

Population Dynamics of *Ips pini* and *Ips grandicollis* in Red Pine Plantations in Wisconsin: Within- and Between-Year Associations with Predators, Competitors, and Habitat Quality

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Environ. Entomol. 31(6): 1043–1051 (2002)

ABSTRACT We sampled bark beetle (Coleoptera: Scolytidae) populations in 17 declining and healthy red pine plantations in Wisconsin over 3 yr. We tested for potential relationships among numbers of bark beetles, conspecifics and competitors, and predators within and among flight seasons to help identify factors affecting population densities. The two most common bark beetle species obtained were *Ips pini* (Say) and *Ips grandicollis* (Eichhoff). The predominant predators obtained were *Thanasimus dubius* (F.) (Cleridae), *Platysoma cylindrica* (Paykull) (Histeridae), and *Platysoma parallelum* Say. Declining stands contained significantly more *Ips* than did healthy stands during the early portion of the season. Healthy stands had more predators than declining stands. There were strong delayed inverse relationships between *I. pini* and predators at the site level, both within and between flight seasons. The number of *I. pini* caught during the late portion of the season was lower when each of the above predators was more abundant earlier in the season, during both 1998 and 1999. Likewise, numbers of *I. pini* and *I. grandicollis* caught during the early portion of the year were inversely related to numbers of predators caught during the previous year. Although *Ips* trap counts showed significant correlations with each predator species, simple predator–prey models did not necessarily improve fits based on habitat quality (i.e., *Ips* numbers regressed on prior *Ips* numbers). We did not observe evidence for interspecific competition among *Ips* spp. This pattern is consistent with the view that host plant quality and predation jointly affect *I. pini* and *I. grandicollis* population dynamics. These results emphasize the importance of interactions among host tree physiology, predation, and dispersal in the population dynamics of phloeophagous herbivores, and have implications to forest management.

KEY WORDS population dynamics, *Ips*, predators, *Thanasimus*, *Platysoma*, conifer

BARK BEETLES (Coleoptera: Scolytidae) colonize the subcortical tissues of woody plants and play important roles in forest health, ecological processes, and economics. Several species kill large numbers of living trees during outbreaks; some exert intermittent losses following various predisposing stresses; and others degrade harvested timber by excavating galleries and vectoring fungi (Paine et al. 1984, Witcosky et al. 1986). Many species release aggregation pheromones that attract mates and additional colonizers, which can contribute to their tree-killing potential (Wood 1982). The underlying factors affecting the population dynamics of bark beetles have been investigated for several species in Europe, Asia, and North America.

These studies emphasize to varying degrees the roles of host availability (Safranyik et al. 1975, Berryman 1976, Paine et al. 1984, Zhang et al. 1992, Lawson et al. 1995), natural enemies (Weslien 1994, Reeve et al. 1998, Turchin et al. 1999), intra- and inter-specific competition (Thomson and Sahota 1981, Anderbrant 1990, Zhang et al. 1992, Lawson et al. 1995), and weather (Kalkstein 1976, Safranyik 1978, Werner and Holsten 1985, Bentz et al. 1991).

A progressive decline of red pine, *Pinus resinosa* (Aitman), plantations in the Great Lakes region of North America is initiated by a complex of predisposing factors that reduce host defenses against subsequent lethal attack by bark beetles (Klepzig et al. 1991, 1995). The predominant tree-killing species is the pine engraver, *Ips pini* (Say). Adult males select weakened trees as hosts and attract females; their brood larvae feed and develop in the phloem (Schenk and Benjamin 1969). In Wisconsin, males produce racemic ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale et al. 1991, Seybold et al. 1995, Miller et al. 1997). The most frequent congeneric

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associate of *I. pini* in Wisconsin is *Ips grandicollis* (Eichhoff), the eastern fivespined ips (Klepzig et al. 1991, Raffa 1991, Erbilgin and Raffa 2001a). Males produce the pheromone ipsenol (Vité et al. 1972).

There is no cross attraction between *I. pini* and *I. grandicollis* (Erbilgin and Raffa 2000). *I. pini* is multivoltine. In the laboratory, each generation requires ≈ 33 d (Aukema and Raffa 2002), and there are typically three generations per year in Wisconsin (Schenk and Benjamin 1969, Raffa 1991). *I. grandicollis* in the Great Lakes states may be bivoltine (Aukema et al. 2000a, 2000b) or univoltine (Ayres et al. 2001), presumably depending on temperature and latitude. *Ips perroti* Swaine is also present, but accounts for $<1\%$ of *Ips* spp. coming to mixtures of pheromone blends and logs in central Wisconsin (Aukema et al. 2000a, 2000b). No direct tests have been conducted on dispersal by *I. pini* or *I. grandicollis*, but experiments with other *Ips* spp. [e.g., *Ips typographus* L., *Ips perturbatus* (Eichhoff)] suggest that almost all beetles fly <200 m, which is substantially less than most *Dendroctonus* spp. (Zumr 1992, Duelli et al. 1997, Werner and Holsten 1997).

