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Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida

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Abstract

Wildfires burned over 200,000 ha of forest lands in Florida from April to July 1998. This unique disturbance event provided a valuable opportunity to study the interactions of summer wildfires with the activity of pine feeding insects and their associates in the southeastern United States. We compared tree mortality with abundance of bark and ambrosia beetles, reproduction weevils and wood borers relative to fire severity. Over 27% of residual live trees in stands that experienced high fire severity died between October 1998 and May 1999. An additional 2–3% of trees that initially survived the fire died during the second year compared to <1% mortality in unburned stands. One year after the fire, more than 75% of the trees surviving in high fire severity stands had roots infected with one or more species of *Leptographium* and/or *Graphium* spp. and nearly 60% of the sampled roots were infected. No such fungi were recovered from roots of trees in unburned stands. Significantly, more root weevils, *Hylobius pales* and *Pachylobius picovorus*, were captured in unbaited pitfalls in the moderate and high fire severity stands than in the controls. Mean trap catches of *Ips grandicollis*, *Dendroctonus terebrans* and *Hylastes salebrosus*, three common bark beetles that feed on phloem tissue of pines, were lower in Lindgren traps in the fire-damaged areas than in the control stands. In contrast, catches of the ambrosia beetles, *Xyleborus* spp. and *Monarthrum mali*, were higher in burned stands than in control stands. The generalist predator, *Temnochila virescens* (Coleoptera: Trogositidae), showed a strong positive relationship between abundance and fire severity, while the flat bark beetle, *Silvanus* sp. (Coleoptera: Sylvanidae), exhibited the reverse trend. Our results show that most tree mortality occurred within 1 year of the fire. *Ips* or *Dendroctonus* bark beetle populations did not build up in dead and weakened trees and attack healthy trees in nearby areas. The prevalence of *Leptographium* spp. in roots may be a symptom of, or result in, weakened trees that may affect the trees' susceptibility to bark beetles in the future.
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1. Introduction

In 1998, wildfires burned more than 200,000 ha of forest land in Florida, creating opportunities for studying the relationships between fire and populations of bark beetles and reproduction weevils in the southern United States. Rarely has such a large area of southern pine forests been damaged by intense summer fires in this region. In March 1956, the Buckhead wildfire burned nearly 46,000 ha of the Osceola National Forest in northern Florida. However, the fire occurred in late winter when temperatures were low (12 °C) and burned through the forest within 2 days (Storey and Merkel, 1960). In contrast, the

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wildfires of 1998 occurred in June and July during an extended drought when Keetch-Byram drought indices were above 700 and temperatures exceeded 34 °C on most days. The fires directly killed large numbers of trees. However, the fate of the remaining live trees is uncertain, particularly with respect to threats from bark beetles and reproduction weevils.

The pine bark beetle complex (Coleoptera: Scolytidae) in the southern United States includes five common species that can cause tree mortality: the southern pine beetle, *Dendroctonus frontalis* (Zimmermann); the pine engravers, *Ips grandicollis* (Eichhoff), *I. calligraphus* (Germar), and *I. avulsus* (Eichhoff); and the black turpentine beetle, *D. terebrans* (Olivier). Of these, the southern pine beetle is the most aggressive, routinely killing relatively healthy trees over large areas across the south during outbreaks (Price et al., 1997). *Ips* spp. are less aggressive than southern pine beetle, with tree-killing attacks generally restricted to stressed or damaged trees. *Ips* spp. populations often build up in logging slash, as well as windthrown, drought-stressed or lightning struck trees. From these population foci, subsequent generations can emerge to attack apparently healthy adjacent trees (USDA Forest Service, 1985). Thatcher (1960) estimated that pine engravers were responsible for 3.7 million m^3 of timber loss annually in the southern United States, while Baker (1972) reported 1.1 million m^3 was killed annually in Florida alone. Black turpentine beetle is attracted to stumps and injured trees. Trees damaged or weakened by fire, old age, adverse weather or harvesting operations are frequently attacked. Although black turpentine beetle is usually considered a secondary pest which attacks only weakened or damaged trees, irregular outbreaks resulting in extensive tree mortality have occurred in all states along the Gulf of Mexico (USDA Forest Service, 1985).

The pine reproduction weevils, *Hylobius pales* (Herbst) and *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae), breed in the stumps and roots of recently cut, killed or severely damaged trees. Adults feed on the phloem tissue of seedlings or small branches of larger trees. Concentrated feeding by adults on seedlings often results in seedling mortality. Reproduction weevils can fly over 3 km to reach breeding sites, and adults can live 9 months or longer in the field (Bullard and Fox, 1969). Attraction of weevils to burned areas (Fox and Hill, 1973), and subsequent increases in weevil populations can seriously affect pine regeneration. Reproduction weevils have been implicated in the transmission of *Leptographium procerum* (Kendrick) Wingfield, a root infecting fungus reportedly capable of killing larger, mature pine trees (Nevill and Alexander, 1992a) and associated with red pine (*Pinus resinosa* Aiton) decline in northcentral USA (Klepzig et al., 1991).

We hypothesized that bark beetles and reproduction weevils would affect the long-term health of the forests in the vicinity of wildfires. Large numbers of dead and severely damaged trees would provide abundant host material to allow bark beetle populations to build up. As this initial host material was used up or deteriorated, we speculated that the beetles could go on to kill weakened trees that might otherwise have survived the fires. In addition, high beetle populations could spill over into nearby unburned areas killing seemingly healthy trees. The availability of large numbers of severely weakened trees could allow engraver beetles and black turpentine beetle to maintain high population levels over several years resulting in a prolonged cycle of forest decline, possibly compounded by *Leptographium* spp. infection.

We examined tree mortality, and the relative abundance of bark and ambrosia beetles, reproduction weevils and wood borers in areas impacted by the wildfires of 1998 in Florida. In addition, we estimated fire severity at the onset of the study, monitored tree mortality within study stands over a 2-year period, and sampled roots of live trees to determine the prevalence of *Leptographium* spp. 1 year after the wildfire.

2. Methods

2.1. Study area

We conducted the study on the Osceola National Forest in Baker and Columbia counties, Florida where approximately 8000 ha burned in July 1998 (82°30′W, 30°20′N). The area provided a full range of fire severity classes in a relatively small area. A further advantage of the site was that results from a previous wildfire on the forest were available for comparison (Storey and Merkel, 1960). The burned area included a variety of stand conditions ranging from slash pine (*Pinus elliottii* Engelm.) plantations to naturally regenerated longleaf pine (*Pinus palustris* Mill.) stands. The stands are typical of the coastal plain flatwoods with an understory dominated by saw palmetto (*Serenoa repens* Bartr.), gallberry (*Ilex glabra* L.), *Vaccinium* spp. and wiregrass (*Aristida beyrichiana*).

