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Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens

Nadir Erbilgin*, Kenneth F. Raffa

Department of Entomology, University of Wisconsin, 345 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA

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Abstract

Declining red pine, *Pinus resinosa* (Aitman), stands in the Great Lakes region appear to arise from a complex of biotic and abiotic factors. We monitored stem and root colonizing beetles in declining and healthy plantations in Wisconsin from 1997 to 1999. We also conducted systematic field excavations and laboratory isolations of various root pathogens. Multiple funnel traps were baited with the synthetic aggregation pheromones of the two most common bark beetle (Coleoptera: Scolytidae) species in the region, *Ips pini* (Say) and *Ips grandicollis* (Eichhoff). Lower-stem flight traps were baited with 1:1 (+)-α-pinene:75% ethanol, and pitfall traps were baited with 1:1 (−)-α-pinene:75% ethanol. Healthy stands had higher populations of predators, particularly *Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae), and *Platysoma parallelum* Say than declining stands. Seasonal abundance patterns of predators and *Ips* also varied between declining and healthy stands. Declining stands had higher numbers of *Ips* and lower numbers of predators early in the season, whereas healthy stands had higher predator populations in the early season. Declining stands had more lower stem infesting bark beetles *Dendroctonus valens* LeConte (Scolytidae) and weevils (Curculionidae) *Pissodes* spp. Surprisingly, healthy stands had more root weevils, *Hylobius pales* (Herbst) and *Hylobius radicis* Buchanan, and root bark beetle *Hylastes porculus* Erichson, over the entire season. However, spatial by temporal patterns again were important. Populations of root colonizing insects were higher in healthy stands early in the season, but higher in declining stands throughout much of the ovipositional period. These results suggest dispersal patterns and overwintering behaviors are important in the interactions among herbivores, predators, and host plant condition in Red Pine Decline. The principal fungi isolated from roots were *Leptographium procerum* (Kendr.) Wingfield and *Leptographium terebrantis* Barras & Perry. These were more prevalent in declining than healthy stands. Staining fungi were more frequently isolated from roots of trees at the pocket margin than from trees in the asymptomatic portion of declining stands. *Heterobasidion annosum* (Fr.) Bref. was not isolated from root samples or stem disks, despite 40% recovery in positive controls using the latter method. Likewise, *Armillaria* spp. were not associated with declining plantations. Our results further support the view that forest declines are due to complex interactions among multiple biotic and abiotic stresses, and exhibit particular spatial and temporal patterns. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Forest decline; Scolytidae; *Hylobius*; Predators; *Leptographium*; Dispersal

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[*] Corresponding author. Present address: University of California, Department of Environmental Science, Policy & Management, 219 Wellman Hall, Division of Insect. Biology, Berkeley, CA 94720-3113. Tel.: +1-(510)-642-8414; fax: +1-(510)-642-7428.
E-mail addresses: erbilgin@nature.berkeley.edu (N. Erbilgin), raffa@entomology.wisc.edu (K.F. Raffa).

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1. Introduction

Red pine, *Pinus resinosa* (Aitman), plantations undergoing decline have been reported among 30–50-year-old stands throughout the Great Lakes region (Klepzig et al., 1991, 1995). Declining stands are characterized by a zone of tree mortality that spreads from an epicenter, termed a "pocket" (Klepzig et al., 1991). No or very few living red pines remain in this epicenter, and the resulting gap is colonized by early successional plants. Trees along the pocket margin usually show reduced radial and crown growth, whereas trees further into the stand show no symptoms. As the pocket expands, more trees die and additional trees show signs of stress along the new margin.

A complex of scolytids and curculionids colonizing stems and roots has been described within declining red pine plantations (Klepzig et al., 1991, 1995). The pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae) is the most common conifer-infesting bark beetle in the Great Lakes region (Schenck and Benjamin, 1969), and *Ips grandicollis* (Eichhoff) is a frequent associate. *Ips perroti* Swaine is sometimes present in small numbers, accounting for <1% of the trap catch in southern and central Wisconsin (Aukema et al., 2000). *Ips* selectively attack trees stressed by factors such as severe drought, defoliation, or root disease (Schenck and Benjamin, 1969; Miller et al., 1989; Klepzig et al., 1991; Wallin and Raffa, 2001). Male *I. pini* and *I. grandicollis* in Wisconsin produce the pheromones racemic ipsdienol plus lanierone, and ipsenol, respectively (Miller et al., 1989; Teale et al., 1991; Seybold et al., 1995a). These aggregation pheromones attract both sexes of their respective conspecifics. There is no cross attraction (Erbilgin and Raffa, 2000).

Under laboratory conditions, *I. pini* requires approximately 33 days to develop (Aukema and Raffa, unpublished data). In Wisconsin, this species typically undergoes three generations per year (Schenck and Benjamin, 1969). Dispersal has not been quantified in *I. pini*, but two related species have been examined. Over 95 and 90% of *Ips typographus* L. flew <200 m in studies by Zumr (1992) and Duellie et al. (1997), respectively. Most *Ips perturbatus* (Eichhoff) were collected within 30 m of their release point (Werner and Holsten, 1997).

Klepzig et al. (1991) observed higher populations of root and lower-stem-infesting beetles, and their associated *Leptographium* fungi, in declining than healthy plantations. This complex includes four weevils (Coleoptera: Curculionidae), the pine root collar weevil, *Hylobius radicis* Buchanan, the pales weevil, *Hylobius pales* (Herbst), the pitch eating weevil, *Pachylobius picivorus* (Germar), and the pine root tip weevil, *Hylobius assimilis* (Boheman) (*H. rhizophagus* Millers, Benjamin, and Warner). Two bark beetles, *Dendroctonus valens* LeConte and *Hylastes porculus* Erickson, colonize the lower stem and lateral roots, respectively, of stressed pines, including those colonized by *I. pini* and *I. grandicollis* (Owen et al., 1987; Klepzig et al., 1991). This decline appears to follow a sequence in which (1) root and lower stem insects colonize trees and introduce *Leptographium*, (2) root infestation reduces tree resistance against *Ips* attack, and (3) *Ips* colonization of root-infested trees is the ultimate source of tree mortality. This model is supported by higher trap catches of *Hylobius*, *Hylastes*, and *Dendroctonus* in declining than healthy stands (Klepzig et al., 1991), reduced measures of tree resistance in root-infested trees, persistent survival of those root-infested trees not subsequently attacked by *Ips*, and a high association of *Ips* with tree death within stands, despite equivalent *Ips* trap catches among stands (Klepzig et al., 1991, 1995, 1996).

