

# 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 (+)- $\alpha$ -pinene:75% ethanol, and pitfall traps were baited with 1:1 (-)- $\alpha$ -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 radialis* 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. © 2001 Published by Elsevier Science B.V.

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

## 1. Introduction

Red pine, *Pinus resinosa* (Aitman), plantations undergoing decline have been reported among 30–

\* Corresponding author. Tel.: +1-608-262-4755;

fax: +1-608-262-3322.

E-mail addresses: erbilgin@entomology.wisc.edu (N. Erbilgin), raffa@entomology.wisc.edu (K.F. Raffa).

40 50-year-old stands throughout the Great Lakes region  
 41 (Klepzig et al., 1991, 1995). Declining stands are  
 42 characterized by a zone of tree mortality that spreads  
 43 from an epicenter, termed a “pocket” (Klepzig et al.,  
 44 1991). No or very few living red pines remain in this  
 45 epicenter, and the resulting gap is colonized by early  
 46 successional plants. Trees along the pocket margin  
 47 usually show reduced radial and crown growth,  
 48 whereas trees further into the stand show no symp-  
 49 toms. As the pocket expands, more trees die and  
 50 additional trees show signs of stress along the new  
 51 margin.

52 A complex of scolytids and curculionids colonizing  
 53 stems and roots has been described within declining  
 54 red pine plantations (Klepzig et al., 1991, 1995). The  
 55 pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae)  
 56 is the most common conifer-infesting bark beetle in  
 57 the Great Lakes region (Schenck and Benjamin,  
 58 1969), and *Ips grandicollis* (Eichhoff) is a frequent  
 59 associate. *Ips perroti* Swaine is sometimes present in  
 60 small numbers, accounting for <1% of the trap catch in  
 61 southern and central Wisconsin (Aukema et al., 2000).  
 62 *Ips* selectively attack trees stressed by factors such as  
 63 severe drought, defoliation, or root disease (Schenck  
 64 and Benjamin, 1969; Miller et al., 1989; Klepzig et al.,  
 65 1991; Wallin and Raffa, 2001). Male *I. pini* and *I.*  
 66 *grandicollis* in Wisconsin produce the pheromones  
 67 racemic ipsdienol plus lanierone, and ipsenol, respec-  
 68 tively (Miller et al., 1989; Teale et al., 1991; Seybold  
 69 et al., 1995a). These aggregation pheromones attract  
 70 both sexes of their respective conspecifics. There is no  
 71 cross attraction (Erbilgin and Raffa, 2000).

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

83 Klepzig et al. (1991) observed higher populations of  
 84 root and lower-stem-infesting beetles, and their asso-  
 85 ciated *Leptographium* fungi, in declining than healthy  
 86 plantations. This complex includes four weevils  
 87 (Coleoptera: Curculionidae), the pine root collar wee-

vil, *Hylobius radialis* Buchanan, the pales weevil, 88  
*Hylobius pales* (Herbst), the pitch eating weevil, 89  
*Pachylobius picivorus* (Germar), and the pine root 90  
 tip weevil, *Hylobius assimilis* (Boheman) (*H. rhizo-* 91  
*phagus* Millers, Benjamin, and Warner). Two bark 92  
 beetles, *Dendroctonus valens* LeConte and *Hylastes* 93  
*porculus* Erickson, colonize the lower stem and lateral 94  
 roots, respectively, of stressed pines, including those 95  
 colonized by *I. pini* and *I. grandicollis* (Owen et al., 96  
 1987; Klepzig et al., 1991). This decline appears to 97  
 follow a sequence in which (1) root and lower stem 98  
 insects colonize trees and introduce *Leptographium*, 99  
 (2) root infestation reduces tree resistance against *Ips* 100  
 attack, and (3) *Ips* colonization of root-infested trees is 101  
 the ultimate source of tree mortality. This model is 102  
 supported by higher trap catches of *Hylobius*, 103  
*Hylastes*, and *Dendroctonus* in declining than healthy 104  
 stands (Klepzig et al., 1991), reduced measures of tree 105  
 resistance in root-infested trees, persistent survival of 106  
 those root-infested trees not subsequently attacked by 107  
*Ips*, and a high association of *Ips* with tree death within 108  
 stands, despite equivalent *Ips* trap catches among 109  
 stands (Klepzig et al., 1991, 1995, 1996). 110

111 Several components of this model remain unknown,  
 112 however. For example, the population dynamics of *Ips*  
 113 are only partially understood, particularly the interac-  
 114 tion between host condition and natural enemies.  
 115 Predators can exert important effects on the population  
 116 dynamics of bark beetles (Weslien, 1994; Reeve,  
 117 1997; Turchin et al., 1999), but whether their impacts  
 118 relate to varying stand conditions is not well under-  
 119 stood. Secondly, the life history of root colonizing  
 120 insects is only partially known, and little is known  
 121 about the role of dispersal in their population  
 122 dynamics and impact. In Europe, closely related spe-  
 123 cies undergo pronounced seasonal dispersal (Norden-  
 124 hem, 1989; Nordlander et al., 1997), and in the  
 125 southern USA, dispersal by some of the same species  
 126 present in the Great Lakes region is pronounced.  
 127 Conversely, root colonizing insects in the northern  
 128 USA and Canada are believed to fly only short dis-  
 129 tances (Wilson and Millers, 1983). Third, the role of  
 130 root-colonizing fungi in declining red pine stands is  
 131 not fully described. Although Klepzig et al. (1991)  
 132 reported relative incidence of root staining and pro-  
 133 vided qualitative information on *Leptographium*,  
 134 quantitative data on infection are not available. Fourth,  
 135 the low frequency of *Armillaria* spp. in reported