We established study plots in October 1998 (approximately 3 months after the fires) in three stands in each of the following fire severity classes: (1) no burn; (2) low severity fire (no crown damage); (3) moderate severity fire (some crown damage and resin exudation from bark near tree base) and; (4) high severity (almost complete crown scorch plus resin exudation). Fire severity classes could not be applied randomly because the stands were subjected to uncontrolled wildfire. Within each stand, we established five plots spaced 50–100 m apart. At each plot, we chose the 10 dominant or co-dominant living trees (some green foliage visible) closest to plot center. Tree diameter, fire severity (% crown scorch) and height of stem char were recorded for each tree along with the presence or absence of bark beetle or wood borer activity. Table 1 lists tree species and average diameter (cm) at breast height of the 50 trees selected in each stand. The trees were re-evaluated in January, May, July and October 1999, and June 2000 for mortality. In addition to our initial visual assessment of fire severity, we determined initial fire-caused tree mortality in each stand by conducting a 10 or 20 m wide strip cruise through each stand along a line connecting our five plots in January 1999. The width of the strips varied among stands depending on stand density, but we examined at least 100 trees per stand. All living and dead trees within the strips were counted and recorded.

2.2. *Insect trapping*

2.2.1. *Crawl and pitfalls traps*

In each of the five plots/stand, we installed one crawl trap (Hanula and New, 1996) on the bole of a live tree approximately 1 m above the ground to catch adult reproduction weevils crawling up the trees. Crawl traps consisted of a modified metal funnel inverted, attached, and sealed to the bark of a tree. A collection container was attached over the upturned spout of the funnel so that insects crawling up the tree bole move through the funnel and into the container. A "drift fence" constructed of 12 cm wide aluminum sheet metal was wrapped around the tree bole to increase the number of weevils captured. A gap in the fence beneath the crawl trap allowed weevils to move into the trap. The sheet metal was sealed to the bark with silicone caulk so insects could not go under it.

Pitfall traps consisted of 480 ml capacity plastic cups with drain holes in the bottom which were buried in the soil so the tops were even with the soil surface.

Table 1
Tree species and average ($\bar{x} \pm$ S.E.) diameters ($n = 50$ trees/stand), percentage of crown scorch and bole char height of trees in stands experiencing varying fire severities as a result of a wildfire on the Osceola National Forest, Baker County, FL, in July 1998

Fire severity	Compartment[a]	Tree species	Diameter (cm)	Percentage of crown scorch	Bole char[b] (m)
None (control)	88	Slash	24.4 ± 0.96	0 ± 0	1.7 ± 0.15
None (control)	98	Longleaf	27.9 ± 0.78	0 ± 0	2.2 ± 0.16
None (control)	98	Longleaf	31.5 ± 1.18	0 ± 0	2.0 ± 0.19
Low	68	Slash	28.6 ± 0.86	0 ± 0	1.7 ± 0.15
Low	66	Longleaf	31.7 ± 0.72	0 ± 0	2.3 ± 0.12
Low	49	Slash	25.5 ± 0.81	0 ± 0	4.1 ± 0.20
Moderate	42	Slash	23.8 ± 0.68	58.5 ± 4.08	8.2 ± 0.44
Moderate	67	Slash	30.0 ± 0.73	12.9 ± 2.12	6.3 ± 0.24
Moderate	65	Longleaf	31.4 ± 0.85	8.8 ± 2.22	5.8 ± 0.21
High	41	Slash	26.3 ± 0.93	70.6 ± 3.24	11.7 ± 0.43
High	42	Slash	22.2 ± 0.52	74.0 ± 18.65	11.4 ± 0.28
High	42	Slash	25.0 ± 0.64	63.2 ± 2.87	10.9 ± 0.37

[a] Compartment designations are those of the Osceola National Forest.

[b] Bole scorch in control plots was due to prescribed burns conducted 3–4 years before the start of the study.

A second collection cup filled with preservative solution (1% formaldehyde in a saturated NaCl solution) was placed inside the first. A funnel set inside the mouth of the larger cup directed weevils into the smaller cup. The funnel was coated with Fluon (Northern Products, Woonsocket, RI) to prevent weevils from escaping once they entered the trap. Following installation of the pitfall, four 1 m long pieces of aluminum sheet metal (20 cm wide) drift fence were inserted into the soil (15 cm above ground), so that the edges touched the pitfall cup and the drift fence sections radiated out from the trap at right angles with the trap in the center. Each trap was covered by a $15 \times 15\,\text{cm}^2$ piece of aluminum sheet metal supported by 30 cm long plastic garden stakes to reduce trap flooding by rainfall. Both crawl traps and pitfalls were operated continuously from October 1998 through June 1999, approximately 1 year after the fire. Samples were collected once per month, sorted, stored in 70% ethanol, identified and counted. Traps in the three control plots were relocated on 12 January 1999 due to prescribed burns scheduled for the previously selected control plots. We included data from trap catches in the original plots since all of the control plots were in the same general area and they were comparable in tree species, size and understory composition.

2.2.2. *Multiple-funnel traps*

In February 1999, three Lindgren 8-unit multiple-funnel traps (Lindgren, 1983) (Phero Tech, Delta, BC) were placed in each stand (36 traps total) to sample pine foraging species. Lindgren multiple-funnel traps are an effective tool for assessing the diversity and abundance of forest Coleoptera (Chénier and Philogène, 1989a; Miller and Maclauchlan, 1998). In each stand, traps were suspended between two trees on a rope within three of the five plots such that the top funnel of each trap was 1.3–1.5 m above ground. No trap was within 2 m of any tree. Each collection cup contained a small square ($5\,\text{cm}^2$) of Vapona (a.i. dichlorvos) to kill captured insects and prevent predation. Traps were operated continuously, and catches were collected at interval of 1–3 weeks until termination on 9 November 1999.

Two traps were baited with (±)-α-pinene from Aldrich Chemical (Milwaukee, WI), released from closed 30 ml Nalgene low-density polyethylene bottles (Fisher International, Atlanta, GA) at a rate of about 0.1–0.2 g/day at 25 °C and a longevity of about 120 days. (±)-α-Pinene is the most abundant monoterpene in the resin of longleaf pine (Mirov, 1961). The lure on one trap in each stand was replaced with a commercially produced (Phero Tech) high-release device consisting of a blue plastic pouch of (−)-α-pinene (chemical purity >95%) and a black plastic pouch of 95% ethanol, each with longevity of about 100 days. (−)-α-Pinene is the predominant monoterpene in slash pine (Mirov, 1961), while ethanol is a common host attractant for bark and wood-boring beetles (Fatzinger, 1985; Fatzinger et al., 1987; Chénier and Philogène, 1989b). The release rates of (−)-α-pinene and ethanol were about 1–3 g/day at 25 °C. All traps received new lures in February, May and August.