Several components of this model remain unknown, however. For example, the population dynamics of *Ips* are only partially understood, particularly the interaction between host condition and natural enemies. Predators can exert important effects on the population dynamics of bark beetles (Weslien, 1994; Reeve, 1997; Turchin et al., 1999), but whether their impacts relate to varying stand conditions is not well understood. Secondly, the life history of root colonizing insects is only partially known, and little is known about the role of dispersal in their population dynamics and impact. In Europe, closely related species undergo pronounced seasonal dispersal (Nordenhem, 1989; Nordlander et al., 1997), and in the southern USA, dispersal by some of the same species present in the Great Lakes region is pronounced. Conversely, root colonizing insects in the northern USA and Canada are believed to fly only short distances (Wilson and Millers, 1983). Third, the role of root-colonizing fungi in declining red pine stands is not fully described. Although Klepzig et al. (1991) reported relative incidence of root staining and provided qualitative information on *Leptographium*, quantitative data on infection are not available. Fourth, the low frequency of *Armillaria* spp. in reported declining stands, in contrast to its association with bark beetles and forest gap formation elsewhere (e.g. Goheen and Hansen, 1993; Rizzo et al., 2000), and the recent discovery of *Heterobasidion annosum* (Fr.) Bref. in Wisconsin (Stanosz et al., 1995), suggest a need for further evaluation. Because of the high damaging potential of *H. annosum* (Alexander et al., 1981), this pathogen was of particular interest.

The objective of our study was to quantify the populations of bark beetles, predators, root and lower stem colonizing beetles, and the incidences of their associated fungi, in declining and healthy red pine stands throughout several growing seasons. Our purpose was to compare populations among stands of various conditions, and to test for possible within-season patterns in these relationships.

2. Materials and methods

2.1. Study site and experimental design

Field experiments were conducted in seventeen *P. resinosa* sites throughout south-western, south-central, and west-central Wisconsin, USA (Table 1). Stands showing an actively expanding margin of dead and poorly growing trees were designated as declining. Two types of control plots were established: symptomatic controls consist of portions of declining stands that are distant from the mortality zone and do not show any symptoms of decline; asymptomatic (true) controls consist of plots in stands that do not show any sign of mortality or stress. The distance between declining and symptomatic control plots was 200 m. The average distance between declining stands and asymptomatic control plots was 500 m.

Plots in stands that contained pockets were established at the margin of tree mortality. Plots in stands that did not contain pockets were established randomly inside the stand. The study plots were established in 1997, and monitored from early spring through late summer for 3 consecutive years, during the activity periods of bark beetles and root insects.

2.2. Insect sampling

Each plot contained three types of traps. Four 12-unit multiple funnel traps (Lindgren, 1983), separated by 20–30 m, were placed in each plot to sample bark beetles that colonize the main part of the stem, and

Table 1
Plot locations and stand conditions for sampling root and stem colonizing insects and fungi in red pine plantations in Wisconsin during 1997–1999

Site	County	Location	Age (year)	Stand condition[a]
1	Chippewa Falls	T.29N.-R.10W-Sec.19 (Howard)	42	Declining
2	Chippewa Falls	T.29N.-R.10W-Sec.19 (Howard)	42	Symptomatic control
3	Chippewa Falls	T.31N.-R.6W-Sec.7 (Brunet Island State Park)	50	Declining
4	Chippewa Falls	T.31N.-R.6W-Sec.7 (Brunet Island State Park)	50	Declining
5	Chippewa Falls	T.32N.-R.6W-Sec.24 (Birch Creek)	44	Asymptomatic control
6	La Crosse	T.18N.-R.6W-Sec.2	44	Declining
7	La Crosse	T.18N.-R.6W-Sec.2	44	Declining
8	La Crosse	T.18N.-R.6W-Sec.2	44	Declining
9	La Crosse	T.18N.-R.6W-Sec.2 (German Davison)	44	Symptomatic control
10	La Crosse	T.18N.-R.6W-Sec.2 (German Davison)	44	Symptomatic control
11	La Crosse	T.18N.-R.6W-Sec.2 (German Davison)	42	Asymptomatic control
12	Buffalo	T.20N.-R.13-12W-Sec.36 (Merrick State Park)	52	Declining
13	Buffalo	T.20N.-R.13-12W-Sec.36 (Merrick State Park)	52	Asymptomatic control
14	Buffalo	T.24N.-R.14-14W-Sec.25 (Tiffany State Wildlife Area)	48	Declining
15	Buffalo	T.24N.-R.14-14W-Sec.25 (Tiffany State Wildlife Area)	48	Symptomatic control
16	Monroe	T.19N.-R.3W-Sec.19 (New Lyme)	42	Declining
17	Monroe	T.19N.-R.4W-Sec.24 (Northeast Park Little Falls)	42	Asymptomatic control

[a] Declining: stand shows continual mortality of trees from an epicenter; symptomatic control: non symptomatic portions of declining stands; asymptomatic controls: stands that do not show sign of mortality or stress.

their predators. Traps were suspended from a rope stretched between two trees. The top of each trap was approximately 3–4 m above ground. The funnel traps were arranged in two rows extending along edges of the pocket, and each row contained two funnel traps. The location of the first row was determined randomly, and the second row was established adjacent to and clockwise from the first row. One trap in each row was baited at random with either racemic ipsdienol (chemical purity (CP): 98%) plus lanierone (CP: 98%), or racemic ipsenol (CP: 98%). Pheromones were obtained from Phero Tech, Inc. (Delta, BC) and released from 20 mg bubblecaps. No-pest strips (Pest STRIP, Loveland Industries, Inc., Greeley, CO) were placed in the collection jars to kill arriving insects and prevent predation. Funnel traps were sampled every 2 weeks from late April through the end of September, based on known seasonal distribution patterns (Raffa, 1991). Monitoring began during the second week of May and continued through the last week of September in 1997, and began during the first week of May and continued through the last week of September in 1998 and 1999.

Lower-stem flight traps sample adult insects in flight (Klepzig et al., 1991). This trap was constructed from a 3.78 l (1 gal) plastic milk jug by removing three sides, and retaining one large flat side as a striking surface, and two supporting columns. The jug is inverted, and the striking surface is attached to the stem by wrapping wire around the tree approximately 25 cm above the ground. A plastic jar fits tightly over the mouth of the jug. Two holes in the bottom of this jar facilitate drainage. Each trap was baited with 1:1 ratio of (+)-α-pinene and 75% ethanol, each released separately from an open 5 ml glass vial suspended inside the inverted jug (Phillips et al., 1988; Erbilgin et al., 2001).

The pitfall traps were as described by Tilles et al. (1986) and modified by Hunt and Raffa (1989), and are designed to sample adult root colonizing insects as they walk on the soil surface. The 20 cm high × 10 cm diameter PVC drain pipe sections containing eight equally spaced holes around the circumference near one end were placed in the soil, with the holes at ground level. Insects enter these traps through the holes, and a thin layer of liquid teflon on the inner surface prevents escape. The ends are capped with plastic lids, two small holes in the bottom lid allow drainage, and the top lid is removed to collect captured insects at each sampling interval. Two 5 ml glass vials containing 1:1 ratio of (−)-α-pinene and 75% ethanol (Erbilgin et al., 2001) were suspended from a wire inserted through two small holes in the trap at ground level.

