*Abies concolor* Gord. and Glend.). The parent material of soils in both areas is partially weathered or decomposed granite. The litter layer is generally denser at the high pollution site than at the low pollution site.

Nine study plots were established at each location. Within each of these plots approximately 20 dominant or codominant pine, with low levels of disease and insect damage were selected for study. Ponderosa pine was used at the high pollution site and a mixture of 55% ponderosa pine and 45% Jeffrey pine was used at the low pollution site. The selected trees within plots were fertilized with Nitroform® (BFC Chemicals, Wilmington, Delaware) slow-release fertilizer (38–0–0). This is a granular ureaformaldehyde fertilizer designed for dry application. Fertilizer was applied with a hand held spreader around each individual tree to a distance of a 4 m beyond the canopy drip line of each tree. At each site, fertilizer was applied to trees at a rate equivalent to 150 kg N ha^{-1} $year^{-1}$ on three plots, three plots at rate of 50 kg N ha^{-1} $year^{-1}$ and three plots were left as unfertilized controls, giving a total of at least 60 trees at each nitrogen addition level at each site. Nitrogen fertilization treatments at these sites began in the fall of 1996 and treatments continued annually through 2002 for a total of six fertilizer applications.

Ozone injury and tree growth rates were assessed before the period of heavy beetle attack. Ozone injury to foliage on pine was assessed for each site in 1997 during September, when ozone injury expression is at a peak (Miller et al., 1996). Tree diameter at breast height (dbh) was determined for all trees in 1997, 1999 and 2001. Yearly mean incremental growth rates were calculated for each tree based on 5 years of growth.

Differences in ozone injury and growth rate among sites and fertilization levels were tested using ANOVA and Fisher's LSD at $\alpha = 0.05$ using SAS (2001).

In the spring of 2003, all trees were assessed for bark beetle activity and tree mortality. Trees in both study areas showed classic patterns of attack by western pine beetle. Beetle galleries at the base of trees were examined in a subset of trees, and were characteristic of western pine beetle. In addition, western pine beetle adults were observed actively attacking trees. Tree mortality for all trees was scored as living or dead. All dead trees surveyed showed signs of beetle activity. In addition, living trees with visible pitch tubes, boring dust and/or emergence holes also were scored as having beetle activity.

We used a *G*-test (Sokal and Rohlf, 1981) to see if mortality or beetle activity differed among fertilization treatments. Tests for the association of beetle activity and nitrogen additions were performed with counts of living trees only and also with counts of all trees, scoring both dead and living trees with beetle activity as having beetle activity. We used stepwise logistic regression (SAS, 2001) to assess the strength of the association of tree growth rate, nitrogen addition level and oxidant injury to tree mortality and frequency of beetle activity. For logistic regression both living and dead trees with beetle activity were counted as having beetle activity. Significant effects were evaluated at $\alpha = 0.05$.

3. Results

Foliar ozone injury was significantly higher at the high pollution site than at the low pollution site. There were no differences in ozone injury among nitrogen addition levels at either site in 1997, seven to nine months after the first nitrogen addition treatment (Fig. 1). Trees at the high pollution site had higher radial growth rates than trees at the low pollution site (Fig. 2). Tree growth rates were not significantly different among nitrogen addition levels at the low pollution site. Trees at intermediate level and high levels of nitrogen addition had significantly higher growth rates than control trees at the high pollution site.

Frequency of both tree mortality and beetle activity was higher at the high pollution site than at the low pollution site for all levels of nitrogen addition (adjusted G statistic (P) for site comparisons: mortality = 17.1 (<0.01), living trees with beetle

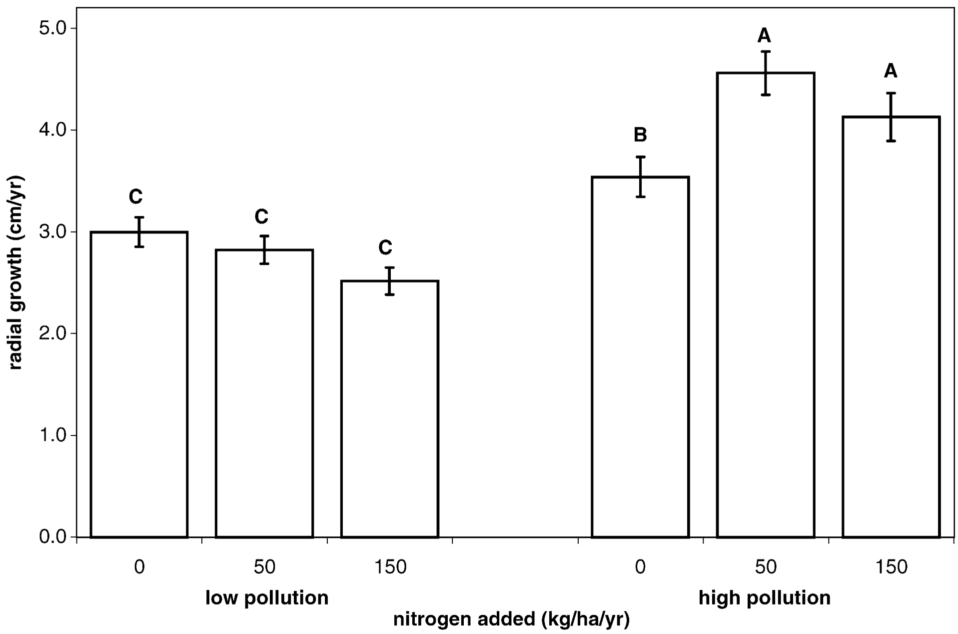

Fig. 2. Radial growth rate (cm/year at breast height) of pines at low and high pollution sites. Radial growth rates were based on measurements obtained from 1997 to 2001. Bars with different letters are significantly different at $P = 0.05$.

