Seasonal Dynamics of Mites and Fungi and Their Interaction with Southern Pine Beetle

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ABSTRACT We evaluated whether *Dendroctonus frontalis* Zimmermann populations were influenced by nontrophic interactions involving commensal mites, their mutualistic bluestain fungus *Ophiostoma minus* (Hedgc.) H. and P. Sydow, and beetle-mutualistic mycangial fungi. We tested for effects of delayed, nonlinear, or positive feedback from *O. minus* and mites on *D. frontalis* population growth. We predicted that (1) high mite densities have demographic consequences for beetles by influencing the prevalence of *O. minus* and antagonistic interactions between *O. minus* and mycangial fungi, and (2) inter-relations and abundances of mites and fungi differentially vary throughout the year in a seasonally variable climate. Surveys of *D. frontalis* populations revealed that temporal and spatial patterns in abundance of mites and their mutualistic fungus, *O. minus* were inversely related with beetle population growth. Negative demographic effects of *O. minus* on *D. frontalis* were nonlinear, only affecting beetle per capita reproduction when fungi colonized >35% of phloem habitat. Mite abundance was strongly correlated with *O. minus* and was an important driving force in promoting bluestain prevalence within trees. Spring abundances of mites and the prevalence of *O. minus* during *D. frontalis* infestation formation were strong predictors of beetle population decline later that year. The two mutualistic fungi associated with *D. frontalis* cycled seasonally but did not seem to influence beetle population dynamics.

KEY WORDS mutualism, bark beetle, *Tarsonemus*, *Ophiostoma*, *Dendroctonus*

UNDERSTANDING THE CAUSES AND consequences of pest outbreaks is a primary goal in the study of population biology. While some outbreaks are apparently linked to exogenous factors (such as climatic effects or disturbances), others seem to be driven by endogenous feedback with delays and/or nonlinearities (Kendall et al. 1999). Endogenous feedback can result from intraspecific processes such as maternal (Wellington 1960) and genetic effects (Chitty 1967) or from interactions with predators (Huffaker 1958), pathogens (Anderson and May 1980), mutualists (Bronstein 1994), competitors (Grosholtz 1992), or resources (Ehrlich and Birch 1967, Haukioja 1980). While the effects of endogenous feedback from direct interactions on population abundance and dynamics have been well studied in many systems, multiple or indirect interactions are often overlooked (Krebs et al. 2001).

Dendroctonus frontalis Zimmermann (Curculionidae: Scolytinae), a keystone species and an important insect pest in pine forests in the southern United States (Price et al. 1997), undergoes extreme temporal and spatial fluctuations in abundance (Turchin et al. 1991). Time-series of annual populations indicate that the epidemic tendency of this bark beetle is primarily driven by endogenous forces, such as predators (Turchin et al. 1999).

Local populations of *D. frontalis* (called infestations or "spots") can grow to 1×10^6 beetles per infestation within a single summer (Thatcher 1967, Coulson 1980), causing considerable damage to pine forests. Infestations start in spring (April–May) after a dispersal period (Heddon and Billings 1979). The onset of infestations is attributed to increased access to weakened trees that allow beetle populations to grow and overwhelm the defenses of neighboring pine trees (Hodges et al. 1979). Infestation growth in spring is influenced by predator–prey interactions (Turchin et al. 1999), extreme temperatures (McClelland and Hain 1979), and beetle dispersal behavior (Gara 1967). However, epidemic populations during the summer are often too large to be effectively reduced by predators or resin defenses (Reeve et al. 1995, Reeve 2000). Indirect negative effects of bluestain fungi on *D. frontalis* are well documented (Barras 1970, Franklin 1970, Bridges 1983, Goldhammer et al. 1990, Hofstetter et al. 2006) but have been given little consideration in local population dynamics of *D. frontalis* (Bridges 1983, Coppedge et al. 1994, Lombardero et al. 2003).