In 1997, each plot contained 10 lower-stem flight and 10 pitfall traps. The two types of traps were alternated within a row, with 5–6 m between traps, and placed on the two rows containing funnel traps along the pocket margin. In 1998 and 1999, we tested for possible effects of trap location by deploying 20 pitfall and 20 lower-stem flight traps at 9 of 17 sites. Traps were assigned in the four cardinal directions surrounding the pocket. The traps were sampled and rebaited every 2 weeks from late April through the end of July. Monitoring with pitfall and lower-stem flight traps began during the second week of May and continued until the end of July in 1997, and began during the first week of May and continued until the last week of July in 1998 and 1999, based on known seasonal distribution patterns (Hoffman et al., 1997).

The physical properties and sources of chemicals used for pitfall and flight traps were (−)-α-pinene (CP: >99%; enantiomeric ratios (ER): 96.6%(−)/3.4%(+)), (+)-α-pinene (CP: >99%; ER: 95%(+)/5%(−)) (Aldrich Chemical Co., Milwaukee, WI), and 75% ethanol (25% distilled water). Volatilization rates under laboratory conditions (23°C) were 200 mg/24 h for ethanol and 40 mg/24 h for α-pinene.

2.3. Fungal sampling

We conducted a series of systematic root excavations and isolations in four declining and four healthy stands that were randomly selected during October 1998. In the declining sites, a circular transect was established around the pocket margin, and another was located 4 m further into the stand. Healthy plantations were sampled in a similar fashion. We divided each circle into four quarters, and within each quarter, one tree was selected randomly. At 0.5 m from the tree center, a 0.5 m deep trench was dug on the pocket side halfway around the tree. The soil between the trench and the tree was removed with a trowel to expose a 180° sector of the root collar and roots. Two primary lateral root segments greater than 2 cm in diameter were examined, and portions of the bark were removed with a knife or chisel to examine for signs and symptoms of fungi, using the method of Klepzig et al. (1991). Root samples from each tree were placed separately in a plastic bag, kept on ice, brought to the laboratory (≤8 h), and stored at 4°C. Eight trees were sampled on each of the eight plots in this study.

Intensive root excavation and sampling were conducted in three of nine declining sites during October 1998. A 15 m long × 1.2 m deep × 70 cm wide trench was excavated by Wisconsin Department of Natural Resources personnel using a backhoe. The trench extended from 6 m inside the pocket margin to 9 m into the stand. Root samples were removed at trees (or stumps) at 6 and 3 m inside the pocket margin, at the pocket margin (0 m) and at 3, 6, and 9 m from the pocket margin. At each interval, one tree (or stump) was selected randomly. A total of six trees were selected in each of the declining sites. Roots on two primary lateral root segments were examined. Sample roots were placed separately in plastic bags on ice, returned to the laboratory, and stored at 4°C.

Roots obtained from both procedures were rinsed under a stream of water to remove soil, and phloem and xylem were exposed by removing bark with a flame-sterilized scalpel. If root samples had any staining or resinosis, samples for isolation were collected at the margins of such features. In the absence of staining or resinosis, four samples were randomly taken along the root sample. Samples from roots were sectioned into small pieces (>2 mm) using a scalpel sterilized in bleach (12% Cl) for 0.5–2 min, rinsed in sterile water, and transferred to potato dextrose agar (PDA). The PDA contained acidified 2% malt extract agar amended with 250 ppm chloramphenicol, 50 ppm *ortho*-phenylphenol, and 8 ppm benomyl and malt extract agar (MEA) with *ortho*-phenyl phenol medium. Plates were incubated at 20°C in growth chambers (24 h light and 60% humidity) and checked for fungal growth. Fungal species were identified by comparing cultures with reference cultures from Dr. T.C. Harrington (Iowa State University).

Additional field experiments were conducted to test whether *H. annosum* is associated with declining red pine stands in Wisconsin. Previous workers demonstrated that airborne spores can germinate on recently exposed wood, such as stump surfaces (e.g. Ross, 1969; Bendz-Hellgren and Stenlid, 1998). We modified the methods of Ross (1969) and Bendz-Hellgren and Stenlid (1998) by using stem disks (3 cm thick and 15 cm diameter) removed from freshly cut red pine trees. Each disk was placed in a petri dish (3 cm height × 16 cm diameter) containing a wet filter paper, and immediately taken to the field on ice in March 1999. Ten stem disks were placed in each of the 17 sites. They were randomly placed along the pocket margin in declining stands, or in a ring around the center of symptomatic and asymptomatic control plots. As a positive control, 10 disks were placed in a red pine plantation in the Arena school forest, Iowa County, WI, that is known to be infected with *H. annosum* (Stanosz et al., 1995). After 4 h, the disks were brought to the laboratory over ice and incubated in plastics bags at 20°C (24 h light and 60% humidity) for 7–10 days in growth chambers, and examined for presence of conidiophores. Fungi were identified by comparing cultures with pure cultures maintained by Dr. J.N. Bruhn (University of Missouri-Columbia) and a pure culture isolated from fruiting bodies of *H. annosum* obtained from the Arena school forest.

2.4. Statistical analyses

Data were analyzed using analysis of variance (ANOVA). Since data from 1997 are not complete, they are presented for informational purposes, but were excluded from statistical comparisons. For insect species which were caught in more than one type of trap, we limited statistical analysis to the type in which most were obtained. The only exception for this criterion was *H. porculus*, because this species was frequently caught in both flight and pitfall traps (see Section 3). We also limited statistical analysis to species for which substantial numbers of insects were obtained. This number varied with feeding guild, and was 3500 per 2-year for bark beetles and 1000 per 2-year for predators in funnel traps, and 1000 per 2-year for insects in lower-stem flight traps and root insects in pitfall traps. All statistical analyses were conducted within a single trap type.

We examined residual plots of each dependent variable from all traps. Square root ($\sqrt{x}$) transformation of raw data from funnel traps in conjunction with mixed models satisfied assumptions of normality and homogeneity of variance (Neter et al., 1983). Dependent variables were analyzed by repeated measure analysis in Proc Mixed (SAS Institute, 1996).

Assumptions for our model were that site and site × trap interactions are random effects. If variance of these terms was zero, we fit the model by omitting that term from the random statement. We tested several covariance structures in preliminary models, e.g. compound symmetric (CS), and unstructured (UN), and autoregressive order 1 (AR(1)), and determined that variance components of AR(1) were most appropriate. When significant treatment differences were indicated, means were separated by Fisher's Protected LSD test ($P = 0.05$).