The use of high-release devices on one trap per plot was designed to increase trap competitiveness with the natural host tree attractants, since some stands contained large numbers of dead and dying trees. The use of low-release devices of (±)-α-pinene ensured consistency with longleaf pine monoterpene constituents and as a contingency against trap saturation. Trapping with multiple-funnel traps was repeated in 2000 by placing only one trap baited with the high-release devices in each stand. Traps were operated in the same manner from 1 March to 5 June 2000.

Traps baited with low-release devices caught substantially fewer beetles than those baited with high-release devices. Therefore, only catches in traps baited with high-release devices were used in analyses. The catches were summed for the period of 8–26 February, 8 March–2 April, and 12 April–30 July due to the late deployment of the high-release devices and from animal damage to several traps that resulted in lost trap catches during the periods of 26 February–8 March and 2–12 April. In 2000, catches were summed for the period 1 March–5 June.

2.3. *Leptographium on roots and weevils*

During the period August to October 1999, we sampled roots of six living pine trees per stand using a modified two-root excavation method (Alexander et al., 1981) to determine the prevalence of *Leptographium* spp. Segments (10–25 cm long) of two or sometimes three primary lateral roots were taken from each tree. Sampled root segments were isolated and transported in individual plastic bags. In the laboratory, individual roots were brushed free of debris and visually examined for the presence of insects or evidence of insect infestation (e.g., galleries, entrance holes, etc.). Roots then were split, debarked and 1–1.5 cm^2 chips of resin-soaked, stained or clear wood tissue were excised. These were surface sterilized by dipping in 95% ethanol followed by brief flaming. Surfaced sterilized sections were plated onto cycloheximide-amended (500 ppm) malt extract medium (Hicks et al., 1980). Plates were incubated under ambient laboratory conditions for 7–10 days and then examined for fungal growth and conidiophores characteristic of *Leptographium* spp.

We isolated *Leptographium* spp. from living *H. pales* and *P. picivorus* because regeneration weevils have been implicated in the transmission of *L. procerum* (Nevill and Alexander, 1992a). Adult weevils were collected from stands in high and moderate fire severity classes in August 1999, using fresh, split slash pine billets baited with a 1:1 mix of turpentine:ethanol. Each trap was made of 6–8 split billets (30 cm long and 5–10 cm wide) stacked on the ground over a piece of fine mesh fabric, covered with green boughs and baited. One billet trap was placed in each of five of the study stands and live weevils found beneath them were collected six days later. Fungal isolations were made from 52 weevils by gently rolling them across the surface of cycloheximide-amended malt extract medium. Plates were held for 10 days at ambient laboratory conditions and examined for colonies of *Leptographium* spp.

2.4. Statistical analysis

Tree mortality, pitfall and crawl trap data were analyzed using the SAS (1985) ANOVA procedure and Fisher's least significant difference multiple comparison test ($P \leq 0.05$). Weevil count data were transformed using the $\sqrt{x} + 0.5$ transformation, and beetle count data were transformed by $\ln(x + 1)$ to remove heteroscedasticity (Sokal and Rohlf, 1981). The SYSTAT 8.0 (SPSS, Chicago, IL) ANOVA and Fisher's least significant difference (LSD) multiple comparison test ($P \leq 0.05$) was used for analyses of Lindgren funnel trap data and *Leptographium* spp. prevalence data.

3. Results

3.1. Fire severity and tree mortality

Fire-related tree mortality, estimated from strip cruises about 6 months after the fire, validated the relationship between selection criteria and fire severity. Control stands contained an average of 1.6% (S.E. = 0.95) dead trees, low fire severity stands averaged 8.8% (S.E. = 8.0) dead trees, moderate fire severity stands averaged 37.6% (S.E. = 4.47) dead trees and high severity stands averaged 63.6% (S.E. = 7.66) dead trees. Estimated bole char height was a better predictor (based on correlation coefficient) of subsequent stand level mortality 1 year after the fire than estimates of percent crown scorch (Fig. 1).

Between 3 and 6 months after the fire, sample trees experienced an average mortality of 13.3% in the high severity stands which was higher ($F_{3,8} = 5.44$, $P = 0.025$) than tree mortality in the control, low or moderate fire severity stands for the same period (Fig. 2). Mortality among sample trees in the stands experiencing high fire severity continued beyond 6 months, doubling to 27.3% by May 1999. Mortality among sample trees in the stands that experienced moderate severity fires also doubled between 6 and 11 months after the fire but was still not significantly different from the controls. Almost all of the tree mortality occurred during the 11 months following the fire. Tree mortality continued to increase by 2–3% from July 1999 to June 2000 in the stands that received high and moderate intensity fires, while stands receiving no fire or low severity burns lost less than 1% of their trees.

3.2. Prevalence of Leptographium spp.

L. procerum and *L. terebrantis* Barras and Perry were recovered from roots and identified from stored cultures (determined by L. Eckhardt, Louisiana State University, Baton Rouge). Species determinations were not available at the time of the study, so we are uncertain which species was more prevalent.

A high proportion of the remaining live trees in the high fire severity stands had roots infected with *Leptographium* spp. 1 year after the fire (Fig. 3). Over 75% of the sampled trees in high fire severity stands had at least one root with *Leptographium* spp.