136 declining stands, in contrast to its association with  
 137 bark beetles and forest gap formation elsewhere (e.g.  
 138 Goheen and Hansen, 1993; Rizzo et al., 2000), and the  
 139 recent discovery of *Heterobasidion annosum* (Fr.)  
 140 Bref. in Wisconsin (Stanosz et al., 1995), suggest a  
 141 need for further evaluation. Because of the high  
 142 damaging potential of *H. annosum* (Alexander et al.,  
 143 1981), this pathogen was of particular interest.

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

## 152 2. Materials and methods

### 153 2.1. Study site and experimental design

154 Field experiments were conducted in seventeen *P.*  
 155 *resinosa* sites throughout south-western, south-cen-  
 156 tral, and west-central Wisconsin, USA (Table 1).

157 Stands showing an actively expanding margin of dead  
 158 and poorly growing trees were designated as declin-  
 159 ing. Two types of control plots were established:  
 160 symptomatic controls consist of portions of declining  
 161 stands that are distant from the mortality zone and do  
 162 not show any symptoms of decline; asymptomatic  
 163 (true) controls consist of plots in stands that do not  
 164 show any sign of mortality or stress. The distance  
 165 between declining and symptomatic control plots was  
 166 200 m. The average distance between declining stands  
 167 and asymptomatic control plots was 500 m.

168 Plots in stands that contained pockets were estab-  
 169 lished at the margin of tree mortality. Plots in stands  
 170 that did not contain pockets were established ran-  
 171 domly inside the stand. The study plots were estab-  
 172 lished in 1997, and monitored from early spring  
 173 through late summer for 3 consecutive years, during  
 174 the activity periods of bark beetles and root insects.

### 175 2.2. Insect sampling

176 Each plot contained three types of traps. Four 12-  
 177 unit multiple funnel traps (Lindgren, 1983), separated  
 178 by 20–30 m, were placed in each plot to sample bark  
 179 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 <sup>a</sup>
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

<sup>a</sup> 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.

180 their predators. Traps were suspended from a rope  
 181 stretched between two trees. The top of each trap was  
 182 approximately 3–4 m above ground. The funnel traps  
 183 were arranged in two rows extending along edges of  
 184 the pocket, and each row contained two funnel traps.  
 185 The location of the first row was determined randomly,  
 186 and the second row was established adjacent to and  
 187 clockwise from the first row. One trap in each row was  
 188 baited at random with either racemic ipsdienol (che-  
 189 mical purity (CP): 98%) plus lanierone (CP: 98%), or  
 190 racemic ipsenol (CP: 98%). Pheromones were  
 191 obtained from Phero Tech, Inc. (Delta, BC) and  
 192 released from 20 mg bubblecaps. No-pest strips (Pest  
 193 STRIP, Loveland Industries, Inc., Greeley, CO) were  
 194 placed in the collection jars to kill arriving insects and  
 195 prevent predation. Funnel traps were sampled every 2  
 196 weeks from late April through the end of September,  
 197 based on known seasonal distribution patterns (Raffa,  
 198 1991). Monitoring began during the second week of  
 199 May and continued through the last week of Septem-  
 200 ber in 1997, and began during the first week of May  
 201 and continued through the last week of September in  
 202 1998 and 1999.

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

217 The pitfall traps were as described by Tilles et al.  
 218 (1986) and modified by Hunt and Raffa (1989), and  
 219 are designed to sample adult root colonizing insects as  
 220 they walk on the soil surface. The 20 cm high  $\times$  10 cm  
 221 diameter PVC drain pipe sections containing eight  
 222 equally spaced holes around the circumference near  
 223 one end were placed in the soil, with the holes at  
 224 ground level. Insects enter these traps through the  
 225 holes, and a thin layer of liquid teflon on the inner  
 226 surface prevents escape. The ends are capped with  
 227 plastic lids, two small holes in the bottom lid allow

228 drainage, and the top lid is removed to collect captured  
 229 insects at each sampling interval. Two 5 ml glass vials  
 230 containing 1:1 ratio of (–)- $\alpha$ -pinene and 75% ethanol  
 231 (Erbilgin et al., 2001) were suspended from a wire  
 232 inserted through two small holes in the trap at ground  
 233 level.

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

250 The physical properties and sources of chemicals  
 251 used for pitfall and flight traps were (–)- $\alpha$ -pinene (CP:  
 252 >99%; enantiomeric ratios (ER): 96.6%(–)/3.4%(+)),  
 253 (+)- $\alpha$ -pinene (CP: >99%; ER: 95%(+)/5%(–))  
 254 (Aldrich Chemical Co., Milwaukee, WI), and 75%  
 255 ethanol (25% distilled water). Volatilization rates  
 256 under laboratory conditions (23°C) were 200 mg/  
 257 24 h for ethanol and 40 mg/24 h for  $\alpha$ -pinene.