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Dendroctonus frontalis larvae depend on the mutualistic fungi *Ophiostoma ranaculosum* (J. R. Bridges and T. J. Perry) Hausner (syn. *Ceratocystiopsis ranaculosus,* Jacobs and Kirisits, 2003) and *Entomocorticium* sp. A (Hsiau and Harrington 1997) deposited by adult female beetles during gallery excavation (Barras and Perry 1972, Barras 1973). Female beetles have specialized prothoracic mycangia that store these fungi (Francke-Grosmann 1967, Barras and Perry 1972, Happ et al. 1976). These mycangial fungi grow in the phloem layer where they often compete with a bluestain fungus, *Ophiostoma minus* (Hedgcock) H. and P. Sydow that is introduced through the surface of attacking *D. frontalis* (Barras 1970). The mycangial fungi vary in their ability to compete with *O. minus* (Klepzig and Wilkens 1997, Hofstetter et al. 2005) and this disparity may lead to differential survival of beetle larvae. *O. minus* spores are also carried by *Tarsonemus* mites (Acarina: Tarsonemidae) that travel on *D. frontalis* (Bridges and Moser 1983, Moser 1985). *Tarsonemus* spp. can occur in high densities on attacking beetles (Moser and Bridges 1986) and likely release fungal spores throughout newly excavated beetle galleries (Lombardero et al. 2000). *Tarsonemus* seem to have no direct negative affect on beetles or mycangial fungi (Moser et al. 1995). The qualitative and quantitative dynamics of mites and fungi and their interrelation with beetle populations are not well understood (Klepzig et al. 2001a). Positive feedback between mites and *O. minus* (e.g., mutualism, Lombardero et al. 2000, 2003) could result in high bluestain abundances within trees and reduce *D. frontalis* per capita reproduction and infestation growth.

Few studies have measured *D. frontalis* population dynamics at the scale of generations. Here, we present evidence that *D. frontalis* populations (at the time scale of beetle generations) are influenced by community interactions involving mutualistic fungi, antagonistic fungi, and phoretic mites. We also show that fungi and mites respond to seasonal changes and *D. frontalis* densities throughout the year. We evaluated whether within-year population dynamics of *D. frontalis* is influenced by endogenous feedbacks involving fungi and mites (Fig. 1). We tested three hypotheses that feedback from mites and fungi affect beetle population dynamics: beetle population dynamics are affected by delayed feedback from mites and fungi (hypothesis 1 [H1]), affected by positive and/or nonlinear feedbacks from mites and fungi (hypothesis 2 [H2]), or are not affected by feedback from mites and fungi but from exogenous effects (i.e., factors other than mites and fungi; hypothesis 3 [H3]). H1 predicts that phoretic *Tarsonemus* and *O. minus* introduced by attacking beetles will have effects on beetle offspring (larval) survival. More specifically, H1 predicts that high mite densities will have demographic consequences for beetles by influencing the prevalence of *O. minus* within trees and antagonistic interactions between *O. minus* and mycangial fungi. H2 predicts that negative effects of phoretic *Tarsonemus* and *O. minus* on beetle survival will occur only when a threshold is reached (i.e., when percent area covered of *O. minus* in bark exceeds 40%; Hofstetter et al. 2006). In this case, nonlinear effects may only occur when conditions for *Tarsonemus* and *O. minus* growth are favorable. For instance, inter-relations and abundances of mites and fungi may differentially vary throughout the year because of seasonal climate. H3 predicts that fluctuations in beetle survival arise independent of *Tarsonemus* abundance and prevalence of *O. minus* within trees and are thus influenced by other variables such as climate, predation, intra- or interspecific competition, or resources.

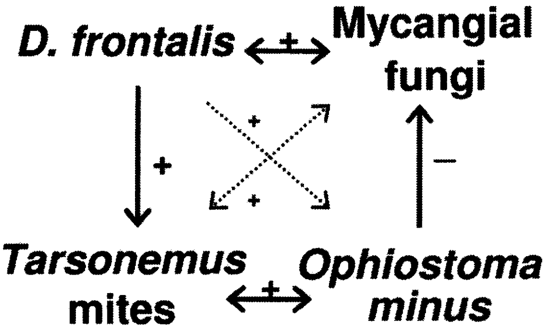

Fig. 1. Hypothesized interactions among phoretic *Tarsonemus* mites, *O. minus* (a bluestain fungus), mycangial fungi, and *D. frontalis.* Solid arrows indicate direct positive (+) or negative (−) effects of abundance (or frequency) of one species on per capita growth of the other species. Dotted arrows indicate potential passive introduction of *O. minus* by beetles and the apparent mutualism between *Tarsonemus* and *O. ranaculosum* (one of the mycangial fungi).