Because assumptions of normality and homogeneity of variance were not met using raw data or standard transformations for pitfall and lower stem flight traps, we used Generalized Linear Mixed Models (Glimmix) with repeated measures analysis in Proc Mixed (Wolfinger and O'Connell, 1993; SAS Institute, 1996). Glimmix estimates the parameters of a linear model using maximum likelihood based on a Poisson distribution of the data, and extends mixed models to accommodate nonnormal errors by adjusting the mean and variance (see Steel and Torrie, 1980; Snedecor and Cochran, 1989). We first tested whether trap locations within stands affected our results. Cardinal direction, position within row, and their interactions had no effect, with the lowest P-value being 0.4 among eight species and two trap types. We then proceeded to test the effect of stand condition. The Glimmix model was $Y = m + \text{site}_i + \text{treatment}_j + (\text{site} \times \text{treatment})_{ij} + \text{time}_k + (\text{treatment} \times \text{Time})_{jk}$, where m is the mean, site_i the site effect, treatment_j the treatment effect, $(\text{site} \times \text{treatment})_{ij}$ the site × treatment interaction (whole plot error), and $(\text{treatment} \times \text{time})_{jk}$ the treatment × time interaction. Assumptions for the model were that site and site × trap were random effects. If the site or site × trap variance component estimate was zero, we refit the model by omitting it from the random statement. When significant treatment differences were indicated, means were separated by Fisher's Protected LSD test ($P = 0.05$).

Logistic regression methods using PROCLOGIST (SAS Institute, 1996) were used to analyze the incidence of staining fungi in declining versus healthy stands, to contrast the incidence of staining fungi between inner and outer circular transects in declining stands, and to evaluate the level of infection of staining fungi with respect to the various distances from pocket margin.

3. Results

We captured a total of 156,530 beetles from 27 species in eight families (Table 2). The phloeophagous herbivores included three *Ips* associated with the main stem, two Cerambycidae associated with the phloem and sapwood of the main stem, one *Orthotomicus* (Scolytidae) associated with the upper stem and branches, two species (*D. valens* and *Pissodes* spp.) associated with the lower stem, and one bark beetle (*Hylastes*) and four weevils (*Hylobius*, *Pachylobius*) associated with roots. One ambrosia beetle (*Gnathotrichus*) was captured in large numbers. Ten species of predators in three families (Cleridae, Histeridae, Tenebrionidae) were obtained. Fourteen species comprised >95% of the total insect catch, and were obtained in sufficient numbers to conduct statistical comparisons. Of these, eleven were phloeophagous beetles and three were predators of bark beetles. *Ips pini* accounted for 64% of all bark beetles captured. The clerid *Thanasimus dubius* (F.) and the histerids *Platysoma cylindrica* (Paykull) and *Platysoma parallelum* Say accounted for 84% of all predators. *Hylobius pales* accounted for 68% of all root weevils.

Each insect species was caught almost exclusively within a single trap type. For example, 95% of all *Ips* and 82% of all predators were caught in funnel traps, 76% of *D. valens* and 81% of *Pissodes* were caught in lower-stem flight traps, and 93% of *Hylobius* and 98% of *Pachylobius* were caught in pitfall traps. The only exception to this pattern was *H. porculus*, which was attracted to both lower-stem flight traps (53%) and pitfall traps (43%) in high numbers, and another 4% were caught in funnel traps.

In funnel traps, the most abundant beetles were *I. pini* and *I. grandicollis*. *Ips perroti* was also obtained, but comprised only 2% of total *Ips* caught during 1998 and 1999. Together, *Ips* spp. and predators accounted for more than 95% of all insects caught in the funnel traps. The most abundant beetles captured in lower-stem flight traps were five scolytids, *G. materiarius*, *I. grandicollis*, *H. porculus*, *O. caelatus*, and *D. valens*, and the curculionid *Pissodes* spp. Lower-stem flight traps also captured substantial numbers of clerid predators, primarily *T. dubius* and *Enoclerus nigripes* (Say). The numbers of root weevils collected in flight traps were substantially lower than those collected in

Table 2
Phloeophagous and predatory beetles captured in red pine plantations in Wisconsin during 1997–1999

Species	Funnel traps			Lower-stem flight traps			Pitfall traps			Total
	1997	1998	1999	1997	1998	1999	1997	1998	1999	
(a) Phloeophagous herbivores and ambrosia beetles										
Scolytidae										
Ips pini (Say)	11045	25865	48007	100	147	106	5	17	7	85299
Ips grandicollis (Eichhoff)	3050	3966	13177	474	885	3947	24	27	94	25644
Ips perroti Swaine	–[b]	1056	1214	–	0	0	0	0	0	2270
Hylastes porculus Erichson	45	133	174	668	1499	1867	–	2031	1196	7613
Gnathotrichus materiarius Fitch	22	45	78	1879	3946	774	58	47	17	6866
Orthotomicus caelatus Eichhoff	3	123	315	328	1835	971	28	260	185	4048
Dendroctonus valens LeConte	93	135	131	194	160	792	52	32	92	1681
Curculionidae										
Hylobius pales (Herbst)	7	17	42	86	123	156	1321	1514	1189	4455
Hylobius radicis Buchanan	1	0	13	0	0	0	472	542	435	1463
Hylobius assimilis (Boheman)	0	0	0	0	0	0	158	182	145	485
Pachylobius picivorus (Germar)	0	2	0	0	0	0	16	55	46	119
Pissodes spp.[a]	57	41	36	606	527	583	61	105	92	2108
Cerambycidae										
Rhagium inquisitor (Gyllenberg)	30	44	30	172	200	144	12	5	6	643
Monochamus carolinensis (Olivier)	80	62	80	0	0	0	0	0	0	222
Trogossitidae										
Grynocharis quadrilineata (Melsheimer)	–	65	29	0	0	0	0	0	0	94
Bostrichidae										
Apate monacha (F.)	–	265	115	156	166	161	0	0	0	863
(b) Predators										
Cleridae										
Thanasimus dubius (F.)	3086	2487	1232	352	318	244	4	24	4	7751
Thanasimus undatulus (Say)	14	79	52	78	49	28	0	0	0	300
Enoclerus nigripes (Say)	322	74	21	285	150	153	8	9	7	1029
Enoclerus nigrifrons (Say)	1	12	28	0	0	0	0	0	0	41
Zenodosus sanguineus Say	–	98	30	–	0	0	0	0	0	128
Histeridae										
Platysoma cylindrica (Paykull)	841	598	289	0	0	0	0	0	0	1728
Platysoma parallelum Say	648	379	147	0	0	0	0	0	0	1174
Platysoma aequum LeConte	3	4	1	0	0	0	0	0	0	8
Tenebrionidae										
Corticeus parallelus (Melsheimer)	–	174	148	0	0	0	0	0	0	322
Tenebroides collaris (Sturm)	–	63	108	0	0	0	0	0	0	171
Total										156530

[a] Mostly *Pissodes nemorensis* Germar, but not always distinguishable from *Pissodes strobi* Peck. Funnel traps baited with either ipsdienol plus lanierone or ipsenol; flight traps baited with 1:1 ratio of (+)-α-pinene:ethanol; pitfall traps baited with 1:1 ratio of (−)-α-pinene:ethanol.