Thanasimus dubius (F.) (Coleoptera: Cleridae), *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae), and *Platysoma parallelum* Say are the most abundant predators of *Ips* spp. in the Great Lakes region (Schenk and Benjamin 1969, Herms et al. 1991, Raffa 1991, Aukema et al. 2000b, Erbilgin and Raffa 2001a). Adult *T. dubius* feed on adult *Ips* during colonization and then deposit eggs within crevices in the bark. After hatching, *T. dubius* larvae enter *Ips* galleries and prey on larvae within the phloem. In laboratory assays, these predators substantially reduce *I. pini* emergence at densities occurring in nature (Aukema and Raffa 2002). The *Platysoma* spp. feed on *Ips* eggs. All three predators are attracted to ipsdienol and ipsenol, to approximately equal degrees (Erbilgin and Raffa 2001a). These predators are "habitat specialists" in that they feed almost entirely on the fauna within trees colonized by scolytids, but consume many species within the subcortical habitat once they locate such trees (Schenk and Benjamin 1969, Miller 1986, Erbilgin and Raffa 2001b). The major predators are univoltine (Reeve 1997). In laboratory rearing, development of *T. dubius* in red pine averaged 65 ± 6 d (Aukema and Raffa 2002). Differences in development times between predators and prey have been proposed to contribute to time-delayed interactions in other bark beetle species (Reeve et al. 1996, Reeve 1997, Turchin et al. 1999).

There is increasing evidence that coleopteran predators can have important effects on the population dynamics of bark beetles. Evidence comes from predator exclusion experiments, laboratory assays, life tables, and time-series analyses of field populations (Miller 1986; Turchin et al. 1991, 1999; Weslien 1994; Schroeder 1996; Reeve 1997). However, the role of predators in the overall population dynamics and outbreak behavior of bark beetles remains unclear. For example, exclusion experiments can be less definitive with bark beetles than other herbivores because pred-

ators, additional colonizers, and competitors arrive simultaneously in response to scolytid pheromones (Lawson et al. 1997). Moreover, exclusion experiments do not permit analysis of individual predator species. Laboratory studies can provide controlled estimates of within-tree predation by particular species but do not relate directly to natural systems. Likewise, life table studies can quantify within-tree mortality but they cannot always identify effects of specific predators or distinguish predation from competition and allow only indirect estimates of mortality during dispersal. Time series analyses can detect correlations over long periods and can be especially powerful in detecting delayed density dependence. However, several authors (e.g., Williams and Liebhold 1995, Hunter and Price 1998) have identified concerns over time series analyses, including that they underestimate the importance of periodicity in abiotic factors (e.g., weather) and hence are prone to spurious correlations. Additionally, Ives et al. (2000) demonstrated that periodic mortality events, specifically winter in northern climates, can disrupt predator-prey oscillations, so within-season analyses are crucial for understanding population dynamics in multivoltine species.

We followed the approach of Wilson et al. (1991) of simultaneously sampling herbivore and predator populations across multiple stands within a relatively small region throughout several seasons. Our objective was to test for relationships between prey and predator densities at the site level, both within single flight seasons of a multivoltine bark beetle and over several flight seasons. These analyses were intended to complement the empirical studies and long-term data sets described previously. Simultaneous examinations of multiple populations provide more realistic conditions, but less experimental control, than direct manipulations. Likewise, they reduce the environmental variation inherent in time series analyses, but lack the long-term profile.

We evaluated data from 3 yr of trapping *Ips* spp. and predators in red pine plantations. We developed time-delayed models between *Ips* and their major predators at the site level. Based on our previous observations, we examined the model:

$$I p_{t+1} = \beta_0 + \beta_1 * I p_t - \beta_2 * T d_t - \beta_3 * P p_t - \beta_4 * P c_t - \beta_5 * I g_t + \epsilon \quad [1]$$

*I*_{*p*} is *I. pini*, *T*_{*d*} is *T. dubius*, *P*_{*p*} is *P. parallelum*, *P*_{*c*} is *P. cylindrica*, *I*_{*g*} is *I. grandicollis* (see Results), *t* is time, and ϵ is a random noise term. The β s are regression coefficients, and the given algebraic signs reflect prior expectations. We started with this model because known predators and congeneric species might be expected to yield negative relationships, and conspecifics might yield a positive relation because of reproduction, and these assumptions are tested in our analyses. Time is indicated by *t*, and *t*+1 (time at a later date) could refer to either later in the season or to the following year, depending on whether we were testing