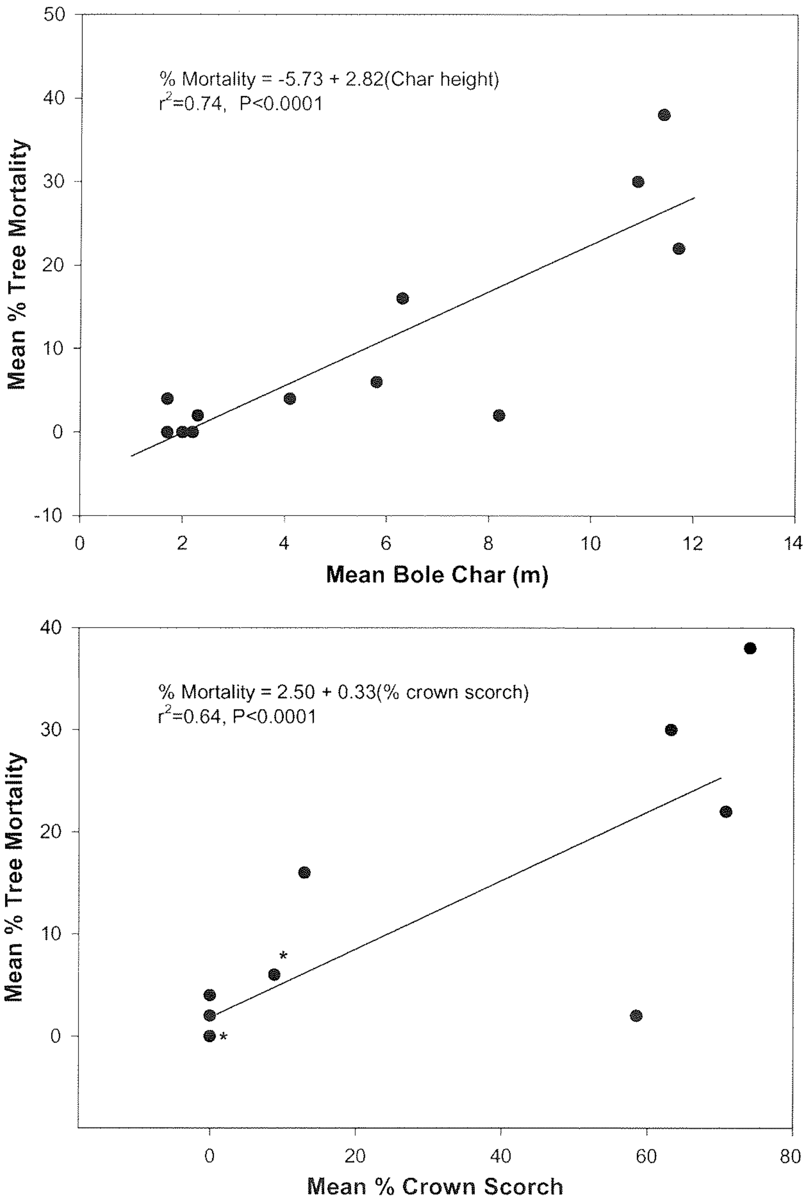

Fig. 1. Relationship of pine mortality 1 year after a wildfire in the Osceola National Forest in Florida to height of stem char and percent crown scorch estimated 3 months after the fire. Asterisks denote multiple observations per point.

infection. All of the roots were damaged at our sampling depth of 15–20 cm on the 18 trees sampled in the high fire severity stands, and nearly 60% of the sampled roots were infected. No *Leptographium* spp. were recovered from roots of sampled trees in the control stands, and less than 10% of the sampled roots and trees in stands that experienced low fire intensities were infected with *Leptographium* spp. fungi.

Reproduction weevil larval galleries were found in 15–20% of the sampled roots in stands in the high severity classes. Stands with no or low severity fires had 0–4% of the roots with evidence of weevil activity. *Leptographium* spp. were recovered from 50% of the

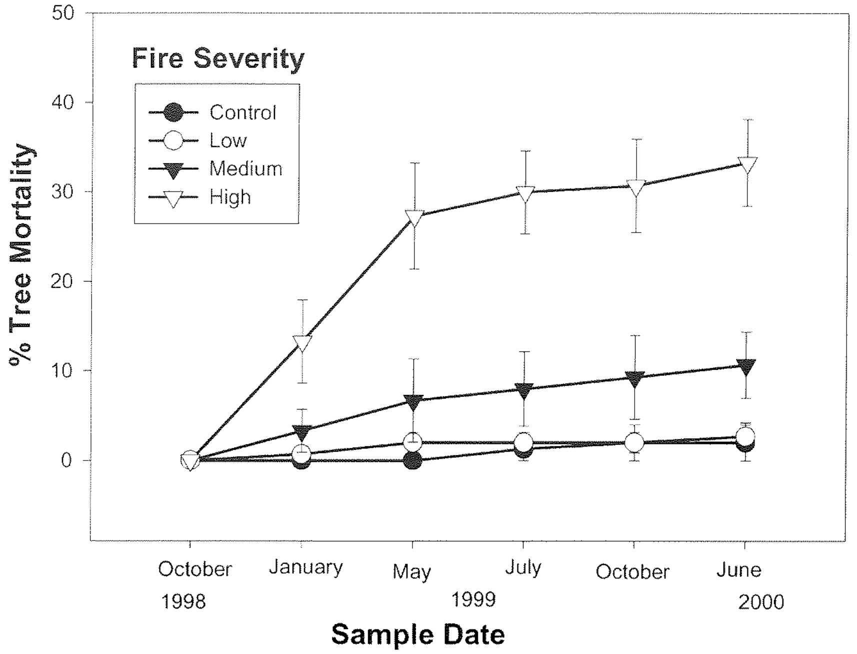

Fig. 2. Mortality of pine trees following a wildfire in July 1998 in stands experiencing differing fire severities on the Osceola National Forest in Florida.

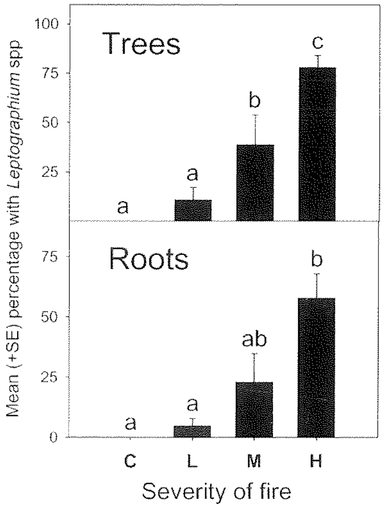

Fig. 3. Mean percentage of trees and roots infected with *Leptographium* spp. Two to three roots were sampled per tree from eight live trees/stand in stands that experienced low (L), moderate (M) and high (H) severity fire (as determined by bole and crown scorch) and control (C) stands on the Osceola National Forest, Florida, during the period August–October 1999. A tree was considered infected if *Leptographium* spp. were cultured from one root. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

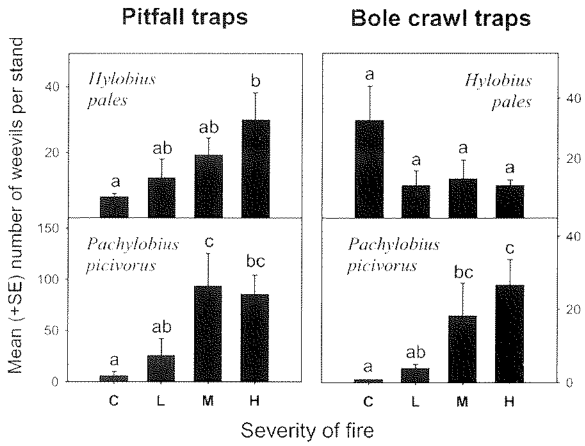

Fig. 4. Mean number of the reproduction weevils *H. pales* and *P. picivorus* captured in crawl traps on the boles of live trees and pitfall traps in the soil of stands that experienced wildfire of varying severities (low, L; moderate, M; high, H; severity fire and control, C stands) during the summer of 1998. Traps were operated continuously from October 1998 through June 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

pales weevils and 36% of the pitch-eating weevils collected from beneath pine billets in moderate and high fire severity stands.