[b] –: Indicates that species was not counted.

pitfall traps. In pitfall traps, the most frequently captured beetles were the scolytid *H. porculus* and two curculionids, *H. pales* and *H. radicis*. *Hylobius assimilis* was captured in low numbers.

Bark beetles and predators showed different distribution patterns with respect to stand conditions (Table 3). The numbers of *I. pini* and *I. grandicollis* did not vary among stand conditions. In contrast, the

Table 3
Stem and root colonizing beetles obtained in red pine plantations of various conditions[a]

Species	Stand condition[b] (mean number ± S.E.)			d.f. (ND, DD)	*F*	*P*
	Declining	Symptomatic control	Asymptomatic control			
Funnel trap						
I. pini	112.9 ± 16.4	100.1 ± 24.0	110.1 ± 24.0	2, 790	0.37	0.69
I. grandicollis	26.9 ± 4.2	25.8 ± 6.3	21.1 ± 6.2	2, 794	0.61	0.5
T. dubius	3.5 ± 0.3 a	3.5 ± 0.3 a	5.3 ± 0.8 b	2, 794	3.6	0.027
P. cylindrica	0.7 ± 0.1 a	1.0 ± 0.2 ab	1.5 ± 0.3 b	2, 794	10.7	0.0001
P. parallelum	0.4 ± 0.1 a	0.5 ± 0.1 a	1.0 ± 0.2 b	2, 796	8.2	0.0003
Lower stem flight trap						
G. materiarius	1.6 ± 0.3	1.3 ± 0.3	2.0 ± 0.4	2, 2589	2.54	0.08
I. grandicollis	1.9 ± 0.4 b	1.0 ± 0.2 a	1.4 ± 0.3 ab	2, 2589	4.2	0.015
H. porculus	1.2 ± 0.2 ab	1.0 ± 0.1 a	1.4 ± 0.1 b	2, 2589	4.2	0.015
O. caelatus	1.0 ± 0.1 b	0.5 ± 0.06 a	1.1 ± 0.11 b	2, 2589	8.5	0.0002
D. valens	0.4 ± 0.03 b	0.3 ± 0.04 a	0.2 ± 0.02 a	2, 2589	5.5	0.004
Pissodes spp.	0.5 ± 0.04 b	0.5 ± 0.04 b	0.3 ± 0.02 a	2, 2589	15.7	0.0001
Pitfall traps						
H. pales	0.8 ± 0.08 a	0.5 ± 0.05 b	1.3 ± 0.1 c	2, 2821	22.8	0.0001
H. porculus	1.1 ± 0.1 b	0.8 ± 0.08 a	1.2 ± 0.1 b	2, 2821	4.6	0.01
H. radicis	0.3 ± 0.02 b	0.2 ± 0.01 a	0.5 ± 0.05 c	2, 2821	25.5	0.0001

[a] Data show mean number (±S.E.) of insects caught per trap per 15-day sample period. Data for each trap type are averaged among sites within each stand condition, over 1998 and 1999. Data from 1997 were excluded from analysis because of differences in sampling dates.

[b] Means followed by the same letter within a row are not significantly different ($P < 0.05$, repeated measure analysis in Proc Mixed). Fisher's Protected LSD test ($P < 0.05$) was used for multiple comparisons of means of transformed data ($\sqrt{x}$). Untransformed means were reported.

predators *T. dubius* and *P. parallelum* were significantly more abundant in the asymptomatic stands than in either tree mortality zones within declining stands or in asymptomatic sections of declining stands. Similarly, *P. cylindrica* were more abundant in healthy stands than in plots containing pockets, but their numbers were not different between the two types of controls.

Bark beetles and predators showed strong stand condition × time interaction effects (*I. pini*: $F_{18,757} = 1.7$, $P = 0.03$; *I. grandicollis*: $F_{18,795} = 2.7$, $P = 0.00017$; *T. dubius*: $F_{18,795} = 2.5$, $P = 0.0005$; *P. cylindrica*: $F_{18,797} = 2.04$, $P = 0.007$; *P. parallelum*: $F_{18,795} = 1.9$, $P = 0.013$). Both *I. pini* and *I. grandicollis* were significantly more abundant in declining than healthy stands early in the season (Fig. 1A). Later in the season, however, their numbers were significantly higher in healthy than declining stands. Predators showed different seasonal patterns than bark beetles (Fig. 1B). *Thanasimus dubius* were more abundant throughout the season in the healthy than declining stands. *Platysoma* spp. showed patterns similar to *T. dubius*, and were almost always higher in asymptomatic controls than in other stand conditions.

The mean number of *D. valens* was significantly higher in plots located at the pocket margin than plots in either asymptomatic or symptomatic controls (Table 3). Populations of *Pissodes* were higher in stands that contain pockets, both in the declining and symptomatic regions, and in stands that do not contain pockets. There were no treatment × time interactions for any of the species caught in lower stem flight traps (*Pissodes* spp.: $F_{10,2587} = 1.4356$, $P = 0.1581$; *D. valens*: $F_{10,2586} = 1.53$, $P = 0.1213$; *H. porculus*: $F_{10,2586} = 0.68$, $P = 0.741$; *I. grandicollis*: $F_{10,2586} = 1.6534$, $P = 0.0861$; *O. caelatus*: $F_{10,2586} = 1.2317$, $P = 0.2647$; *G. materiarius*: $F_{10,2586} = 1.47$, $P = 0.1442$).

Surprisingly, the numbers of *H. pales* and *H. radicis* were significantly higher in the asymptomatic controls than in stands that contained pockets (Table 3). However, there were strong stand condition × time interaction for *H. pales* ($F_{10,2818} = 5.25$, $P < 0.0001$), *H. radicis* ($F_{10,2818} = 5.75$, $P < 0.0001$), and *H. porculus* ($F_{10,2817} = 5.22$, $P < 0.0001$), indicating that their relative trap catches among various stand conditions varied throughout the season. This pattern is illustrated in Fig. 2. *Hylobius pales*, *H. radicis*, and *H. porculus* were significantly more abundant in asymptomatic stands than in pockets at the first collection period. In contrast, later in the season, their numbers were usually higher in the declining stands than in the asymptomatic controls (Fig. 2). *Hylastes pales* and *H. radicis* were more abundant in pockets than in either control for three of the remaining sample periods, and *H. porculus* were more abundant in pockets than asymptomatic controls for three of the remaining sample periods.