Table 1. Seasonal distribution of *I. pini* and predators in *Pinus resinosa* plantations of varying stand conditions

Species	Mean no. (\pm SE)/Trap			Statistics ^a		
	Declining	Symptomatic control	Asymptomatic control	df (dn/dd)	F	P
<i>I. pini</i>						
Early season	116.9 \pm 12.8a	47.3 \pm 7.9c	88.8 \pm 11.7b	2,14	3.86	0.046
Mid season	50.3 \pm 6.7a	58.9 \pm 11.6a	51.8 \pm 8.3a	2,14	2.77	0.09
Late season	282.4 \pm 41.51a	292.5 \pm 50.9a	273.2 \pm 58.9a	2,14	2.16	0.152
<i>T. dubius</i>						
Early season	5.9 \pm 0.5b	6.0 \pm 0.9b	9.6 \pm 1.4a	2,14	5.13	0.021
Mid season	1.2 \pm 0.2b	1.1 \pm 0.2b	2.7 \pm 0.6a	2,14	5.02	0.023
Late season	0.4 \pm 0.1b	0.8 \pm 0.3b	2.1 \pm 0.5a	2,14	5.66	0.016
<i>P. cylindrica</i>						
Early season	1.2 \pm 0.4b	1.3 \pm 0.3b	2.2 \pm 0.4a	2,14	4.94	0.024
Mid season	0.4 \pm 0.1b	0.2 \pm 0.1b	0.9 \pm 0.2a	2,14	5.07	0.022
Late season	0.2 \pm 0.05a	0.4 \pm 0.1a	0.4 \pm 0.1a	2,14	2.80	0.095
<i>P. parallellum</i>						
Early season	0.7 \pm 0.1a	0.7 \pm 0.1a	1.3 \pm 0.2b	2,14	4.33	0.034
Mid season	0.4 \pm 0.1a	0.1 \pm 0.05b	0.5 \pm 0.1a	2,14	4.51	0.031
Late season	0.1 \pm 0.03a	0.01 \pm 0.01a	0.1 \pm 0.01a	2,14	2.01	0.170

Means followed by the same letter within a row are not significantly different ($P < 0.05$, Repeated Measures Analysis in Proc Mixed, SAS Institute 1996). Means are based on averages over sites over 1998 and 1999. Fisher's protected LSD test ($P < 0.05$) was used for multiple comparisons of means of log-transformed data. Untransformed means and standard errors are shown.

^a Test of significance among stand conditions within single portion of the season.

for intra- or inter-seasonal relationships. We likewise searched for similar relationships with *I. grandicollis*:

$$I_{g,t+1} = \beta_0 + \beta_1 * I_{g,t} - \beta_2 * Td_t - \beta_3 * Pp_t - \beta_4 * Pc_t - \beta_5 * Ip_t + \epsilon. \quad [2]$$

Materials and Methods

Study Site and Experimental Design. We conducted field experiments in 17 red pine plantations in west-central Wisconsin during 1997–1999. Site features are described in Erbilgin and Raffa (2002). The plantations ranged from 42 to 52 yr old (46 ± 1), were located within a 64-km radius, and were not subjected to management over the course of the study. We monitored *Ips* and predator populations in three kinds of stand conditions, using traps baited with *Ips* pheromones. Nine declining stands contained gaps of dead trees and peripheral zones of stressed trees and exhibited progressive spread of symptoms into healthy sections. Four “symptomatic controls” consisted of healthy portions of stands that contain a neighboring section displaying the above symptoms. Four “asymptomatic controls” consisted of plots in healthy stands, i.e., in which no portion of the stand showed any sign of mortality or stress. The edges of asymptomatic stands were located ≈ 500 m from the edges of declining stands. Plots within declining stands were established at the gap margin, and plots within symptomatic controls were established at least 200 m away from gaps. Plots within healthy stands (asymptomatic controls) were established randomly within the stands.

We deployed four 12-unit multiple funnel traps in each site (Lindgren 1983), with ≈ 25 m between traps. Each trap was suspended from a rope between two trees. The traps were arranged in two rows of two traps each, extending along edges of the pocket as described

in Erbilgin and Raffa (2002). One trap in each row was baited at random either with racemic ipsdienol (chemical purity, 98%) plus lanierone (chemical purity, 98%), or ipsenol alone (chemical purity, 98%). *I. pini* and *I. grandicollis* counts were based on traps with ipsdienol with lanierone and ipsenol, respectively; and predator counts were based on all traps. Pheromones were obtained from Phero Tech (Delta, British Columbia) and released from 20-mg bubblecaps. No-pest strips (Pest STRIP, Loveland Industries, Greeley, CO) in the collection jars killed arriving insects and prevented predation. Funnel traps were sampled every 2 wk from the second week of May through the last week of September in 1997, and from the last week of April through the last week of September in 1998 and 1999.