### 258 2.3. Fungal sampling

259 We conducted a series of systematic root excava-  
 260 tions and isolations in four declining and four healthy  
 261 stands that were randomly selected during October  
 262 1998. In the declining sites, a circular transect was  
 263 established around the pocket margin, and another was  
 264 located 4 m further into the stand. Healthy plantations  
 265 were sampled in a similar fashion. We divided each  
 266 circle into four quarters, and within each quarter, one  
 267 tree was selected randomly. At 0.5 m from the tree  
 268 center, a 0.5 m deep trench was dug on the pocket side  
 269 halfway around the tree. The soil between the trench  
 270 and the tree was removed with a trowel to expose a  
 271 180° sector of the root collar and roots. Two primary  
 272 lateral root segments greater than 2 cm in diameter  
 273 were examined, and portions of the bark were

274 removed with a knife or chisel to examine for signs  
275 and symptoms of fungi, using the method of Klepzig  
276 et al. (1991). Root samples from each tree were placed  
277 separately in a plastic bag, kept on ice, brought to the  
278 laboratory ( $\leq 8$  h), and stored at 4°C. Eight trees were  
279 sampled on each of the eight plots in this study.

280 Intensive root excavation and sampling were con-  
281 ducted in three of nine declining sites during October  
282 1998. A 15 m long  $\times$  1.2 m deep  $\times$  70 cm wide trench  
283 was excavated by Wisconsin Department of Natural  
284 Resources personnel using a backhoe. The trench  
285 extended from 6 m inside the pocket margin to 9 m  
286 into the stand. Root samples were removed at trees (or  
287 stumps) at 6 and 3 m inside the pocket margin, at the  
288 pocket margin (0 m) and at 3, 6, and 9 m from the  
289 pocket margin. At each interval, one tree (or stump)  
290 was selected randomly. A total of six trees were  
291 selected in each of the declining sites. Roots on two  
292 primary lateral root segments were examined. Sample  
293 roots were placed separately in plastic bags on ice,  
294 returned to the laboratory, and stored at 4°C.

295 Roots obtained from both procedures were rinsed  
296 under a stream of water to remove soil, and phloem  
297 and xylem were exposed by removing bark with a  
298 flame-sterilized scalpel. If root samples had any stain-  
299 ing or resinosis, samples for isolation were collected at  
300 the margins of such features. In the absence of staining  
301 or resinosis, four samples were randomly taken along  
302 the root sample. Samples from roots were sectioned  
303 into small pieces ( $> 2$  mm) using a scalpel sterilized in  
304 bleach (12% CI) for 0.5–2 min, rinsed in sterile water,  
305 and transferred to potato dextrose agar (PDA). The  
306 PDA contained acidified 2% malt extract agar  
307 amended with 250 ppm chloramphenicol, 50 ppm  
308 *ortho*-phenylphenol, and 8 ppm benomyl and malt  
309 extract agar (MEA) with *ortho*-phenyl phenol med-  
310 ium. Plates were incubated at 20°C in growth cham-  
311 bers (24 h light and 60% humidity) and checked for  
312 fungal growth. Fungal species were identified by  
313 comparing cultures with reference cultures from Dr.  
314 T.C. Harrington (Iowa State University).

315 Additional field experiments were conducted to test  
316 whether *H. annosum* is associated with declining red  
317 pine stands in Wisconsin. Previous workers demon-  
318 strated that airborne spores can germinate on recently  
319 exposed wood, such as stump surfaces (e.g. Ross,  
320 1969; Bendz-Hellgren and Stenlid, 1998). We mod-  
321 ified the methods of Ross (1969) and Bendz-Hellgren

and Stenlid (1998) by using stem disks (3 cm thick and 322  
15 cm diameter) removed from freshly cut red pine 323  
trees. Each disk was placed in a petri dish (3 cm 324  
height  $\times$  16 cm diameter) containing a wet filter 325  
paper, and immediately taken to the field on ice in 326  
March 1999. Ten stem disks were placed in each of the 327  
17 sites. They were randomly placed along the pocket 328  
margin in declining stands, or in a ring around the 329  
center of symptomatic and asymptomatic control 330  
plots. As a positive control, 10 disks were placed in 331  
a red pine plantation in the Arena school forest, Iowa 332  
County, WI, that is known to be infected with *H.* 333  
*annosum* (Stanosz et al., 1995). After 4 h, the disks 334  
were brought to the laboratory over ice and incubated 335  
in plastics bags at 20°C (24 h light and 60% humidity) 336  
for 7–10 days in growth chambers, and examined for 337  
presence of conidiophores. Fungi were identified by 338  
comparing cultures with pure cultures maintained by 339  
Dr. J.N. Bruhn (University of Missouri-Columbia) and 340  
a pure culture isolated from fruiting bodies of *H.* 341  
*annosum* obtained from the Arena school forest. 342

#### 2.4. Statistical analyses 343

Data were analyzed using analysis of variance 344  
(ANOVA). Since data from 1997 are not complete, 345  
they are presented for informational purposes, but 346  
were excluded from statistical comparisons. For insect 347  
species which were caught in more than one type of 348  
trap, we limited statistical analysis to the type in which 349  
most were obtained. The only exception for this 350  
criterion was *H. porculus*, because this species was 351  
frequently caught in both flight and pitfall traps (see 352  
Section 3). We also limited statistical analysis to 353  
species for which substantial numbers of insects were 354  
obtained. This number varied with feeding guild, and 355  
was 3500 per 2-year for bark beetles and 1000 per 2- 356  
year for predators in funnel traps, and 1000 per 2-year 357  
for insects in lower-stem flight traps and root insects in 358  
pitfall traps. All statistical analyses were conducted 359  
within a single trap type. 360