Table 2
Frequency of tree mortality and beetle activity at low and high pollution sites

Site	Nitrogen added (kg ha^{-1} year^{-1})	Number of trees	Percentage of dead trees	Percentage of living trees with activity	Total percentage affected by beetles
Low pollution	0	65	0	1.5	1.5
	50	61	1.6	1.7	3.3
	150	62	8.1	15.8	22.6
Adjusted G			7.36*	12.09**	19.19**
High pollution	0	62	9.5	50.9	55.6
	50	60	16.7	16.0	30.0
	150	62	19.4	24.0	38.7
Adjusted G			2.59	16.85**	8.53*

The G-test was used to examine if rates of tree mortality and beetle activity were significantly different among sites and fertilization treatments.

* Frequency of tree mortality and beetle activity within each site was significantly associated with fertilization level at $P < 0.05$.

** Frequency of tree mortality and beetle activity within each site was significantly associated with fertilization level at $P < 0.01$.

activity = 38.3 (<0.01), total trees affected by beetles = 55.6 (<0.01)). Tree mortality increased significantly with increased nitrogen additions at the low pollution site (Table 2). Tree mortality also tended to be higher among fertilized trees at the high pollution site, but this difference was not significant. Beetle activity, for all trees, living and dead, and for living trees only was significantly associated with nitrogen addition levels both at the low pollution site and the high pollution site. At the low pollution site, increased beetle activity, like tree mortality, was associated with higher levels of nitrogen addition. Trees at the high pollution site showed the opposite trend, where trees from control plots had the highest beetle activity.

Stepwise logistic regression indicated differences in tree mortality for both sites combined were significantly associated with increased ozone injury and fertilization level (Table 3). At the low pollution site, trees included a mix of Jeffrey and ponderosa pine. However, neither tree mortality nor beetle activity were affected by tree species ($P = 0.95$). Frequency of beetle activity for both sites combined was significantly associated with ozone injury, which was higher at the high pollution site than the high pollution site. Fertilization showed a significant relationship with tree mortality and beetle activity for trees at the low pollution site. Among the high pollution site trees, tree mortality was not associated with fertilization level, ozone injury or tree growth rates. Increased frequency of beetle activity at the high pollution site was positively associated with ozone injury and negatively associated with tree growth rate.

Table 3
Model statistics for stepwise logistic regression testing the effect of foliar ozone injury, tree growth rate and nitrogen additions on tree mortality and beetle activity within trees

	Model	Parameter	Wald's χ^2	P
Tree mortality	Overall	Ozone injury	10.77	0.001
		Fertilization	6.63	0.01
	Within sites			
	CAO	Fertilization	4.55	0.03
	CP	None		
Beetle activity	Overall	Ozone injury	33.08	<0.001
	Within sites			
	CAO	Fertilization	12.16	<0.001
	CP	Growth	8.28	0.004
		Ozone injury	4.47	0.03

The overall model tested for effects associated with beetle activity and tree mortality for both sites combined, while within sites models tested for effects associated with beetle activity and tree mortality within each site.

4. Discussion

Many studies have shown a correlation between air pollution and patterns of outbreaks in forest insects (e.g. Führer, 1985). Increased susceptibility of ponderosa pine to western pine beetle and mountain pine beetle has been associated with ozone exposure in the San Bernardino Mountains (Stark et al., 1968; Cobb and Stark, 1970). In the 1960s, researchers working at similar plots in the San Bernardino Mountains found that oxidant injury was associated with traits in pine that increased susceptibility to beetle attack, including resin flow and exudation pressure (Cobb et al., 1968; Stark and Cobb, 1969). Forty years later in 2003, we continue to see a strong association between ozone injury and beetle attack. We also found a strong association between nitrogen additions and tree mortality due to bark beetles.

Although ozone injury was strongly associated with differences in tree mortality and beetle activity between sites, it was not associated with patterns of mortality within each site. This is counter to what was expected based on studies in the San Bernardino Mountains in the 1960s, particularly at the high pollution site where ozone injury to ponderosa pine is high (Stark et al., 1968). However, Stark et al. (1968) compared classes of trees selected on the basis of the severity of ozone injury while pines in this study were selected without regard to ozone injury. Both studies compared trees within similar age classes. In addition, Stark et al. (1968) observed the greatest frequency of beetle attacks in trees with the most severe ozone injury. Many of the most ozone sensitive pine have subsequently died (Pronos et al., 1999). The effects of nitrogen deposition may also have played a role in diminishing the link between ozone injury and pine susceptibility to beetle attacks. High nitrogen deposition has offset some aboveground growth reductions associated with ozone exposure (Grulke and Balduman, 1999).