Insect numbers from each feeding guild varied by year (Table 4). Overall, the numbers of *I. pini* and *I. grandicollis* increased by 43 and 25%, respectively, from 1998 to 1999. Trap captures of *T. dubius*, *P. cylindrica*, and *P. parallelum* declined by 60, 61, and 64%, respectively. Relative population changes

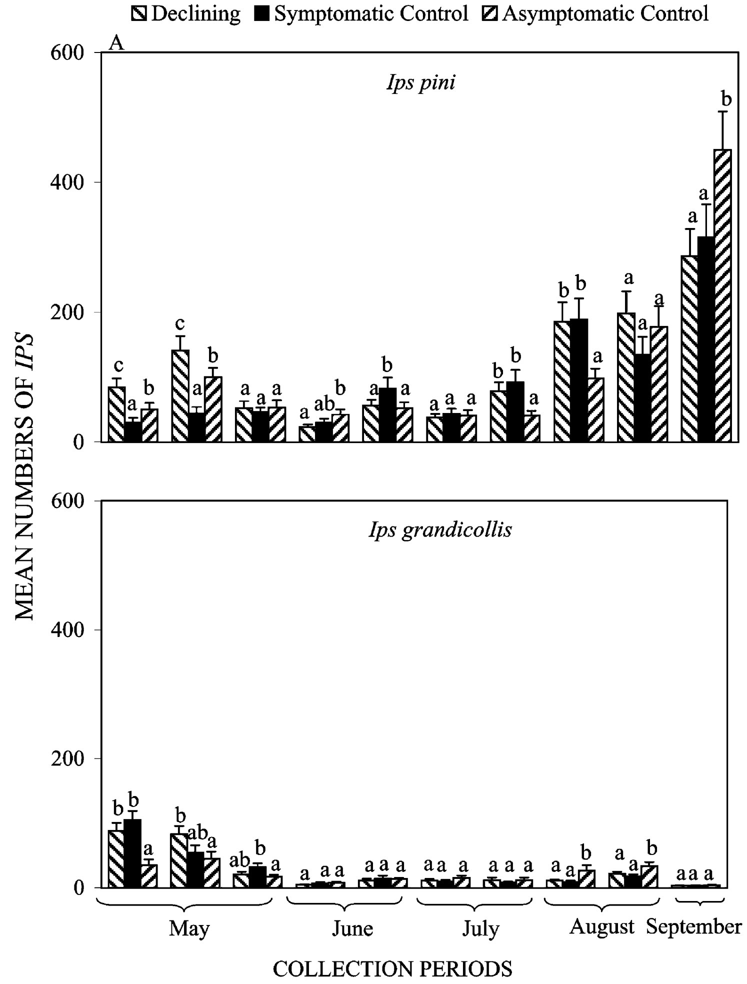

Fig. 1. Temporal distributions of bark beetles and predators in *Pinus resinosa* plantations of various stand conditions. (A) *Ips pini* and *Ips grandicollis*, (B) *Thanasimus dubius*, *Platysoma cylindrica*, and *Platysoma parallelum*. Data show mean number (±S.E.) of insects caught per trap per 15-day sample period. Data for each multiple funnel trap are averaged among sites within each stand condition, over 1998 and 1999. Bars with the same letter at each collection period are not significantly different ($P > 0.05$), Proc Mixed and Tukey's Protected LSD test.

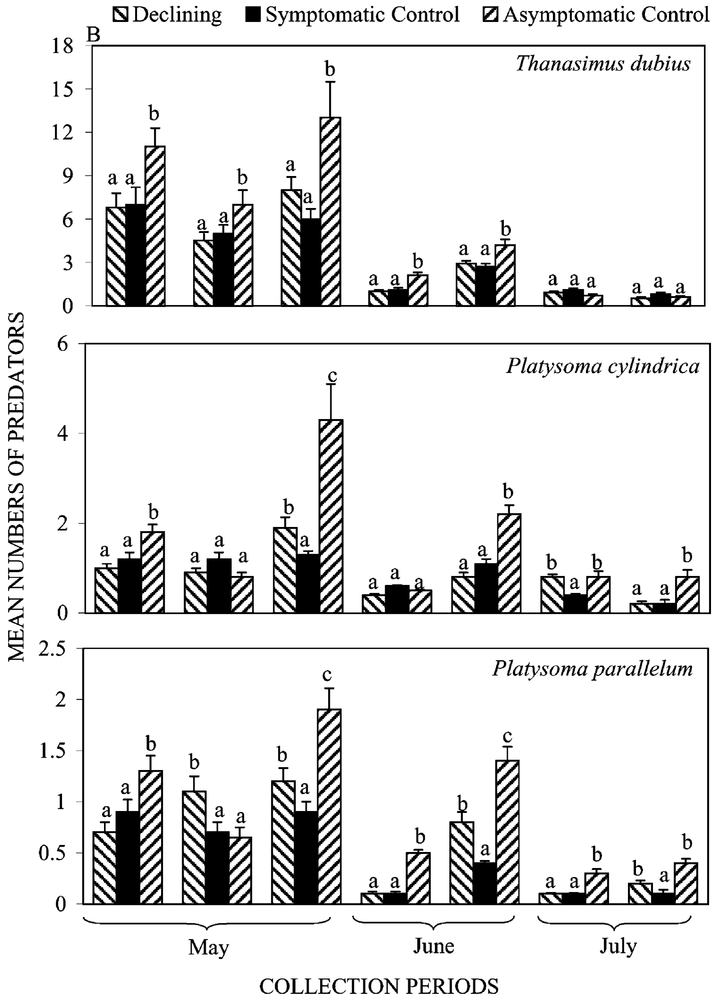

Fig. 1. (*Continued*).

between *Ips* and predators were consistent with a time-delayed interaction at the site level. Ten of the 11 sites in which trap catches of *I. pini* increased from 1998 to 1999 were accompanied by decreases in trap catches of *T. dubius*. Conversely, four of the six sites in which trap catches of *I. pini* decreased were accompanied by increases in trap catches of *T. dubius*. Likewise, trap catches of *T. dubius* decreased in 11 of the 16 sites in which the trap catches of *I. grandicollis* increased. Numbers of some other phloeophagous insects, particularly *O. caelatus*, *H. pales*, and *H. radicis*, and the ambrosia beetle, *G. materiarius*, declined from 1998 to 1999, with reductions ranging from 20 to 87%. Trap catches of the lower stem feeding insects *D. valens* and *Pissodes* spp. increased by 240 and 33%, respectively, from 1998 to 1999.