3.3. *Insect abundance*

Insect trapping did not commence until October—3 months after the fire. Reproduction weevils were more abundant in pitfalls in stands where fire intensities reached moderate to high levels. Significantly, more pales and pitch-eating weevils were captured in unbaited pitfalls in the high fire severity stands than in the controls (Fig. 4). Pitch-eating weevils also were significantly greater in moderate fire severity stands. Abundance in unburned control stands and stands with low severity fires were similar for both weevil species.

Table 2

Mean number (±S.E.) per plot of reproduction weevils, bark beetles, wood borers and some predators captured in Lindgren multiple-funnel traps operated in mature pine stands from February 1999 to November 1999 and February 2000 to June 2000. The stands differed in the severity of wildfire that occurred in July 1998

Insect species	Fire severity[a]				F	P
	None	Low	Moderate	High		
Reproduction weevils						
H. pales[b]	145 ± 45	184 ± 43	117 ± 50	75 ± 10	1.28	0.346
P. picivorus[b]	23 ± 3	43 ± 5	32 ± 13	16 ± 3	2.48	0.135
Phloem feeders						
D. terebrans[c]	153 ± 37 a	34 ± 8 b	41 ± 34 b	12 ± 4 b	6.25	0.017
H. salebrosus[c]	106 ± 21 a	15 ± 9 b	19 ± 17 b	4 ± 3 b	10.9	0.003
Hylastes tenuis[c]	23 ± 12	8 ± 3	3 ± 1	4 ± 3	2.01	0.191
I. Grandicollis[c]	725 ± 47 a	232 ± 41 b	238 ± 41 b	195 ± 18 b	42.9	<0.001
Orthotomicus caelatus[c]	12 ± 5	2 ± 1	3 ± 2	3 ± 1	2.93	0.1
Xylem feeders						
Monoarthum mali[c]	16 ± 5	53 ± 22	102 ± 18	89 ± 43	2.25	0.16
Platypus flavicornis[d]	26 ± 17	34 ± 4	41 ± 13	38 ± 5	0.35	0.791
Xyleborus spp.[c]	541 ± 81 a	1371 ± 122 a	3245 ± 390 b	2874 ± 578 b	12.7	0.002
Xyloborinus saxeseni[c]	1539 ± 411	2188 ± 635	2420 ± 72	2041 ± 312	0.82	0.517
Xylosandrus crassiusculus[c]	50 ± 19	54 ± 18	88 ± 9	85 ± 11	1.8	0.224
Wood borers						
Acanthocinus nodus[e]	11 ± 2	41 ± 16	44 ± 10	19 ± 2	2.71	0.116
Acanthocinus obsoletus[e]	21 ± 5	94 ± 35	104 ± 8	81 ± 15	3.65	0.064
Arophalus rusticus[e]	40 ± 14	38 ± 9	26 ± 12	8 ± 2	1.98	0.195
Monochamus titillator[e]	6 ± 2	21 ± 11	16 ± 5	8 ± 4	1.22	0.363
Xylotrechus sagittatus[e]	41 ± 15	69 ± 10	46 ± 14	24 ± 3	2.61	0.123
Chalcophora georgiana[f]	34 ± 14	7 ± 2	5 ± 4	3 ± 2	3.57	0.067
Associated beetles						
Lasconotus sp.[g]	115 ± 61	66 ± 19	76 ± 8	70 ± 25	0.43	0.74
Silvanus sp.[h]	105 ± 30 a	29 ± 6 b	38 ± 12 b	34 ± 11 b	4.36	0.043
T. virescens[i]	292 ± 65 a	739 ± 40 ab	1062 ± 237 b	1775 ± 255 c	12.3	0.002

[a] Means within rows followed by the same letter are not significantly different according to the LSD procedure.

[b] Coleoptera: Curculionidae.

[c] Coleoptera: Scolytidae.

[d] Coleoptera: Platypodidae.

[e] Coleoptera: Cerambycidae.

[f] Coleoptera: Buprestidae.

[g] Coleoptera: Colydiidae.

[h] Coleoptera: Silvanidae.

[i] Coleoptera: Trogositidae.

Bole traps, which capture insects crawling up trees, also had significantly more *P. picivorus* in moderate and high fire severity stands but equal numbers of *H. pales*. In contrast, Lindgren traps captured approximately equal numbers of both reproduction weevils in all treatments over the entire study period (Table 2). However, fewer ($F_{3,8} = 6.13, P = 0.018$) *P. picivorus* were captured in Lindgren traps in the high severity stands during the spring 1999 trapping period than in stands that experienced less severe wildfire (Fig. 5) and more ($F_{3,8} = 6.34, P = 0.017$) were captured in the fall in stands experiencing low severity fire.

Lindgren traps captured significant numbers of bark and wood-boring beetles. Mean trap catches of *I. grandicollis* and *D. terebrans* were lower in the fire-damaged areas than in the control stands (Table 2). Likewise, *Hylastes salebrosus* Eichhoff was captured in higher numbers in stands that were outside the wildfire area. *I. grandicollis* was captured in higher numbers (spring 1999, $F_{3,8} = 24.58, P < 0.001$; fall 1999, $F_{3,8} = 7.66, P = 0.01$; spring 2000, $F_{3,8} = 10.97, P = 0.003$) in control plots throughout the study, although the greatest numbers were captured in spring of 1999 (Fig. 6). Catches of *D. terebrans* also were higher ($F_{3,8} = 5.10, P = 0.029$) in spring 1999 in control stands, but numbers were approximately equal in all stands during other trapping periods. *H. salebrosus* were captured in higher numbers in the control stands during spring ($F_{3,8} = 4.46, P = 0.04$) and fall 1999 ($F_{3,8} = 6.41, P = 0.016$).