Statistical Analyses. The raw data (counts) were log ($y+1$) transformed to satisfy assumptions of homogeneity of variance (Neter et al. 1983). Because sampling began later in 1997, only those analyses based on late-year samples were used for that year.

Within-Year Analyses. A seasonal pattern of *I. pini* of three generations per year has been reported for this region by Schenk and Benjamin (1969) and later substantiated in the laboratory by (Aukema and Raffa 2002). Our analysis is based on combining the bi-weekly trap counts into three distinct periods. We formally tested for and verified the presence of three distinct periods using analysis of variance (ANOVA) and pair-wise contrasts within an autoregressive repeated measures analysis using SAS Proc ANOVA (SAS Institute 1996). Data within each putative time period were combined using pooled data from 1998 and 1999. We termed the three distinct flight periods as early, mid, and late (see Results) and structured our comparisons among stand conditions and analyses re-

Table 2. Results for regression of trap counts of *I. pini* and its associated insects among different portions of single flight seasons at the site level

Intercept	Td _{EM}	Pc _{EM}	Pp _{EM}	Ip _{EM}	Ig _{EM}	MSE	F	df	P	R ²
1998										
4.210	-0.959					0.1189	44.80	1,15	<0.0001	0.749
3.348		-0.848				0.1576	30.11	1,15	<0.0001	0.667
3.338			-0.912			0.1869	23.02	1,15	0.0002	0.606
-2.562				1.763		0.1717	26.40	1,15	<0.0001	0.638
-1.313					1.693	0.2569	12.67	1,15	0.0029	0.458
-2.888				1.389	0.625	0.1668	14.30	2,14	0.0004	0.671
4.037	-0.950			0.378	-0.413	0.1273	14.28	3,13	0.0002	0.767
2.573	-0.764			0.450		0.1220	22.14	2,14	<0.0001	0.760
0.391		-0.515		0.916		0.1337	19.59	2,14	<0.0001	0.737
-0.173			-0.494	1.092		0.1409	18.22	2,14	<0.0001	0.722
1999										
4.454	-0.806					0.0687	20.98	1,15	0.0004	0.583
3.562		-0.599				0.0752	17.85	1,15	0.0007	0.543
3.544			-0.587			0.1053	8.47	1,15	0.0108	0.361
-0.612				1.280		0.0512	33.27	1,15	<0.0001	0.689
-0.354					1.265	0.0519	32.62	1,15	<0.0001	0.685
-0.956				0.732	0.708	0.0393	24.44	2,14	<0.0001	0.777
-2.524	0.283			0.807	1.028	0.0405	16.01	3,13	<0.0001	0.787
0.930	-0.309			0.927		0.0490	18.20	2,14	<0.0001	0.722
0.123		-0.139		1.063		0.0532	16.25	2,14	0.0002	0.699
-0.099			-0.145	1.140		0.0524	16.57	2,14	0.0002	0.703

Analyses show relationships of *I. pini* trap counts late in a flight season with abundances of various single species and combinations earlier in the season.

EM: Early and Middle part of year; L: Late part of same year.

Ip: *I. pini*; Td: *T. dubius*; Pc: *P. cylindrica*; Pp: *P. parallelum*; Ig: *I. grandicollis*

A coefficient in italics is not significantly different from zero at $P < 0.05$.

lating herbivore abundance to predators and competitors, accordingly.

Numbers of *I. pini* captured late in the flight season were regressed on insect numbers captured in the sum of the early and mid parts of the flight season, using models with one or more predictor variables. Because most *I. grandicollis* were caught early in the season (Erbilgin and Raffa 2002), we did not perform within-year analyses with this species. The units of replication were the total numbers of insects for a given site averaged across biweekly samples within a period and also across years. Insect associates included the predators *T. dubius*, *P. cylindrica*, and *P. parallelum*, the competitor *I. grandicollis*, and conspecifics (see Results). To aid in interpretation of the effects of predators, we used Pearson correlation coefficients to quantify correlations among all combinations of species pairs among the major predator species.