Materials and Methods

To test for multispecies effects on the demographics of *D. frontalis,* we evaluated relations between beetle abundance (at two hierarchical levels: density of beetles within trees and number of infested trees within each infestation) and the abundances of *Tarsonemus* mites, mycangial fungi, and *O. minus.* To test for possible delayed and nonlinear effects from mites and fungi, we evaluated cross-correlation functions within and among measured traits within infestations (abundance and growth of beetles, mites, and *O. minus*) with time lags of one, two, or three beetle generations (Statistix 7.1; Analytical Software 2002). We also tested for changes in species relations across seasons, as would be expected if the interaction system is subject to exogenous effects from climatic variation.

***D. frontalis* Communities.** We conducted the study in Bankhead National Forest (N. F.), AL, from April 2000 to October 2001. *D. frontalis* populations in the Bankhead N. F. experience colder winters, because of higher elevation (680–720 ft), than other beetle populations in the southern United States. We sampled five *D. frontalis* infestations each separated by >3 km. Infestations were followed for 18 mo (beginning after the initiation of new infestations each spring) at intervals of approximately one beetle generation. We collected adult beetles and infested bark within in-

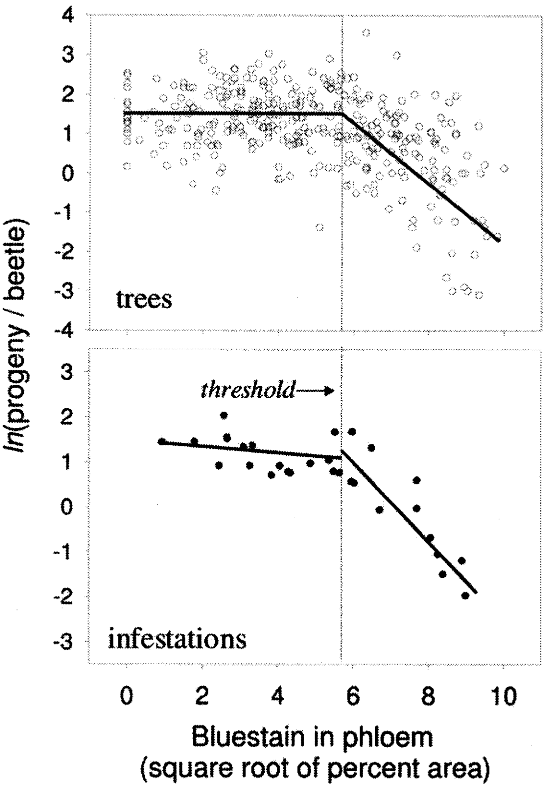

Fig. 2. Relationship between bluestain abundance in phloem (% coverage per unit area) and per capita reproduction of beetles. (A) Each point represents a tree (12 dm^2 of bark). (B) Each point represents the average of bark samples per infestation during one sample period. In back-transformed units, the apparent threshold is at 34% area covered bluestain.

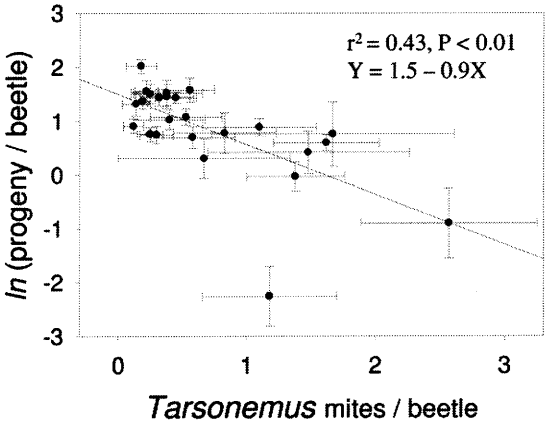

Fig. 3. Relationship between mean *Tarsonemus* mite densities per adult *D. frontalis* and the reproductive success of *D. frontalis* within bark. Each point represents one infestation (±SE based on $n = 5$ trees).