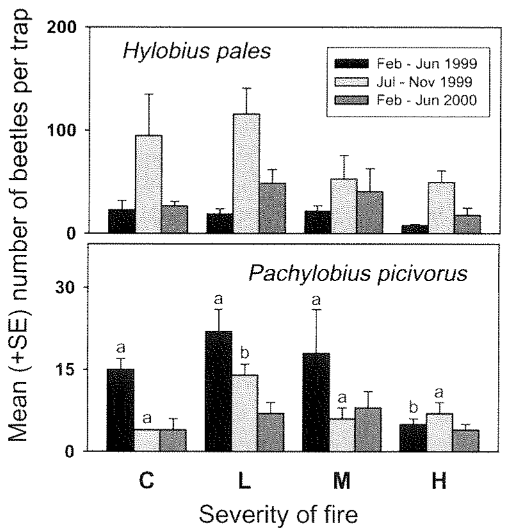

Fig. 5. Mean catches of reproduction weevils (Curculionidae) in multiple-funnel traps baited with ethanol and (−)-α-pinene in stands with low (L), moderate (M) and high (H) severity of fire scorch and control (C) stands on the Osceola National Forest in 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

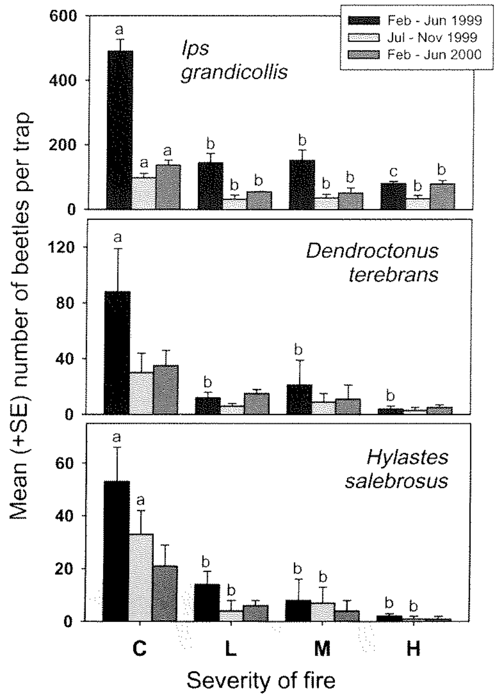

Fig. 6. Mean catches of bark (phloem-feeding) beetles in multiple-funnel traps baited with ethanol and (−)-α-pinene in stands with low (L), moderate (M) and high (H) severity of fire scorch and control (C) stand on the Osceola National Forest in 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

In contrast, catches of ambrosia beetles either were unaffected by fire or captured in higher numbers in the burned area. Total catches of *Xyleborus* spp. (Coleoptera: Scolytidae) were highest in stands within the fire-damaged areas (Table 2). *Xyleborus* spp. ($F_{3,8} = 26.45, P < 0.001$) and *M. mali* (Fitch) ($F_{3,8} = 5.65, P = 0.022$) were captured in higher numbers in burned stands in spring of 1999 (Fig. 7). *Xyleborus* spp. also were captured in higher numbers ($F_{3,8} = 8.98, P = 0.006$) in moderate and high severity stands in fall of 1999 (Fig. 7).

The numbers of wood borers captured were not affected by fire severity (Table 2). Only *Acanthocinus*

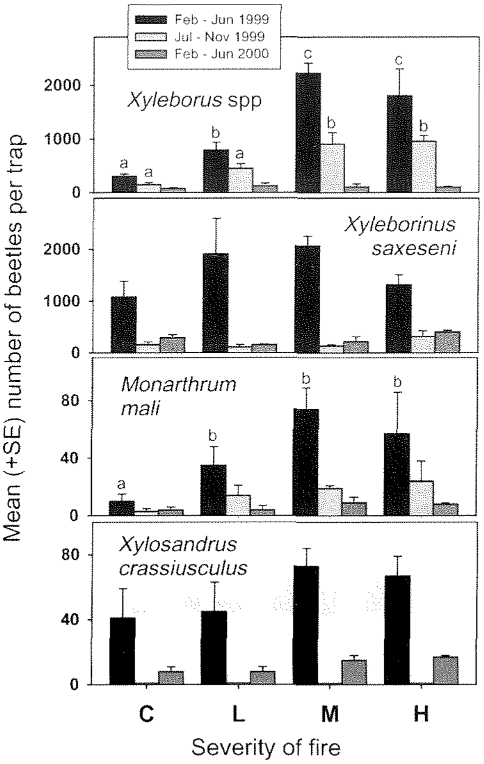

Fig. 7. Mean number of ambrosia (wood-feeding) beetles (Scolytidae and Platypodidae) in multiple-funnel traps baited with ethanol and (−)-α-pinene in stands with low (L), moderate (M) and high (H) severity of fire scorch and a control (C) stand on the Osceola National Forest in 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

nodosus (F.) (Coleoptera: Cerambycidae) was captured in higher numbers ($F_{3,8} = 4.86, P = 0.033$) in spring of 1999 in stands experiencing moderate fire severity (Fig. 8). High fire severity and unburned stands had the lowest numbers of *A. nodosus*.

Other species of beetles associated with bark and wood-boring beetles varied in abundances relative to fire severity. One general predator of bark and ambrosia beetles, *T. virescens* (F.) (Coleoptera: Trogositidae), showed a strong positive relationship between abundance and fire severity (Table 2), but by spring of 2000 the relationship was no longer evident (Fig. 5). The flat bark beetle, *Silvanus* sp. (Coleoptera: Sylvanidae), exhibited a negative relationship with more beetle captures occurring in the unburned control stands (Table 2). The trend was no longer evident in spring of 2000 (Fig. 9).

4. Discussion

Pine tree mortality increased within 6 months after the wildfire of 1998 with most of the mortality occurring during the first year. Mortality continued in the high and moderate fire severity stands through June 2000, but at a low rate. Storey and Merkel (1960) reported similar results following the Buckhead fire in 1956, although they found that all of the mortality occurred within 3 months. In comparison, our study started 3 months after the fire and an additional 30% tree mortality occurred in the high fire severity stands between that time and July 1999, 1 year after the fire. Since the two studies occurred in the same forest, the differences are likely due to either differences in fire dynamics, or stand structure and composition.

The 1956 Buckhead fire occurred in March when air temperatures were 12 °C, while the 1998 fire occurred during the summer when temperatures were twice as high. The Buckhead fire was a headfire that moved through the forest in less than 24 h. In contrast, shifting winds in 1998 moved the fire back and forth through the forest over several weeks consuming all of the organic layer on the forest floor in places. The amounts of stem char and crown scorch were similar in the two studies and the tree species were the same. Therefore, root damage may have been an important factor in the extended period of mortality we observed.