Between-Year Analyses. The same groupings of time periods were used for between-year analyses. *I. pini* in the early part of a given year (t+1) were regressed on numbers of insect associates summed over early, mid, and late flight seasons of the previous year (t), as well as concurrent *I. grandicollis* at time t. The units of replication were the numbers of insects averaged across all traps and across years for a given site. Similar analyses were performed for *I. grandicollis* in the early part of given year (t), using associated predators but with *I. pini* as the potential competitor. We used Pearson correlation coefficients to assess the correlations among all combinations of species pairs among the major predator species.

Results

Insect Abundances, Stand Condition, and Flight Activity Periods. The predominant phloeophagous herbivore was *I. pini*, which constituted $\approx 77\%$ of 110,000 *Ips* individuals. More than 95% of all phloeophagous insects caught were *I. pini* and *I. grandicollis*. We therefore limited analyses to these two species. The mean numbers of *I. pini* ($F_{1,178} = 8.37, P = 0.0043$) and *I. grandicollis* ($F_{1,178} = 78.7, P < 0.0001$) varied between years. However, there were no year by stand condition interaction effects on either species ($F_{2,178} = 1.09, P = 0.2979$ for *I. pini*; $F_{2,178} = 1.69, P = 0.1875$ for *I. grandicollis*), indicating that the relative effect of stand condition was the same for both years.

Overall, different abundances of *I. pini* were attributable to different portions of the flight season ($F_{2,32} = 33.89, P < 0.0001$), and paired-contrast comparisons indicated three generally distinct periods. The period of 25 April to 15 June differed from 15 June to 30 July ($F_{1,32} = 9.47, P = 0.0043$), which differed from 30 July to 30 September ($F_{1,32} = 66.44, P < 0.0001$), and the period of 25 April to 15 June differed from 30 July to 30 September ($F_{1,32} = 25.74, P < 0.0001$). Hereafter, these are referred to as early, mid, and late portions of the flight season, respectively, and are treated separately.

Trap catches of *I. pini* showed significant flight period by stand condition interactions ($F_{4,28} = 3.45, P = 0.021$). Declining stands had significantly more *I. pini* than healthy stands during the early portion of the flight season, but there was no difference related to

Table 3. Results for regression of trap counts of *I. pini* and associated insects among flight seasons at the site level

Intercept	Td _(t-1)	Pc _(t-1)	Pp _(t-1)	Ip _(t-1)	Ig _(t)	Ig _(t-1)	MSE	F	df	P	R ²
1997-1998											
3.776	-0.534						0.0516	25.79	1,15	<0.0001	0.632
3.306		-0.417					0.0630	18.36	1,15	0.0007	0.550
3.335			-0.449				0.0614	19.26	1,15	0.0005	0.562
-0.716				1.256			0.0058	346.00	1,15	<0.0001	0.958
0.667					0.937		0.0783	11.85	1,15	0.0036	0.441
1.510						0.580	0.0770	12.33	1,15	0.0032	0.451
-0.789				1.190	0.116		0.0056	179.93	2,14	<0.0001	0.963
3.899	-0.551				-0.041		0.0552	12.05	2,14	0.0009	0.633
-1.466	0.098			1.275	0.231		0.0055	122.76	3,13	<0.0001	0.966
3.429	-0.470					0.105	0.0544	12.33	2,14	0.0008	0.638
-0.676				1.170	0.094		0.0051	198.15	2,14	<0.0001	0.966
-1.173	0.084			1.253	0.145		0.0050	136.38	3,13	<0.0001	0.969
-0.657	-0.009			1.242			0.0062	161.74	2,14	<0.0001	0.959
-0.386		-0.057		1.165			0.0055	185.02	2,14	<0.0001	0.964
-0.537			-0.031	1.207			0.0061	166.57	2,14	<0.0001	0.960
1998-1999											
3.651	-0.552						0.0446	35.88	1,15	<0.0001	0.705
3.215		-0.499					0.0635	20.69	1,15	0.0004	0.580
3.293			-0.583				0.0516	28.95	1,15	<0.0001	0.659
0.075				0.837			0.0453	35.04	1,15	<0.0001	0.700
0.511					0.807		0.0954	8.76	1,15	0.0097	0.369
0.367						0.972	0.0975	8.26	1,15	0.0016	0.355
0.155				0.889	-0.092		0.0482	16.51	2,14	0.0002	0.702
5.460	-0.777				-0.532		0.0407	20.88	2,14	<0.0001	0.749
4.007	-0.568			0.302	-0.477		0.0419	13.70	3,13	0.0003	0.760
4.680	-0.666					-0.352	0.0450	18.17	2,14	<0.0001	0.722
-0.007				0.804	0.078		0.0483	16.45	2,14	0.0002	0.701
3.018	-0.433			0.326	-0.251		0.0464	11.94	3,13	0.0005	0.734
1.933	-0.300			0.410			0.0444	18.56	2,14	<0.0001	0.726
0.698		-0.122		0.680			0.0470	17.32	2,14	0.0002	0.710
1.363			-0.283	0.521			0.0396	21.65	2,14	<0.0001	0.756

Analyses show relationships of *I. pini* trap catches early in a flight season with abundances of various single species and combinations late in the prior season.

t: early part of year; t-1: entire previous year; Ip: *I. pini*; Td: *T. dubius*; Pc: *P. cylindrica*; Pp: *P. parallelum*; Ig: *I. grandicollis*
 A coefficient in italics is not significantly different from zero at $P < 0.05$.

stand condition during the other two periods (Table 1).