festations to estimate abundances of *E.* sp. *A*, *O. ranaculosum*, *Tarsonemus* mites on beetles, and the prevalence of *O. minus* and *Tarsonemus* within trees (adapted from methods of Lombardero et al. 2003, Hofstetter et al. 2006). Within each infestation, we estimated beetle population size by counting the number of trees infested and the beetle densities within trees.

Determination of Mite, Fungal, and Beetle Abundances. To determine the abundance of mycangial fungi, phoretic mites, and *O. minus*, we captured adult beetles near newly attacked trees within each infestation using five unbaited Lindgren funnel traps (Phero Tech, Delta, Canada). We monitored traps until 50–100 beetles per infestation were captured for each beetle generation. We immediately placed each beetle into a 1-ml sterile centrifuge-cap vial (Fisher, Pittsburgh, PA) and stored them at 5°C. We removed phoretic mites from beetles, counted them, and placed them in lactophenol for later identification to genus or species (methods similar to Moser and Bridges 1986). We removed the prothorax from female beetles and identified the fungus within each mycangium by dissecting open the mycangia, mounting them on a slide with lactophenol-blue solution, and viewing the slide using a compound microscope (Barras and Perry 1972). We placed male beetles and the head and abdomen of female beetles on selective media (2% malt extract agar with 0.2% cycloheximide) to determine the incidence of *O. minus* on beetle bodies. We examined phoretic mites for the presence of *O. minus* or *O. ranaculosum* spores. We collected a total of 1,538 *D. frontalis* adults and identified 1,792 phoretic *Tarsonemus spp.* mites. Voucher specimens of mites and fungi were deposited at USDA Southern Research Station, Pineville, LA, in care of J. C. Moser and K. D. Klepzig.

To determine the prevalence of *O. minus* within beetle-infested trees in each infestation, we removed two 6-dm^2 bark samples from each of five infested trees (containing pupae or callow adults of *D. frontalis*) and traced the areas containing blue stain and *O. minus* perithecia onto 8 by 11-in sheets of mylar acetate.

In addition to estimating percent *O. minus* within trees, we used the bark samples to calculate *Tarsonemus*/dm^2, beetle entries/dm^2, larval pupal chambers/dm^2, and beetle gallery length (cm/dm^2) (methods similar to Lombardero et al. 2003). We estimated *Tarsonemus* densities on phloem by counting both male and female adult mites within each of three randomly chosen 1-cm^2 plots in areas of phloem with and without *O. minus*. We also collected 10 mites from *O. minus* and non–*O. minus* areas from each bark sample, identified them to species, and scored them for the presence of fungal spores. We measured beetle gallery lengths by tracing female oviposition galleries within the phloem. We sampled bark from >175 trees (>20 m^2 of bark) from infestations within national forest throughout the year. Our beetle entry density measurements cannot be simply extrapolated to attacks/tree because there is variation within trees (partly random and partly related to height on the bole; Coulson 1980), and thus the entry data and

Table 1. Correlations among measures of beetles, fungi, and mites across *D. frontalis* infestations in the Bankhead National Forest (n = 35: 2 yr × 5 infestations × 3–4 beetle generations)