We examined residual plots of each dependent 361  
variable from all traps. Square root ( $\sqrt{x}$ ) transforma- 362  
tion of raw data from funnel traps in conjunction with 363  
mixed models satisfied assumptions of normality and 364  
homogeneity of variance (Neter et al., 1983). Depen- 365  
dent variables were analyzed by repeated measure 366  
analysis in Proc Mixed (SAS Institute, 1996). 367

Assumptions for our model were that site and site  $\times$  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,  $\text{site}_i$  the site effect,  $\text{treatment}_j$  the treatment effect,  $(\text{site} \times \text{treatment})_{ij}$  the site  $\times$  treatment interaction (whole plot error), and  $(\text{treatment} \times \text{time})_{jk}$  the treatment  $\times$  time interaction. Assumptions for the model were that site and site  $\times$  trap were random effects. If the site or site  $\times$  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										
<i>Ips pini</i> (Say)	11045	25865	48007	100	147	106	5	17	7	85299
<i>Ips grandicollis</i> (Eichhoff)	3050	3966	13177	474	885	3947	24	27	94	25644
<i>Ips perroti</i> Swaine	– <sup>b</sup>	1056	1214	–	0	0	0	0	0	2270
<i>Hylastes porculus</i> Erichson	45	133	174	668	1499	1867	–	2031	1196	7613
<i>Gnathotrichus materiarius</i> Fitch	22	45	78	1879	3946	774	58	47	17	6866
<i>Orthotomicus caelatus</i> Eichhoff	3	123	315	328	1835	971	28	260	185	4048
<i>Dendroctonus valens</i> LeConte	93	135	131	194	160	792	52	32	92	1681
Curculionidae										
<i>Hylobius pales</i> (Herbst)	7	17	42	86	123	156	1321	1514	1189	4455
<i>Hylobius radialis</i> Buchanan	1	0	13	0	0	0	472	542	435	1463
<i>Hylobius assimilis</i> (Boheman)	0	0	0	0	0	0	158	182	145	485
<i>Pachylobius picivorus</i> (Germar)	0	2	0	0	0	0	16	55	46	119
<i>Pissodes</i> spp. <sup>a</sup>	57	41	36	606	527	583	61	105	92	2108
Cerambycidae										
<i>Rhagium inquisitor</i> (Gyllenberg)	30	44	30	172	200	144	12	5	6	643
<i>Monochamus carolinensis</i> (Olivier)	80	62	80	0	0	0	0	0	0	222
Trogossitidae										
<i>Grynocharis quadrilineata</i> (Melsheimer)	–	65	29	0	0	0	0	0	0	94
Bostrichidae										
<i>Apate monacha</i> (F.)	–	265	115	156	166	161	0	0	0	863
(b) Predators										
Cleridae										
<i>Thanasimus dubius</i> (F.)	3086	2487	1232	352	318	244	4	24	4	7751
<i>Thanasimus undatulus</i> (Say)	14	79	52	78	49	28	0	0	0	300
<i>Enoclerus nigripes</i> (Say)	322	74	21	285	150	153	8	9	7	1029
<i>Enoclerus nigrifrons</i> (Say)	1	12	28	0	0	0	0	0	0	41
<i>Zenodosus sanguineus</i> Say	–	98	30	–	0	0	0	0	0	128
Histeridae										
<i>Platysoma cylindrica</i> (Paykull)	841	598	289	0	0	0	0	0	0	1728
<i>Platysoma parallelum</i> Say	648	379	147	0	0	0	0	0	0	1174
<i>Platysoma aequum</i> LeConte	3	4	1	0	0	0	0	0	0	8
Tenebrionidae										
<i>Corticeus parallelus</i> (Melsheimer)	–	174	148	0	0	0	0	0	0	322
<i>Tenebroides collaris</i> (Sturm)	–	63	108	0	0	0	0	0	0	171
Total										156530

<sup>a</sup> 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 (+)- $\alpha$ -pinene:ethanol; pitfall traps baited with 1:1 ratio of (–)- $\alpha$ -pinene:ethanol.

<sup>b</sup> –: Indicates that species was not counted.

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

Bark beetles and predators showed different dis- 467  
tribution patterns with respect to stand conditions 468  
(Table 3). The numbers of *I. pini* and *I. grandicollis* 469  
did not vary among stand conditions. In contrast, the 470

Table 3  
Stem and root colonizing beetles obtained in red pine plantations of various conditions<sup>a</sup>

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

<sup>a</sup> Data show mean number ( $\pm$ 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.

<sup>b</sup> 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.