About 11,000 predators were obtained, of which 89% were three species, *T. dubius* (62%), *P. cylindrica* (16%), and *P. parallelum* (11%). Therefore, analyses were limited to these three species. Predators showed no differences in their responses to the synthetic pheromones of *I. pini* versus *I. grandicollis* ($F_{1,15} = 2.233$, $P = 0.156$ for *T. dubius*; $F_{1,15} = 2.187$, $P = 0.16$ for *P. cylindrica*; $F_{1,15} = 0.503$, $P = 0.489$ for *P. parallelum*). Numbers of *T. dubius* ($F_{1,376} = 51.0$, $P < 0.0001$), *P. cylindrica* ($F_{1,376} = 55.53$, $P < 0.0001$), and *P. parallelum* ($F_{1,376} = 54.74$, $P < 0.0001$) varied between years. However, as with *Ips*, there were no year by stand condition interaction effects on any species ($F_{2,376} = 1.34$, $P = 0.4670$ for *T. dubius*; $F_{2,376} = 2.37$, $P = 0.0946$ for *P. cylindrica*; and $F_{2,376} = 1.80$, $P = 0.1674$ for *P. parallelum*).

The trap catch patterns of predators across stand conditions also changed as the season progressed (Table 1). Healthy stands had higher trap catches of *T. dubius* than either symptomatic or asymptomatic portions of declining stands during all three portions of the flight season, and the ratio of *T. dubius* counts in healthy-to-declining stands rose from 1.6 to 3.5 from the early to late portions of the flight (period by stand condition interaction: $F_{4,28} = 4.32$, $P = 0.007$). Like-

wise, there was a strong flight period by stand condition interaction in the abundance of *P. cylindrica* ($F_{4,28} = 3.44$, $P = 0.021$). Healthy stands had significantly higher *P. cylindrica* counts than either symptomatic or asymptomatic portions of declining stands during the early and mid season, but not late portion of the flight season. Numbers of *P. parallelum* were significantly higher in healthy stands than in declining stands. However, *P. parallelum* showed a pattern opposite that of *T. dubius*, in that the ratio of *P. parallelum* counts in healthy-to-declining sections was highest early in the flight season (1.9), and declined thereafter (1.0 in late season) (period by stand condition interaction: $F_{4,28} = 3.35$, $P = 0.023$).

Relationships Among *I. pini* and Associates During Different Periods of Single-Flight Seasons. Regression models of the form proposed in equation 1 for *I. pini* held for both 1998 and 1999 (Table 2) with a high degree of statistical significance. Using each variable separately (i.e., fitting simple linear regressions for each possible predictor) resulted in relationships that were significant with all P value < 0.003 in 1998 and < 0.011 in 1999. Most relationships were significant with $P < 0.0002$. Moreover, the algebraic sign of the regression coefficient (direction of slope), with the exception of *I. grandicollis*, was always in agreement with equation 1. Pearson correlation coefficients

Table 4. Results for regression of trap counts of *I. grandicollis* and associated insects among flight seasons at the site level