	Percent bluestain	Population size	Entries/ dm^2	Gallery/ dm^2	Progeny/ beetle	Progeny/ dm^2	*Tars.*/ beetle	Percent beetles *E.* sp. A	Percent beetles *O. ranac.*	Percent beetles *O. minus*
Beetle population size	−0.08									
Beetle entries/dm^2	0.37	0.14								
Gallery/dm^2	0.06	0.22	0.53[a]							
Progeny/beetle	−0.68[b]	0.18	−0.56[a]	−0.06						
Progeny/dm^2	−0.65[b]	0.23	−0.33	−0.30	0.90[b]					
Tarsonemus/beetle	0.74[b]	−0.38	0.36	0.32	−0.78[b]	−0.74[b]				
Percent beetles with *E.* sp. A	−0.13	−0.31	−0.29	0.01	−0.19	−0.27	−0.23			
Percent beetles with *O. ranaculosum*	0.26	0.13	0.25	0.39	0.16	0.15	0.32	−0.87[b]		
Percent beetles with *O. minus*	−0.28	0.08	−0.10	−0.08	0.37	0.30	−0.22	−0.09	0.06	
Percent beetles with *Tarsonemus*	0.72[b]	−0.20	0.16	0.32	−0.81[b]	−0.75[b]	0.92[b]	−0.07	0.18	−0.19

[a]$P < 0.05$; [b]$P < 0.01$ (with Bonferroni correction).

number of tree infested are coarse estimates of beetle population size. Measurements of beetle entries and larval densities were not possible for infestations during our September 2000 sampling period because of difficulty in removing large, continuous sections of outer bark during this period.

Statistical Analyses. We tested for relationships between beetle population size (function of the number of infested trees and beetles/tree), beetle entry density (adult pairs/dm^2 bark), or per capita reproduction (pupae/parental adult) and phoretic mites and *O. minus* (percent bluestain in bark, percent beetles with *O. minus* spores) using regression analyses (JMP 5.1, SAS Institute, Inc., Cary, NC USA). We used regression models to characterize the relationship between blue stain and pupae/beetle pair, gallery production/beetle pair, larval survival (pupae/egg), and *Tarsonemus* density. We evaluated larval survival with an analysis of variance (ANOVA) model that included fungus (each species tested separately), beetle entry density, and their interaction. We computed correlations among traits (means for each infestation) using a Pearson product-moment correlation coefficient with a Bonferroni correction. To improve normality and homogenize variances, we arcsine square root-transformed proportion of each fungus, and log-transformed (mites/dm^2 + 1) and (mites/beetle + 1). Phoretic *Tarsonemus* and spores/*Tarsonemus* were analyzed using an ANOVA model that included infestation as a random effect. The fraction of beetles with *O. minus* was analyzed using a nominal logistic model (Wald χ^2) that included infestation as a random effect (JMP 5.1). Female beetles carrying particular fungi were analyzed using a Tukey-Kramer honestly significant difference (HSD). We used Akaike's Information Criterion (AIC; Burnham and Anderson 1998) and C_p (Mallows C_p; Gilmour 1996) to identify the best models to describe beetle population growth based on nine measured traits (percent bluestain, beetle gallery density, pupal density, attack density, percent beetles with *O. minus*, percent female beetles with *E.* sp. *A* or *O. ranaculosum*, percent beetles with *Tarsonemus*, and *Tarsonemus* per beetle). We also evaluated nonlinear models ($Y = a + bX + c\chi^2$), where X = prevalence of *O. minus* in trees, phoretic mites, or percent beetles with mites.

Table 2. Regression analyses and likelihood estimates that explained the effects of measured variables on beetle production (ln progeny/beetle/infestation)

Independent parameter(s)	P value	R^2	Cp	AIC
Single parameter models				
Percent bluestain (quadratic model)[a]	<0.01	0.67	3.2	−27.0
Percent beetles with mites (quadratic model)[a]	<0.01	0.55	8.9	−22.4
Percent bluestain (linear model)	<0.01	0.54	9.7	−21.2
Percent beetles with mites (linear model)	<0.01	0.54	9.5	−21.3
Mites/beetle	<0.01	0.54	9.4	−21.4
Two parameter models				
Percent bluestain + percent *E.* sp. A	<0.01	0.74	1.0	−30.0
Percent bluestain + percent beetles with mites	<0.01	0.69	3.1	−27.0
Three parameter models				
Percent bluestain + percent *E.* sp. A + attacks	<0.01	0.79	−0.28	−33.5
Percent bluestain + percent *E.* + percent beetles w/mites	<0.01	0.72	2.9	−28.2

Only parameters showing best fit (based on Cp and AIC values) from analyses of all possible regressions are represented.