471 predators *T. dubius* and *P. parallelum* were signifi- 492  
472 cantly more abundant in the asymptomatic stands than 493  
473 in either tree mortality zones within declining stands 494  
474 or in asymptomatic sections of declining stands. 495  
475 Similarly, *P. cylindrica* were more abundant in healthy 496  
476 stands than in plots containing pockets, but their 497  
477 numbers were not different between the two types 498  
478 of controls. 499

479 Bark beetles and predators showed strong stand 500  
480 condition  $\times$  time interaction effects (*I. pini*: 501  
481  $F_{18,757} = 1.7$ ,  $P = 0.03$ ; *I. grandicollis*:  $F_{18,795} =$  502  
482  $2.7$ ,  $P = 0.00017$ ; *T. dubius*:  $F_{18,795} = 2.5$ ,  $P =$  503  
483  $0.0005$ ; *P. cylindrica*:  $F_{18,797} = 2.04$ ,  $P = 0.007$ ; *P.* 504  
484 *parallelum*:  $F_{18,795} = 1.9$ ,  $P = 0.013$ ). Both *I. pini* 505  
485 and *I. grandicollis* were significantly more abundant 506  
486 in declining than healthy stands early in the season 507  
487 (Fig. 1A). Later in the season, however, their numbers 508  
488 were significantly higher in healthy than declining 509  
489 stands. Predators showed different seasonal patterns 510  
490 than bark beetles (Fig. 1B). *Thanasimus dubius* were 511  
491 more abundant throughout the season in the healthy 512

than declining stands. *Platysoma* spp. showed patterns 492  
similar to *T. dubius*, and were almost always higher in 493  
asymptomatic controls than in other stand conditions. 494

The mean number of *D. valens* was significantly 495  
higher in plots located at the pocket margin than plots 496  
in either asymptomatic or symptomatic controls 497  
(Table 3). Populations of *Pissodes* were higher in 498  
stands that contain pockets, both in the declining 499  
and symptomatic regions, and in stands that do not 500  
contain pockets. There were no treatment  $\times$  time 501  
interactions for any of the species caught in lower 502  
stem flight traps (*Pissodes* spp.:  $F_{10,2587} = 1.4356$ , 503  
 $P = 0.1581$ ; *D. valens*:  $F_{10,2586} = 1.53$ ,  $P = 0.1213$ ; 504  
*H. porculus*:  $F_{10,2586} = 0.68$ ,  $P = 0.741$ ; *I. grandicol-* 505  
*lis*:  $F_{10,2586} = 1.6534$ ,  $P = 0.0861$ ; *O. caelatus*: 506  
 $F_{10,2586} = 1.2317$ ,  $P = 0.2647$ ; *G. materiarius*: 507  
 $F_{10,2586} = 1.47$ ,  $P = 0.1442$ ). 508

Surprisingly, the numbers of *H. pales* and *H. radialis* 509  
were significantly higher in the asymptomatic controls 510  
than in stands that contained pockets (Table 3). How- 511  
ever, there were strong stand condition  $\times$  time inter- 512

513 action for *H. pales* ( $F_{10,2818} = 5.25, P < 0.0001$ ), *H.*  
 514 *radicis* ( $F_{10,2818} = 5.75, P < 0.0001$ ), and *H. porculus*  
 515 ( $F_{10,2817} = 5.22, P < 0.0001$ ), indicating that their  
 516 relative trap catches among various stand conditions  
 517 varied throughout the season. This pattern is illu-  
 518 strated in Fig. 2. *Hylobius pales*, *H. radicis*, and *H.*  
 519 *porculus* were significantly more abundant in asymp-  
 520 tomatic stands than in pockets at the first collection  
 521 period. In contrast, later in the season, their numbers  
 522 were usually higher in the declining stands than in the  
 523 asymptomatic controls (Fig. 2). *Hylastes pales* and *H.*

524 *radicis* were more abundant in pockets than in either  
 525 control for three of the remaining sample periods, and  
 526 *H. porculus* were more abundant in pockets than  
 527 asymptomatic controls for three of the remaining  
 528 sample periods.

529 Insect numbers from each feeding guild varied by  
 530 year (Table 4). Overall, the numbers of *I. pini* and *I.*  
 531 *grandicollis* increased by 43 and 25%, respectively,  
 532 from 1998 to 1999. Trap captures of *T. dubius*, *P.*  
 533 *cylindrica*, and *P. parallelum* declined by 60, 61, and  
 534 64%, respectively. Relative population changes