Intercept	Td _(t-1)	Pc _(t-1)	Pp _(t-1)	Ig _(t-1)	Ip _(t)	Ip _(t-1)	MSE	F	df	P	R ²
1997-1998											
2.988	-0.403						0.0201	37.73	1,15	<0.0001	0.716
2.604		-0.294					0.0322	17.82	1,15	0.0007	0.543
2.650			-0.336				0.0265	24.85	1,15	0.0002	0.624
0.969				0.585			0.0060	161.39	1,15	<0.0001	0.915
0.910					0.471		0.0394	11.85	1,15	0.0036	0.441
0.629						0.571	0.0427	9.75	1,15	0.0070	0.394
0.926				0.569	0.028		0.0064	76.17	2,14	<0.0001	0.916
3.048	-0.411				-0.016		0.0215	17.62	2,14	0.0002	0.716
1.742	-0.157			0.476	-0.086		0.0046	72.16	3,13	<0.0001	0.943
3.048	-0.411					-0.016	0.0215	17.62	2,14	0.0002	0.716
0.865				0.562		0.055	0.0062	77.59	2,14	<0.0001	0.917
1.847	-0.165			0.464		-0.109	0.0046	71.72	3,13	<0.0001	0.943
1.447	-0.117			0.467			0.0047	105.90	2,14	<0.0001	0.938
1.263		-0.085		0.502			0.0044	144.07	2,14	<0.0001	0.942
1.305			-0.096	0.487			0.0045	100.80	2,14	<0.0001	0.941
1998-1999											
3.397	-0.422						0.0233	40.04	1,15	<0.0001	0.727
3.101		-0.412					0.0258	34.70	1,15	<0.0001	0.698
3.051			-0.383				0.0425	15.19	1,15	0.0014	0.503
0.580				0.876			0.0419	15.59	1,15	0.0013	0.510
1.411					0.457		0.0540	8.76	1,15	0.0097	0.369
0.869						0.572	0.0361	20.57	1,15	0.0004	0.578
0.502				0.670	0.212		0.0402	8.94	2,14	0.0031	0.561
4.414	-0.576				-0.278		0.0213	23.15	2,14	<0.0001	0.768
4.392	-0.573			0.006	-0.277		0.0229	14.33	3,13	0.0002	0.768
4.414	-0.576					-0.278	0.0213	23.15	2,14	<0.0001	0.768
0.401				0.449		0.385	0.0321	12.99	2,14	0.0006	0.650
4.189	-0.542			0.037		-0.215	0.0258	12.28	3,13	0.0004	0.739
3.094	-0.388			0.104			0.0247	18.93	2,14	<0.0001	0.730
2.447		-0.338		0.245			0.0261	17.62	2,14	0.0002	0.716
1.594			-0.240	0.559			0.0330	12.43	2,14	0.0008	0.640

Analyses show relationships of *I. grandicollis* early in a flight season with abundance of various single species, and combinations late in the prior season.

t: early part of year; t-1: entire previous year; Ip: *I. pini*; Td: *T. dubius*; Pc: *P. cylindrica*; Pp: *P. parallellum*; Ig: *I. grandicollis*
 A coefficient in italics is not significantly different from zero at $P < 0.05$.

showed that there is high positive correlation among all of the predator species ($\rho > 0, P < 0.0001$; Table 5). Because of this high correlation among predator species, we simplify Table 2 by only showing complete permutations for one species, *T. dubius*, which composed nearly two-thirds of all predators.

The results of the multiple regression analyses were less clear. The overall pattern is that all equations with two or more predictors improved the fit somewhat, but removal of one or two species caused little reduction in R^2 , and there was little effect based on which species was removed. The lack of consistency of the algebraic signs for certain variables in these models is due to the multicollinearity among the predictor variables. This suggests a high degree of covariance among insect species. In both years, the number of *T. dubius*, *I. pini*, and *I. grandicollis* in the early and mid season provided the best prediction of third-generation *I. pini*, and all other terms could be removed without loss of significance.

Relationships Among Ips and Associates Between Flight Seasons. As in the within-year trends, the type of relationship suggested by equation 1 was strongly validated for both between-year analyses (Table 3). As in the within-year trends, however, the simple linear relationships with *I. grandicollis* were positive. Similar signs and slope magnitudes among predators

was likely due to high positive correlations among their abundances ($\rho > 0, P < 0.0001$; Table 5).

As in the within-year analyses, multiple regression analyses generated highly significant P values and high R^2 values, but also reflected high covariance. That is, removal of individual variables resulted in very small reductions in R^2 , and there was little difference in the effect generated by removal of a species exhibiting similar flight phenology. The variables most consistently associated with *I. pini* population were the number of *I. pini*, *I. grandicollis*, and *T. dubius* in the previous year.

Both between-year analyses on *I. grandicollis* trends agreed with the kind of relationship suggested by equation 2 (Table 4). As with *I. pini*, each single variable was significant and in the predicted direction, except that the effect of *I. pini* was positive. As with *I. pini*, the strongest slope among the predators was generated by *T. dubius* (-0.41), followed by *P. parallellum* (-0.36) and *P. cylindrica* (-0.35). The multiple regression equations with the best fit in both years included *T. dubius*, *I. pini*, and *I. grandicollis*.