[a] Nonlinear analyses of quadratic equation: progeny/beetle = 1 + 0.4 (bluestain) − 0.07(bluestain)^2. Similar results were found with threshold model (Fig. 5). Progeny/beetle = 1.5-2.0 (percent beetles with mites) − 6.6 (percent beetles with mites)^2.

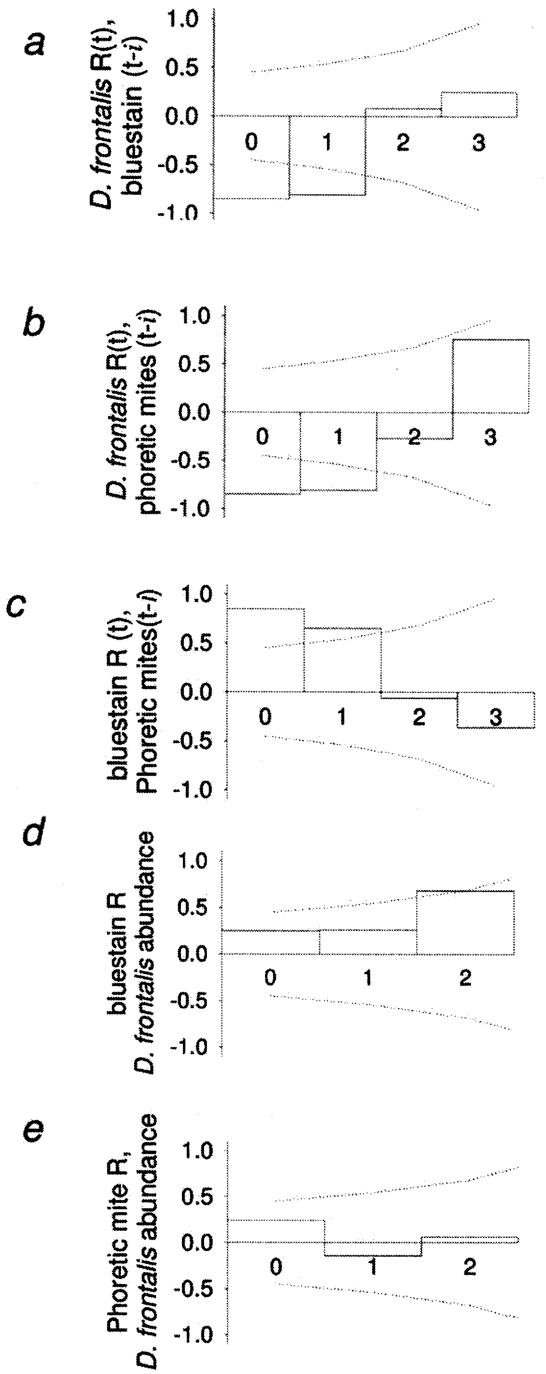

Fig. 4. Time-lagged correlation coefficients of *D. frontalis* per capita reproduction in relation to previous bluestain densities (t-i) and *Tarsonemus* densities (t-i) (graphs a and b), growth of *O. minus* in relation to *Tarsonemus* densities (graph c), and the rate of population change (R_t) in *Tarsonemus* and *O. minus* (graphs d and e) in relation to previous beetle population size. The y-axis represents the sign and size of the correlation coefficients, and the x-axis represents the time lag (previous beetle generations) within infestations.

Results

Test Hypotheses that Delayed (H1), Positive and/or Nonlinear (H2), or No (H3) Feedback from Mites and *O. minus* Affect Beetle Population Growth. Field surveys revealed that beetle per capita reproduction was negatively related to bluestain prevalence within trees (Fig. 2), phoretic *Tarsonemus* abundance (Fig. 3), and beetle attack density (Table 1). Beetle per capita production was unrelated to the relative frequency of each mycangial fungus within infestations (Table 1) or time of year. The relationship between prevalence of bluestain within trees and progeny per beetle was nonlinear (Fig. 2; support for H2), with strong negative effects occurring when percent area of bluestain exceeded 35% of the phloem. No other linear or quadratic models using just one species as a predictor were as good (in terms of r^2, C_p, or AIC) as a quadratic model with X = percent bluestain (Table 2). Models employing mite abundance alone, however, also explained >50% of the variation in per capita growth of beetles. The best model overall (in terms of AIC) was one that included percent bluestain in phloem, percent *E.* sp. *A* and beetle attack density.