The principal fungi isolated from root samples were *Leptographium procerum* (Kendr.) Wingfield and *Leptographium terebrantis* Barras & Perry (Table 5). There was a significantly higher incidence of these fungi in declining than healthy stands ($\chi_1 = 6.3083$, $P = 0.012$). Logistic regression analysis indicated that staining fungi isolated from roots of trees at the pocket margin were significantly higher than those 4 m behind the pocket margin ($\chi_1 = 10.2448$, $P = 0.0014$) (Table 5). In healthy stands, there was

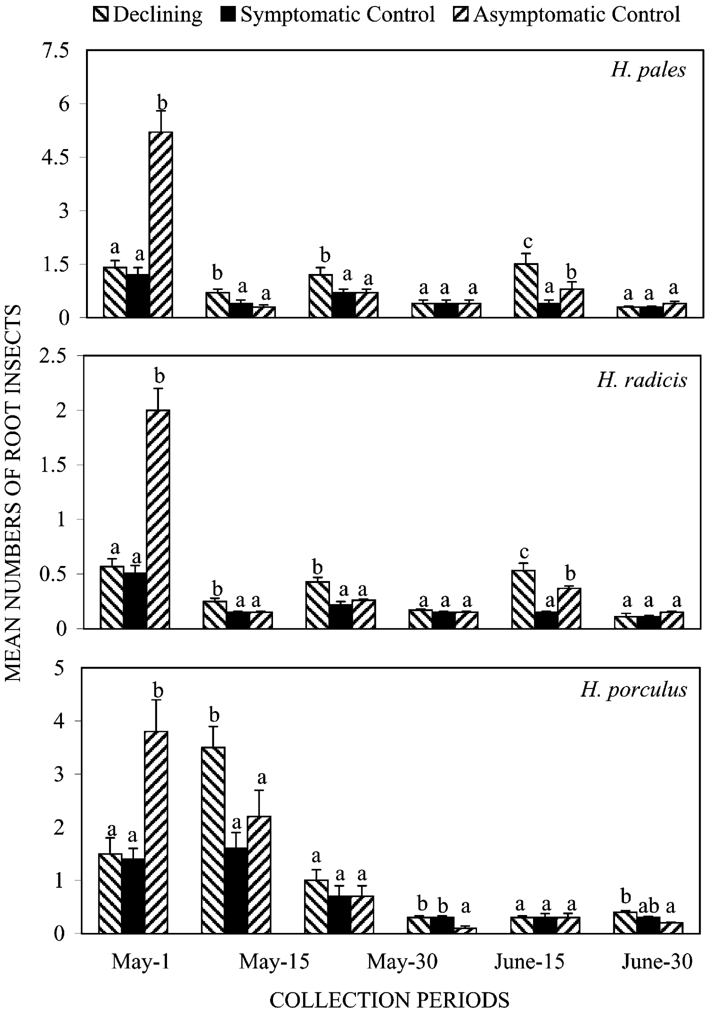

Fig. 2. Temporal distributions of root-colonizing beetles in baited pitfall traps. Data show mean number (±S.E.) of insects caught per trap per 15-day sample period. Data for each pitfall trap are averaged among sites within each stand condition, over 1998 and 1999. Bars with the same letter at each collection period are not significantly different ($P > 0.05$), Glimmix in Proc Mixed and Tukey's Protected LSD test.

no difference in the incidence of staining fungi between the center and margin of plots.

Results obtained from the stand excavation studies were similar to those of circular transect studies. In declining stands, there was a significant effect of distance from the margin on the incidence of staining fungi ($\chi_1 = 27.25, P = 0.0001$) (Fig. 3). The incidence of staining fungi was higher at the pocket margin and 3 m beyond the pocket margin than at other distances. The incidence of fungi declined thereafter.

Heterobasidion annosum and *Armillaria* spp. were not isolated from any root samples or stem disks in declining or healthy stands. However, the recovery rate for capturing airborne spores of *H. annosum* on stem disks in the site known to be infected (i.e. positive control) was almost 40%.

4. Discussion

A major difference between declining and healthy red pine stands is that populations of predators of bark beetles were lower in stands showing high tree mortality. This difference was more pronounced at

Table 4
Between-year variation in populations of stem- and root-colonizing beetles in red pine plantations[a]

Species	Mean numbers[b] (±S.E.)			d.f. (ND, DD)	*F*	*P*
	1997	1998	1999			
Funnel traps						
I. pini	62.1 ± 10.6	95.1 ± 10.1 a	141.2 ± 17.7 b	1, 793	6.5	0.0113
I. grandicollis	20.8 ± 7.1	14.6 ± 3.0 a	38.7 ± 5.4 b	1, 797	7.67	0.0058
T. dubius	12.5 ± 1.7	5.2 ± 0.5 b	2.6 ± 0.2 a	1, 794	79.43	0.0001
P. cylindrica	3.0 ± 0.7	1.3 ± 0.3 b	0.61 ± 0.2 a	1, 795	72.59	0.0001
P. parallelum	2.2 ± 0.5	0.8 ± 0.1 b	0.31 ± 0.03 a	1, 794	39.34	0.0001
Lower stem flight traps						
G. materiarius	4.2 ± 0.6	2.53 ± 0.2 b	0.5 ± 0.04 a	1, 2586	334.7	0.0001
I. Grandicollis	1.0 ± 0.2	0.6 ± 0.08 a	2.5 ± 0.23 b	1, 2586	217.1	0.0001
H. porculus	1.3 ± 0.2	1.0 ± 0.06 b	1.2 ± 0.08 a	1, 2586	4.271	0.0389
O. caelatus	0.7 ± 0.1	1.2 ± 0.1 b	0.6 ± 0.03 a	1, 2586	87.381	0.0001
Pissodes spp.	1.6 ± 0.3	0.3 ± 0.01 b	0.4 ± 0.01 a	1, 2587	10.31	0.0013
D. valens	0.5 ± 0.1	0.1 ± 0.02 a	0.5 ± 0.03 b	1, 2586	150.78	0.0001
Pitfall traps						
H. pales	3.0 ± 0.7	1.0 ± 0.08 b	0.7 ± 0.04 a	1, 2818	27.688	0.0001
H. porculus	0.4 ± 0.06	1.3 ± 0.1 b	0.8 ± 0.05 a	1, 2817	25.26	0.0001
H. radicis	1.1 ± 0.3	0.4 ± 0.03 b	0.2 ± 0.02 a	1, 2818	23.478	0.0001

[a] Data show mean number (±S.E.) of insects caught per trap per 15-day sample period. Data for each trap type are averaged among sites within each stand condition. Comparisons between 1998 and 1999 are reported. Data from 1997 were excluded from analysis because of differences in sampling dates.

[b] Means followed by the same letter within a row are not significantly different ($P < 0.05$, repeated measure analysis in Proc Mixed). Fisher's Protected LSD test ($P < 0.05$) was used for multiple comparisons of means of transformed data ($\sqrt{x}$). Untransformed means are reported.

the between-stand than within-stand level. That is, asymptomatic portions of declining stands had predator trap catches more characteristic of symptomatic areas of declining stands than of healthy stands. This suggests that stand features other than or in addition to prey abundance may partially explain the higher numbers of predators in healthy stands (Table 3). Stand characteristics such as nectar sources have been shown to affect populations of hymenopteran parasitoids of bark beetles (Hougardy and Grégoire, 2000), but we currently lack sufficient information to describe similar stand features for coleopteran predators. However, interactions between temporal patterns and stand condition suggest that dispersal of predators may

Table 5
Incidence of staining fungi in relation to between- and within-stand conditions of *P. resinosa* plantations

Fungus	Percent staining fungi isolated			
	Declining stands		Healthy stands	
	At pocket margin	4 m behind pocket	At center margin	4 m behind pocket
L. terebrantis	25	7	12.5	12.5
L. procerum	50	12	12.5	12.5
Total[a]	63	15	17	16

[a] Since some samples from the same root contained both *Leptographium* spp., total staining is smaller than their sum. Statistical analysis conducted based on the percentage of trees with root staining fungi by PROCLOGIST.