Wade and Johansen (1986) reported a prescribed burn that resulted in mortality of older trees while younger trees survived in a mixed age slash pine stand, although they observed no visible external tree damage. They suggested that the fire killed the upper feeder roots of all of the trees, but only the younger trees were capable of rapid root regeneration and recovery. We found over 75% of the trees and nearly 60% of the roots in stands that experienced high severity fire were infected with *Leptographium* spp. or a related *Graphium* sp. *Leptographium* spp. are pathogens of conifers throughout the world (Harrington and Cobb, 1988). *L. procerum* causes white pine root disease that can result in mortality of eastern white pine, *P. strobus* L. (Alexander et al., 1988), and *L. procerum* and *L. terebrantis* have been implicated in red pine (*P. resinosa*) decline (Klepzig et al., 1991) in Wisconsin. Both pathogens are thought to be transmitted by reproduction weevils and other root- and lower stem-feeding insects (Alexander et al., 1988;

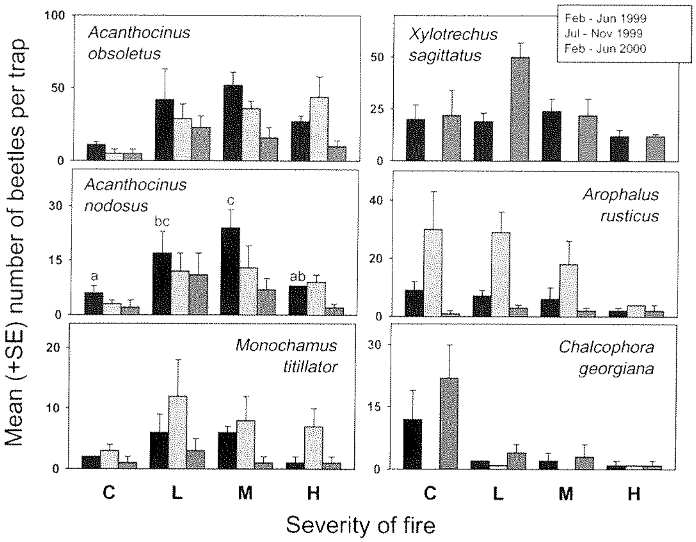

Fig. 8. Mean number of wood-borer beetles (Cerambycidae and Buprestidae) in multiple-funnel traps baited with ethanol and (−)-α-pinene in stands with low (L), moderate (M) and high (H) severity of fire scorch and a control (C) stand on the Osceola National Forest in 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

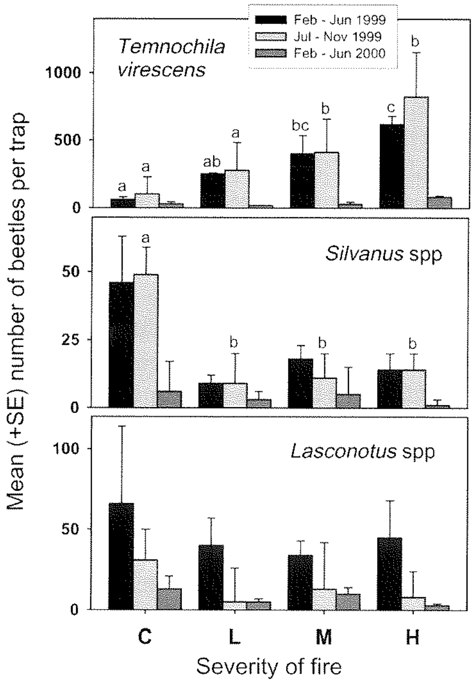

Fig. 9. Mean catches of bark beetle associates (Trogositidae, Silvanidae, and Colydiidae) in multiple-funnel traps baited with ethanol and (−)-α-pinene in stands with low (L), moderate (M) and high (H) severity of fire scorch and a control (C) stand on the Osceola National Forest in 1999. Bars within a graph with different letters above are significantly different at $P = 0.05$ (LSD test).

Wingfield et al., 1988; Klepzig et al., 1991; Nevill and Alexander, 1992a,b; Harrington, 1993; Malloch and Blackwell, 1993). However, the role of these fungi as pathogens of southern pines is uncertain. *Leptographium* spp., such as *L. terebrantis* and *L. procerum*, have been isolated from roots of a number of pine species in the southern United States (Barnard et al., 1985, 1991; Otrosina et al., 1997), but they have not been directly linked to tree mortality. Otrosina et al. (1997) found a higher prevalence of *Leptographium* spp. in roots of trees in stands with southern pine beetle activity, and speculated that infection by these fungi could predispose trees to beetle attack.

Geiszler et al. (1984) reported that percent root kill was the most important factor in determining the likelihood that bark beetles would attack fire-damaged lodgepole pine, *P. contorta* var. *latifolia* (Englm.). Likewise, Amman and Ryan (1991) noted higher than expected mortality of large diameter, thick-barked Douglas fir, *Pseudotsugae menziesii* (Mirb.) Franco, following the 1988 fires in the greater Yellowstone area, and suggested that unmeasured root damage may have been responsible. Despite the high levels of root damage we observed in stands that experienced high severity fires, the direct causes of tree mortality were not clear. We observed ips bark beetle, and occasionally black turpentine beetle, attacks on trees that died during the study. However, since these beetles regularly attack dead trees, it is impossible to know whether the trees died as a result of their activity. Dixon et al. (1984) reported bark beetle activity increased with increasing amounts of stem char on 7–15 year-old slash pine trees. In particular, they found that *I. calligraphus* initiated attacks on heavily damaged trees and then spread to nearby less damaged ones. They also reported finding trees attacked by *I. avulsus*, *I. grandicollis* and *D. terebrans*. Amman and Ryan (1991) studied bark beetle infestation of fire-damaged trees following the 1988 Yellowstone fires. Surveys of bark beetles before the fires showed mountain pine beetle, *D. ponderosae* Hopkins, populations were very low and had been declining over several years. Spruce beetle, *D. rufipennis* (Kirby), populations were low and pine engraver, *I. pini* (Say), populations were present but declining. Only populations of the Douglas fir beetle, *D. pseudotsugae* Hopkins, were increasing before the fires. Following the Yellowstone fires, they found that 67% of the Douglas fir died 2 years after the fires and 46% were attacked by *D. pseudotsugae*. Approximately, 49% of the lodgepole pine died and the majority of the insect attacks were pine engravers, while mountain pine beetles only attacked seven trees. Spruce beetles infested 50% of the Engelmann spruce, *Picea engelmannii* Parry ex. Engelm, trees that died. These data show that when bark beetle populations were present they were able to take advantage of some of the trees killed by fire, but the high numbers of uninfested dead trees suggests that fire killed the trees rather than bark beetles. Storey and Merkel (1960) tried to protect fire-damaged slash and longleaf pine trees following the Buckhead fire by spraying them with insecticide. They saw no difference in mortality of sprayed and unsprayed trees. Most of the mortality we observed occurred within a year of the fire which is similar to other studies in Florida (Storey and Merkel, 1960; Dixon et al., 1984) and we suspect that the trees died of fire-related injuries and not bark beetle attacks.