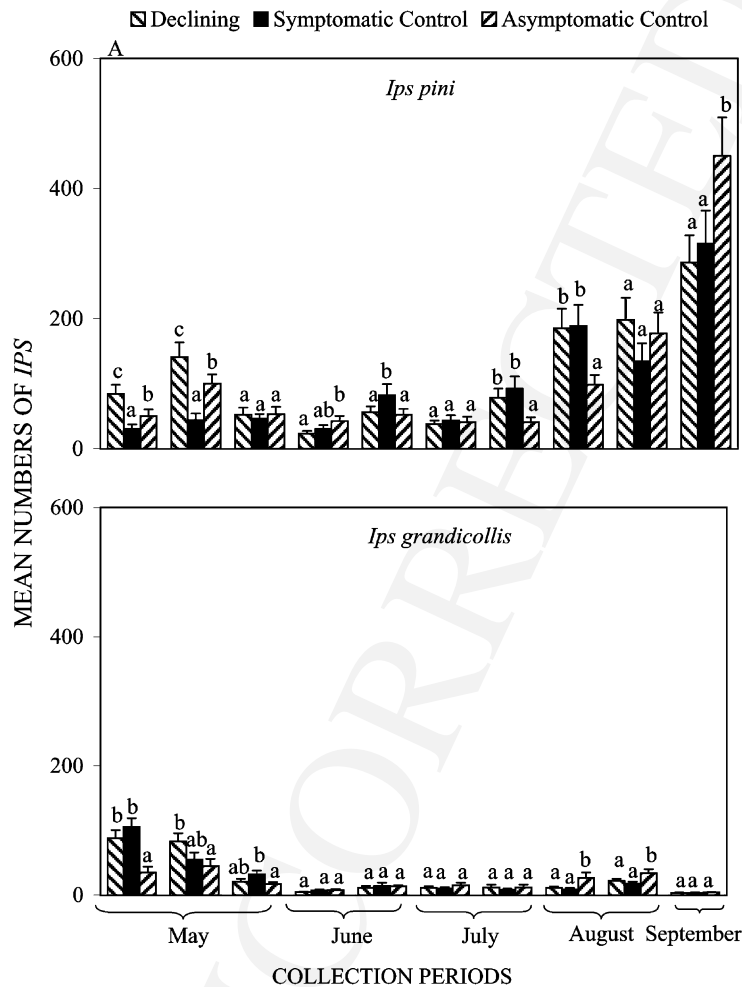


Fig. 1. Temporal distributions of bark beetles and predators in *Pinus resinosa* plantations of various stand conditions. (A) *Ips pini* and *Ips grandicollis*, (B) *Thanasimus dubius*, *Platysoma cylindrica*, and *Platysoma parallelum*. Data show mean number ( $\pm$ S.E.) of insects caught per trap 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.

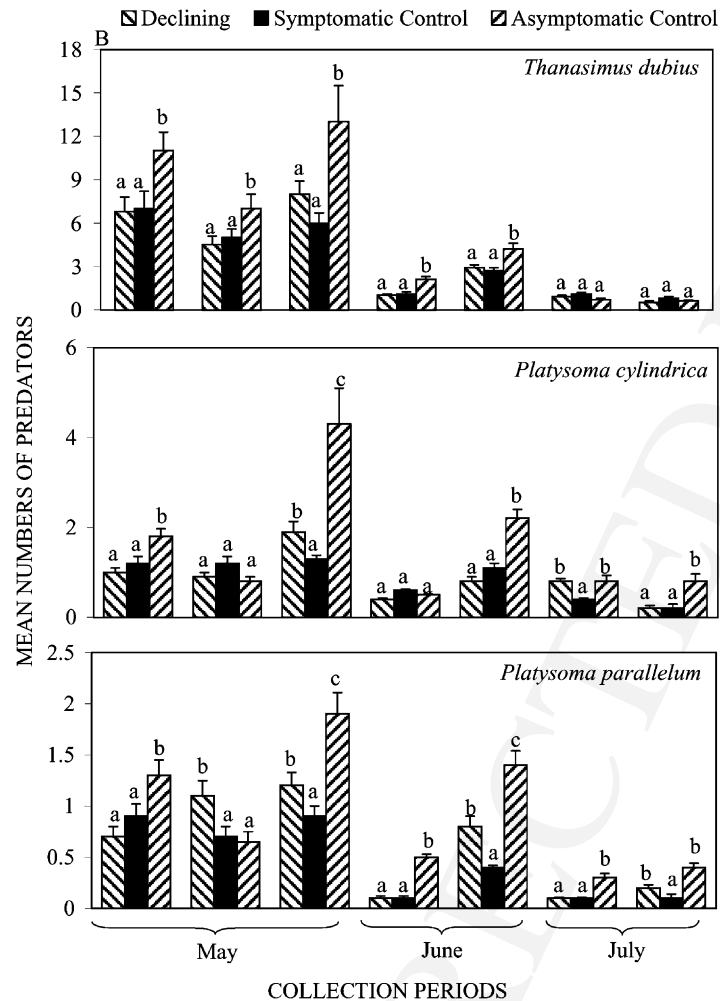


Fig. 1. (Continued).

535 between *Ips* and predators were consistent with a  
 536 time-delayed interaction at the site level. Ten of the  
 537 11 sites in which trap catches of *I. pini* increased from  
 538 1998 to 1999 were accompanied by decreases in trap  
 539 catches of *T. dubius*. Conversely, four of the six sites  
 540 in which trap catches of *I. pini* decreased were  
 541 accompanied by increases in trap catches of *T.*  
 542 *dubius*. Likewise, trap catches of *T. dubius* decreased  
 543 in 11 of the 16 sites in which the trap catches of *I.*  
 544 *grandicollis* increased. Numbers of some other  
 545 phloeophagous insects, particularly *O. caelatus*, *H.*  
 546 *pales*, and *H. radialis*, and the ambrosia beetle, *G.*  
 547 *materiarius*, declined from 1998 to 1999, with reduc-

548 tions ranging from 20 to 87%. Trap catches of the  
 549 lower stem feeding insects *D. valens* and *Pissodes*  
 550 spp. increased by 240 and 33%, respectively, from  
 551 1998 to 1999.

552 The principal fungi isolated from root samples were  
 553 *Leptographium procerum* (Kendr.) Wingfield and *Lep-*  
 554 *tographium terebrantis* Barras & Perry (Table 5).  
 555 There was a significantly higher incidence of these  
 556 fungi in declining than healthy stands ( $\chi_1 = 6.3083$ ,  
 557  $P = 0.012$ ). Logistic regression analysis indicated  
 558 that staining fungi isolated from roots of trees at  
 559 the pocket margin were significantly higher than those  
 560 4 m behind the pocket margin ( $\chi_1 = 10.2448$ ,  
 561  $P = 0.001$ ).