We found that pines with the highest rates of nitrogen addition tended to have higher mortality (Table 2). The difference in tree mortality between control trees and trees at the highest rate of fertilization was similar for both sites (8% at the low pollution site and 10% at the high pollution site) but the association between nitrogen additions and tree mortality was only significant at the low pollution site (Table 2), possibly due to the already high soil nitrogen status at the high pollution site (Fenn et al., 1996). Nitrogen deposition could increase tree susceptibility to bark beetle attack, either through decreasing plant resistance to other pests and pathogens, or by altering plant growth characteristics and nutrient quality (Skeffington and Wilson, 1988; Herms and Mattson, 1992; Waring and Cobb, 1992). The high surface area of pine canopies leads to high levels of atmospheric deposition in dry and wet forms, including deposition from fog, resulting in elevated throughfall fluxes of nitrogen under the canopies (Fenn et al., 2000, 2002). Nitric acid can also directly damage cuticular surfaces and increase plant susceptibility to pests or pathogens (Bytnerowicz et al., 2001).

Beetle activity increased with nitrogen additions at the low pollution site, but showed the opposite pattern at the high pollution site. Beetle activity was much higher in unfertilized trees at the high pollution site. All trees at the high pollution site have considerable atmospheric inputs of nitrogen. The forest floor under pine trees at the high pollution site is reported to receive as much as 194 kg N ha^{-1} $year^{-1}$ in throughfall (Table 1). This exceeded the highest rate of nitrogen additions for fertilized trees at the low pollution site which, combined with atmospheric deposition, were not likely to receive more than 168 kg N ha^{-1} $year^{-1}$. It is likely that nitrogen is frequently already available in excess of biotic demand for all trees at the high pollution site, and therefore, added nitrogen had little further effect on tree mortality. But at the low pollution site, where atmospheric inputs of nitrogen are much lower, additional nitrogen inputs were significantly associated with increased tree mortality and beetle activity. During spring 2003, many control trees at the high pollution site were heavily attacked by western pine beetle. We expect that if drought stress and beetle attacks continue, many more trees at the high pollution site will die and mortality will reach similar levels among all fertilization treatments. While nitrogen additions clearly had an effect on beetle activity at the low pollution site atmospheric nitrogen inputs are high enough at the high pollution site that further nitrogen additions, at most, only contributed to a faster mortality rate for trees already succumbing to the combined stress from drought and beetle attacks.

Lower tree growth has been shown to be correlated with reduced resistance to bark beetles to some degree (Waring, 1983). However, growth effects may be most apparent when comparing among whole stands, where increased tree diameter is associated with increased tree age. Aging trees had a slower metabolism and a slower rate of wound healing which may reduce tree resistance to insects and pathogens (Kozlowski, 1971). Alternatively, growth may be decreased by ozone. Cobb et al. (1968) found decreased radial growth in pines within similar age classes was associated with high oxidant injury.

High nitrogen deposition can offset aboveground growth reductions associated with ozone exposure (Grulke and Balduman, 1999). Interactions between ozone exposure and nitrogen deposition may affect tree susceptibility to bark beetle attack at the high pollution site, where oxidant injury is high, but not at the low pollution site, where trees show very few symptoms of ozone injury (Fig. 1). We found that the lower growth rates of control trees were associated with increased frequency of beetle activity in pines at the high pollution site. Although oxidant injury was similar among all trees at the high pollution site, fertilized trees had higher growth rates. Possibly, high nitrogen availability also offsets other negative effects of ozone exposure that affect tree susceptibility to bark beetles.

Fertilization is often used in management practices to increase tree growth rates and shorten intervals between timber harvest. Fertilization treatments used in management practices have been associated with increased incidence for several pests and pathogens in conifers (Nowak and Berisford, 2000; Sun et al., 2000; Viiri et al., 2001). Similarly, atmospheric deposition of nitrogen compounds may increase susceptibility of ponderosa pine and Jeffrey pine to bark beetle attacks in the San Bernardino Mountains. Incidence of beetle activity on pines at the low atmospheric deposition site was increased 20% in stands treated with nitrogen additions, while beetle activity at a site with high atmospheric input ranged from 30 to 57% of trees affected, regardless of further nitrogen addition. This study suggests that, in addition to drought and oxidant injury, nitrogen deposition appears to affect tree susceptibility to beetle attack.

Acknowledgements

We wish to thank D. Reed, C. Hanlon, J. Charles and C. Casteel for reviewing earlier drafts of the manuscript. The support of the USDA National Research Initiative Competitive Grants Program, Agreement No. 96-35101-3259 to Mark Fenn, Mark Poth and Paul Miller was instrumental in establishing the research plots for this study. The ongoing support of the USDA Forest Service, Pacific Southwest Research Station is also gratefully acknowledged in support of this work. We also thank Dave Jones, Tony Davila, and Susan Schilling for invaluable assistance in field data collection and in applying the annual fertilization treatments.

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