We determined that bark char height was a better predictor of subsequent mortality than crown scorch (Fig. 2). Likewise, Storey and Merkel (1960) found bark char was better for predicting tree mortality of slash and longleaf pines than crown damage. Wade and Johansen (1986) thought bud kill was the critical factor determining whether trees died as a result of fire. They considered crown consumption the best method of assessing bud damage. We saw no evidence of crown consumption in trees that were still living at the beginning of our study, 3 months after the wildfire, so it is unlikely the buds on our study trees were substantially damaged. Thus, basal damage or root damage most likely were the major reasons for tree death.

We saw no evidence of southern pine beetle attacks. Like the mountain pine beetle prior to the 1988 Yellowstone fires, southern pine beetle populations were low in Florida and had been since 1996 (Price et al., 1997; Meeker and Barnard, 1999, 2000), so they may not have been able to take advantage of an abundant resource.

Only four of our sample trees had black turpentine beetle attacks, and the highest numbers of these beetles were in traps in unburned stands. Unlike the southern pine beetle, black turpentine beetle populations were considered high in 1998 and 1999 in the southern United States because of drought-caused tree stress (Meeker and Barnard, 1999, 2000), and we caught relatively large numbers of black turpentine beetles in unburned stands. Therefore, it is doubtful that reduced local abundance accounted for the low numbers of black turpentine beetles in traps or attacks on trees in the burned stands. One possibility is that the large numbers of dead and weakened trees in the burned areas were more attractive than the traps and this resulted in reduced black turpentine beetle catches. However, black turpentine beetle catches were nearly 10 times lower in the low fire severity stands than in control stands, although the low severity stands had the same amount of tree mortality as the controls at the time the traps were operated. Therefore, if competition between traps and trees was a factor, we should have caught the same number of beetles in both the low severity and control stands where very few dead trees were available to compete with the traps.

Black turpentine beetles also attack fire-damaged trees (Dixon et al., 1984). In one study, black turpentine beetles were responsible for approximately 65% of the bark beetle attacks on longleaf pine in small 2 ha prescribed burn plots in South Carolina (B.T. Sullivan, personal communication). In that study, the small plot size may have allowed beetles to move into the plots from the surrounding forest. We are unsure why black turpentine beetles were not captured in higher numbers in traps in our fire-damaged stands, but the low numbers of infested trees suggests that they were not abundant.

We originally hypothesized that an abundance of dead and dying trees in stands of high and moderate fire severities would result in an extended period of tree mortality due to increased ips bark beetle activity. Ips beetles have six or more generations/year in the southern United States and are the most common phloem-feeding bark beetles attacking dead trees in this region. Our results show that most tree mortality occurred within 1 year after the fire. Although ips beetles were present in the forest throughout the study, we did not see prolonged tree mortality in severe and moderate fire severity stands or spread of the beetles into unburned portion of the forest as we hypothesized.

Like the black turpentine beetle, *Ips* spp. populations were considered high in 1998 and 1999 in the southern United States because of drought-caused tree stress and mortality (Meeker and Barnard, 1999, 2000). Only *I. grandicollis* was captured in our traps and they were more abundant in traps in unburned stands. Competition between nearby dead trees and the traps does not explain the differences in trap captures, since stands that experienced low fire severity had the same number of dying trees as the controls but still had significantly lower numbers of *I. grandicollis*. Again, we are unsure why fewer ips bark beetles were captured throughout the burned portion of the forest since *I. grandicollis* readily attacked scorched portions of tree boles in this and other studies (Dixon et al., 1984; Santoro et al., 2001). Other *Ips* spp. also have demonstrated an ability to use fire-damaged trees (Dixon et al., 1984; Geiszler et al., 1984; Werner, 1988; Amman, 1991). We found numbers of *I. grandicollis* declined instead of increased with time after the fire despite an abundance of dead and weakened trees. Ips bark beetles attacked many trees initially killed by the fire and trees that died later also were infested. However, a large number of trees that experienced severe crown and root damage, and should have been susceptible to bark beetle attack, remained alive 2 years after the fire.

In general, phloem-feeding bark beetles were less abundant in burned stands, while other Scolytidae were more abundant or were unaffected by burning. For example, *Xyleborus* spp. and *M. mali* were more abundant in moderate and high severity stands, while other ambrosia beetles were caught in similar numbers regardless of fire severity. Adults of these species tunnel into the sap- and heartwood of trees, seeding the galleries with "ambrosia" fungi (USDA Forest Service, 1985). The young are located several centimeters in the wood where they feed only on the fungi. As a result, they and their breeding material were likely insulated from direct damage by fire.

The higher abundance of reproduction weevils in pitfall traps in stands experiencing severe fires may have been due to attraction of weevils from surrounding areas in response to an abundance of suitable host material (i.e., dead and dying trees) and increased brood production. Fox and Hill (1973) found burned areas were attractive to pitch-eating weevils but not pales weevils. Reproduction weevil larvae develop in below ground portions of stumps and in roots where they and their host material are protected from fire. Most likely, many survived the fire and were able to take advantage of an abundant resource. Reproduction weevils are capable of flying over 3 km to reach breeding sites (Bullard and Fox, 1969), and they are common in mature pine stands in the Osceola National Forest (Hanula, unpublished data). So, it is possible that large numbers moved into the burned area from the surrounding forest.

It is unclear why captures of pales weevils in crawl traps did not exhibit the same trend of increasing numbers with increasing fire severity as in pitfalls while pitch-eating weevils did. Pales weevils may not climb up trees to feed as readily as pitch-eating weevils, although there were no living seedlings for them to feed on.

Captures of pitch-eating weevils in Lindgren traps were the reverse of pitfall traps, i.e., fewer in high severity stands. These weevils fly to terpene and ethanol sources released from black cylindrical silhouettes placed in contact with the ground (Fatzinger et al., 1987), so although the Lindgren traps may have been attractive in some respects, their height may not have been optimal. In addition, in areas with an abundance of breeding material, weevils may fly less and spend more time on the forest floor looking for oviposition sites.

5. Conclusion

Tree mortality caused by the wildfires of 1998 peaked by May 1999, although low levels (2–3%) of additional mortality continued through the following year. Whether this trend will continue is unknown. *Ips* and *Dendroctonus* spp. bark beetles did not build up populations in fire-damaged areas and then move into nearby undamaged forest areas as we originally hypothesized. However, the abundance of roots infected with *Leptograpium* spp. and at least two associated insect vectors in stands that experienced moderate to high severity fires raises the possibility that such stands may continue to undergo long-term delayed mortality similar to that observed by Ferguson et al. (1960) following a fire that caused extensive basal damage. Even without further insect-mediated disease transmission, the current levels of *Leptographium* spp. show that the root systems incurred significant damage as a result of the fires. In addition, the trees displaying high levels of crown scorch in areas where the fires were moderate to high severity. Therefore, those trees are likely to be under considerable stress for several more years and at increased risk of bark beetle attack.

Acknowledgements

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