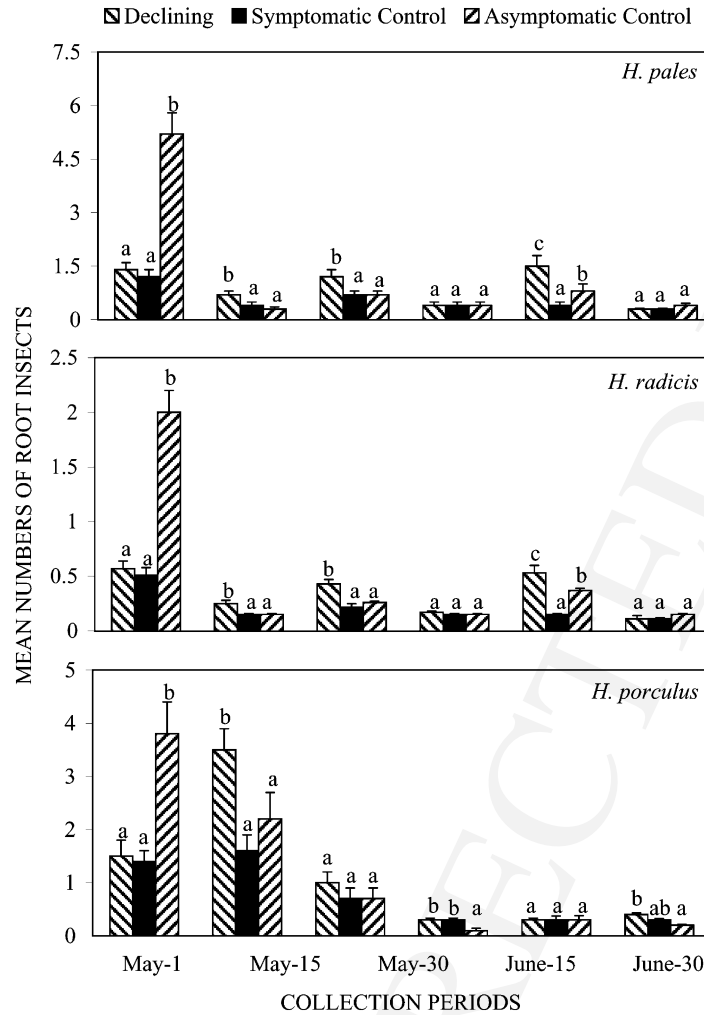


Fig. 2. Temporal distributions of root-colonizing beetles in baited pitfall traps. Data show mean number ( $\pm$ S.E.) of insects caught per trap per 15-day sample period. Data for each pitfall trap are averaged among sites within each stand condition, over 1998 and 1999. Bars with the same letter at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

561  $P = 0.0014$ ) (Table 5). In healthy stands, there was no  
 562 difference in the incidence of staining fungi between  
 563 the center and margin of plots.

564 Results obtained from the stand excavation studies  
 565 were similar to those of circular transect studies. In  
 566 declining stands, there was a significant effect of  
 567 distance from the margin on the incidence of staining  
 568 fungi ( $\chi_1 = 27.25$ ,  $P = 0.0001$ ) (Fig. 3). The inci-  
 569 dence of staining fungi was higher at the pocket  
 570 margin and 3 m beyond the pocket margin than at  
 571 other distances. The incidence of fungi declined there-  
 572 after.

*Heterobasidion annosum* and *Armillaria* spp. were 573  
 not isolated from any root samples or stem disks in 574  
 declining or healthy stands. However, the recovery 575  
 rate for capturing airborne spores of *H. annosum* on 576  
 stem disks in the site known to be infected (i.e. 577  
 positive control) was almost 40%. 578

#### 4. Discussion 579

A major difference between declining and healthy 580  
 red pine stands is that populations of predators of bark 581

Table 4  
Between-year variation in populations of stem- and root-colonizing beetles in red pine plantations<sup>a</sup>

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

<sup>a</sup> Data show mean number ( $\pm$ 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.

<sup>b</sup> 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.

582 beetles were lower in stands showing high tree mortality. This difference was more pronounced at the  
583 between-stand than within-stand level. That is, asymptomatic portions of declining stands had predator trap  
584 catches more characteristic of symptomatic areas of declining stands than of healthy stands. This suggests  
585 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  
591 affect populations of hymenopteran parasitoids of bark beetles (Hougardy and Grégoire, 2000), but we  
592 currently lack sufficient information to describe similar stand features for coleopteran predators. However,  
593 interactions between temporal patterns and stand condition suggest that dispersal of predators may con-  
594  
595  
596  
597

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
<i>L. terebrantis</i>	25	7	12.5	12.5
<i>L. procerum</i>	50	12	12.5	12.5
Total <sup>a</sup>	63	15	17	16

<sup>a</sup> 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.