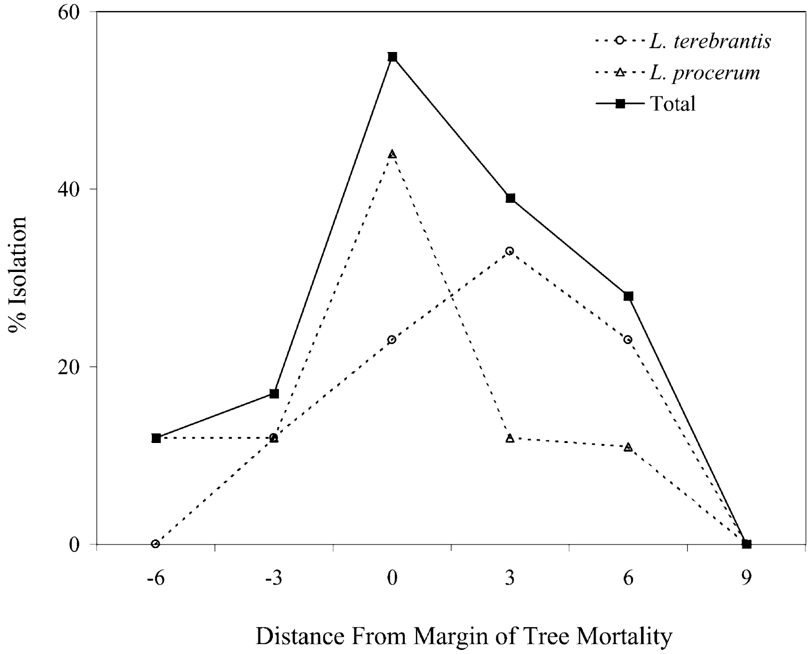

Fig. 3. Isolation of fungi from roots at various distances from margins of epicenter of tree mortality in *Pinus resinosa* plantations. Since some samples taken from the same root contained both *Leptographium* spp., total staining is relatively smaller than their arithmetical total. Statistical analysis was conducted based on the presence or absence of incidence of staining fungi by PROCLOGIST.

contribute to these observed predator-prey dynamics. Currently, we do not know how dispersal of predators varies with respect to that of their bark beetle prey across different stand condition within a season. However, Cronin et al. (2000) observed that *T. dubius* in the southern USA flew an average of 1.25 km, approximately six times more than its principal prey species in the region, *Dendroctonus frontalis* Zimmermann (Thoeny et al., 1992; Turchin and Odendall, 1996).

Our results agree with Klepzig et al. (1991) that populations of *D. valens* are higher in declining than in healthy stands. Root and lower stem colonizing insects also showed an association with declining red pine stands, in agreement with Klepzig et al. (1991), but not in a simple pattern. The higher total trap catch of root insects in the healthy stands was opposite that expected. It appears that temporal by stand condition interactions, rather than total seasonal abundance, are important. The results shown in Fig. 2 suggest that dispersal may be important, with overwintering populations concentrated in stands with closed canopies, followed by immigration into open and declining stands. Direct observations of dispersal in spring and early summer by *Hylobius abietis* (L.) have been made in Europe (Solbreck, 1980; Nordenhem, 1989; Nordlander et al., 1997). Approximately 90% of this flight occurs within 2 weeks of emergence (Solbreck and Gyldberg, 1979; Solbreck, 1980), and most of these weevils disperse over 10 km (Solbreck, 1980; Nilssen, 1984). *Hylobius pales* is known to fly substantial distances in the southern USA, but less is known about its dispersal in the northern USA. Rieske and Raffa (1993) suggested that dispersal of root insects in Wisconsin, particularly *H. pales*, could be substantial when densities are high.

The higher incidence of *Leptographium* in declining than healthy stands is consistent with observations on root staining and mortality by Klepzig et al. (1991), and further supports the view that these fungi contribute to Red Pine Decline. Trees farther than 6–9 m away from the pocket margin have lower levels of root mortality and infection than trees at or near the margin of mortality. *Hylobius*, *Pachylobius*, *Hylastes*, and *Dendroctonus* have been shown to vector *Leptographium* in Wisconsin (Klepzig et al., 1991), which may partially explain the higher frequency of these fungi in declining than in healthy stands (Table 5), and at pocket margins than in asymptomatic regions of declining stands (Fig. 3). Similarly Otrosina et al. (1997) isolated *L. procerum* and *L. terebrantis* more frequently from plots attacked by the southern pine beetle, *D. frontalis* than control plots. The occasional isolation of *Leptographium* from roots in asymptomatic stands suggests that above ground symptoms may not become visible until most of the root system is diseased. Similarly, Kelsey et al. (1998) reported that crown growth parameters did not change significantly until more than one-third of the root system was infected.

Heterobasidion annosum and *Armillaria* spp. were not isolated from roots or stem disks in these declining or healthy stands. The absence of *Armillaria* agrees with previous observations by Klepzig et al. (1991). Successful isolation of *H. annosum* near trees where it was known to be present suggests that the method is sensitive, and supports the view that this pathogen is not widely distributed throughout Wisconsin at present. Likewise, a survey by the Wisconsin Department of Natural Resources yielded few positive observations (Cummings Carlson and Guthmiller, 2000). The lack of association between *H. annosum* and tree mortality to bark beetles is consistent with observations by Otrosina et al. (1997) with *D. frontalis* and *Pinus taeda* L. Because of the damage this pathogen has done elsewhere (Otrosina et al., 1995, 1999; Morrison and Johnson, 1999), continued monitoring of *H. annosum* is warranted.

Our results provide further support to the view that declines of forest stands are due to complex interactions among multiple biotic and abiotic stresses, and exhibit particular spatial and temporal patterns (Manion and Lachance, 1992; Huettl and Muller-Dombois, 1993; Innes, 1993). In the system described here, within-season temporal by inter-stand spatial patterns of natural enemy abundance are important. The current study suggests that a combination of low numbers of predators (Fig. 1) and reduced host tree resistance induced by root colonizing insects (Fig. 2) and pathogens (Fig. 3), may contribute to stand declines. Subsequent studies should identify stand factors that facilitate the development, and attraction of these predators as well as the dispersal of adult weevils.

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