Discussion

Our results are consistent with the view that a combination of factors, particularly habitat quality and

Table 5. Person correlation coefficients among predators within and between flight seasons

Insect species	<i>T. dubius</i>	<i>P. cylindrica</i>	<i>P. parallelum</i>
Within flight seasons			
<i>T. dubius</i>	1	0.87536	0.80469
<i>P. cylindrica</i>	0.87536	1	0.71348
<i>P. parallelum</i>	0.80469	0.71358	1
Between flight seasons			
<i>T. dubius</i>	1	0.84344	0.85859
<i>P. cylindrica</i>	0.84344	1	0.81700
<i>P. parallelum</i>	0.85859	0.81700	1

coleopteran predators most strongly affect within- and between-season population trends of *I. pini* and *I. grandicollis* in the Great Lakes region (Klepzig et al. 1991, Raffa 1991, Aukema et al. 2000b, Ayres et al. 2001, Erbilgin and Raffa 2002). The strong patterns in Table 1 suggest that relationships between dispersal and habitat structure may be important in *Ips*-predator dynamics. In the southern United States, *T. dubius* flies ≈ 6 times farther than its principal prey in the region, *Dendroctonus frontalis* Zimmermann (Scolytidae), and dispersal patterns vary with forest management practices (Thoeny et al. 1992; Turchin and Odendall 1996; Cronin et al. 1999, 2000). A greater dispersal ability of predators than *I. pini* might generate some of the time by stand condition interaction effects observed in this study. Dispersal has not been quantified in *I. pini*, but two related species have been examined. More than 95 and 90% of *Ips typographus* L. flew <200 m in studies by Zurr (1992) and Duelli et al. (1997), respectively. Likewise, most *Ips perturbatus* (Eichhoff) were collected within 30 m of their release point (Werner and Holsten 1997).

We did not find evidence for interspecific competition among herbivores at the site level, i.e., numbers of one herbivore were not inversely related to the other. This suggests that habitat quality, particularly the number of trees experiencing stress, is of overriding importance and that numbers of various *Ips* species largely reflect changes in resource availability. Interspecific competition at the tree level can occur among *Ips* spp. (Ayres et al. 2001), but it can be reduced by pheromone specificity (Lanier and Wood 1975, Birch et al. 1980, Erbilgin and Raffa 2000). A strong effect of habitat quality also appears to diminish any signal of intraspecific competition, even though it is well established at the within-tree level (Anderbrant 1990, Robins and Reid 1997, Aukema and Raffa 2002).

These results help explain results from previous studies on *Ips* distribution among *P. resinosa* stands of varying conditions. *Ips* are the ultimate factor in tree death in plantations showing the specific sequence of events termed "Red Pine Decline" (Klepzig et al. 1991, Erbilgin and Raffa 2002). Yet populations of *Ips* are not consistently higher in declining stands than in healthy stands. Moreover, we have not detected consistent increases in predator populations within declining stands following increased tree mortality. Our results suggest the importance of time by stand condition interactions among host tree resistance, herbivore

populations, and predator impacts. That is, *Ips* populations initially rise in stands containing large numbers of stressed trees (Table 1), particularly trees stressed by root insects and pathogens (Klepzig et al. 1991, Erbilgin and Raffa 2002). Predators likewise reproduce within and/or migrate into these stands and exert significant impacts. But certain poorly understood features of healthy stands, such as alternative food sources and/or protection from environmental extremes, appear to support higher predator populations. Separating cause and effect in the interactions of stand condition and predators of bark beetles remains a significant challenge and an area requiring additional effort.

Adding multiple predator species to single predator models had little effect on improving prediction of *Ips* counts (Tables 3 and 4). Although we have no direct observations on interactions between predators, Ferguson and Stiling (1996) suggested that nonadditive effects between natural enemies reflect interference. There is considerable evidence for interference among multiple predators in other systems (Rosenheim 1998). One possible source of interference may arise from the sequence of predator attacks on different life stages. These results support the view that the potential for interference should be considered when introductions of natural enemies are proposed against invasive bark beetle species.

Acknowledgments

These studies were supported by National Science Foundation grants DEB 9408264 and DEB 9629776, U.S. Department Agriculture NRI AMD 96 04317, the Wisconsin Department Natural Resources (WI-DNR), and the University of Wisconsin (UW)-Madison, College of Agricultural and Life Sciences (CALS). Field assistance by A. Szele, A. Weinstein, E. Hladilek, K. Boland, J. Redmer, and S. LaFontaine, Department Entomol., UW-Madison is greatly appreciated. We thank J. Cummings Carlson, T. Lanigan, and G. Edge, WI-DNR for providing study sites. We thank P. Crump, CALS Computer Facility, UW-Madison, for help with statistical programs. We thank D. Mahr, D. Hogg, Department of Entomology, C. Lorimer, Department of Forest Ecology and Management, UW-Madison, and two anonymous reviewers for their valuable critiques of manuscript.

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Received for publication 17 July 2001; accepted 18 July 2002.