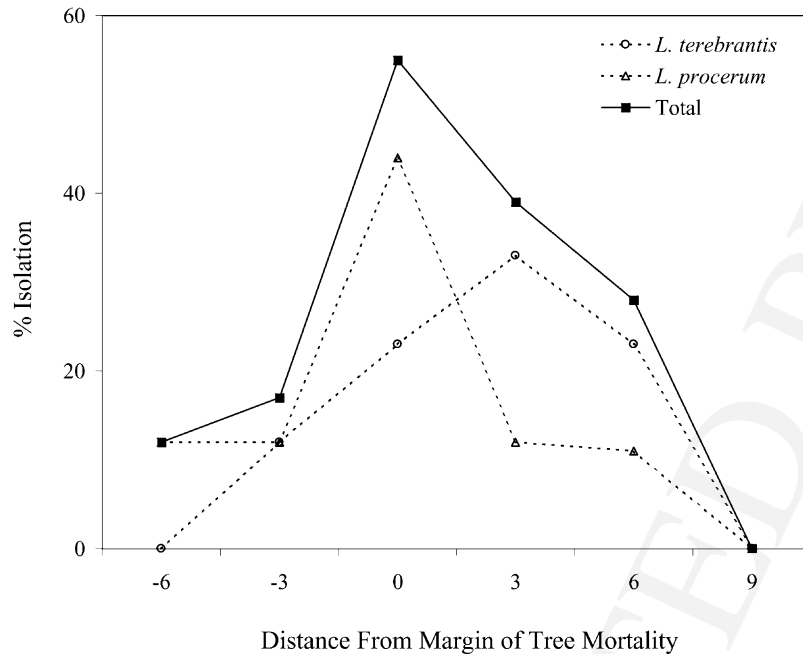


Fig. 3. Isolation of fungi from roots at various distances from margins of epicenter of tree mortality in *Pinus resinosa* plantations. Since some samples taken from the same root contained both *Leptographium* spp., total staining is relatively smaller than their arithmetical total. Statistical analysis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

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

607 Our results agree with Klepzig et al. (1991) that  
 608 populations of *D. valens* are higher in declining than in  
 609 healthy stands. Root and lower stem colonizing insects  
 610 also showed an association with declining red pine  
 611 stands, in agreement with Klepzig et al. (1991), but not  
 612 in a simple pattern. The higher total trap catch of root  
 613 insects in the healthy stands was opposite that  
 614 expected. It appears that temporal by stand condition  
 615 interactions, rather than total seasonal abundance, are  
 616 important. The results shown in Fig. 2 suggest that  
 617 dispersal may be important, with overwintering popu-  
 618 lations concentrated in stands with closed canopies,  
 619 followed by immigration into open and declining

620 stands. Direct observations of dispersal in spring  
 621 and early summer by *Hylobius abietis* (L.) have been  
 622 made in Europe (Solbreck, 1980; Nordenhem, 1989;  
 623 Nordlander et al., 1997). Approximately 90% of this  
 624 flight occurs within 2 weeks of emergence (Solbreck  
 625 and Gyldeberg, 1979; Solbreck, 1980), and most of  
 626 these weevils disperse over 10 km (Solbreck, 1980;  
 627 Nilssen, 1984). *Hylobius pales* is known to fly sub-  
 628 stantial distances in the southern USA, but less is  
 629 known about its dispersal in the northern USA. Rieseke  
 630 and Raffa (1993) suggested that dispersal of root  
 631 insects in Wisconsin, particularly *H. pales*, could be  
 632 substantial when densities are high.

633 The higher incidence of *Leptographium* in declining  
 634 than healthy stands is consistent with observations  
 635 on root staining and mortality by Klepzig et al. (1991),  
 636 and further supports the view that these fungi con-  
 637 tribute to Red Pine Decline. Trees farther than 6–9 m  
 638 away from the pocket margin have lower levels of root  
 639 mortality and infection than trees at or near the margin  
 640 of mortality. *Hylobius*, *Pachylobius*, *Hylastes*, and  
 641 *Dendroctonus* have been shown to vector *Leptogra-*

642 *phium* in Wisconsin (Klepzig et al., 1991), which may  
 643 partially explain the higher frequency of these fungi in  
 644 declining than in healthy stands (Table 5), and at  
 645 pocket margins than in asymptomatic regions of  
 646 declining stands (Fig. 3). Similarly Otrosina et al.  
 647 (1997) isolated *L. procerum* and *L. terebrantis* more  
 648 frequently from plots attacked by the southern pine  
 649 beetle, *D. frontalis* than control plots. The occasional  
 650 isolation of *Leptographium* from roots in asymptomatic  
 651 stands suggests that above ground symptoms  
 652 may not become visible until most of the root system is  
 653 diseased. Similarly, Kelsey et al. (1998) reported that  
 654 crown growth parameters did not change significantly  
 655 until more than one-third of the root system was  
 656 infected.

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

675 Our results provide further support to the view that  
 676 declines of forest stands are due to complex interactions  
 677 among multiple biotic and abiotic stresses, and  
 678 exhibit particular spatial and temporal patterns (Man-  
 679 ion and Lachance, 1992; Huettl and Muller-Dombois,  
 680 1993; Innes, 1993). In the system described here,  
 681 within-season temporal by inter-stand spatial patterns  
 682 of natural enemy abundance are important. The current  
 683 study suggests that a combination of low numbers  
 684 of predators (Fig. 1) and reduced host tree resistance  
 685 induced by root colonizing insects (Fig. 2) and pathogens  
 686 (Fig. 3), may contribute to stand declines. Sub-  
 687 sequent studies should identify stand factors that  
 688 facilitate the development, and attraction of these  
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