Cross-correlation functions with time lags of one, two, or three beetle generations used to test for possible delayed and nonlinear effects from mites and fungi revealed instantaneous and delayed negative effects on beetle population growth from *O. minus* and *Tarsonemus* at t and t-1 beetle generations (Fig. 4; support for H1 and H2).

Temporal Dynamics of Beetles, Fungi, and Mites Across Multiple Infestations. Beetle abundances and reproductive success were highly variable from June 2000 to October 2001 (Figs. 5 and 6). Per capita reproduction of beetles was high and stable throughout infestations in 2000 and declined sharply during the summer of 2001, coinciding with high bluestain within bark and high phoretic mite abundances (Fig. 5). Relative abundances of the two beetle-mutualistic fungi appeared to cycle annually, with *E.* sp. *A* reaching its highest abundance in the spring and summer (March to August) and *O. ranaculosum* being most abundant during the fall and early winter (August to December; Fig. 5B). Less than 3% of adult female beetles carried no fungi within their mycangium. Percent of individual beetles carrying both mycangial fungi (one in each side of the mycangia) averaged 5–25% per infestation.

Prevalence of *O. minus*, as estimated by percent of beetles carrying *O. minus* spores, did not show a clear seasonal pattern although the number of beetles carrying spores declined in 2001 (Fig. 5B). Mites and the prevalence of *O. minus* (bluestain) in phloem increased in 2001 (Fig. 5C). Increase in prevalence of *O. minus* within trees was positively related with phoretic *Tarsonemus* (at t and t-1), but *Tarsonemus* population growth and *O. minus* prevalence within trees were unrelated to *D. frontalis* population size at time t, t-1, or t-2 (Fig. 4) or *D. frontalis* entry densities within trees ($r < 0.08$, $P > 0.78$).

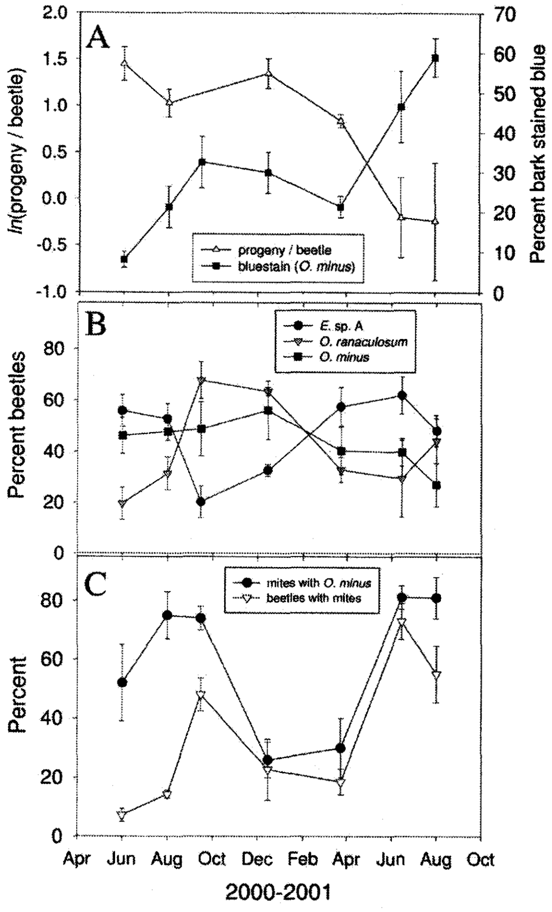

Fig. 5. Temporal dynamics of beetles, fungi, and mites in Bankhead National Forest during 2000 and 2001. (A) Average reproductive success of *D. frontalis* per infestation and percent of bark stained blue per tree (per infestation). (B) Incidence of symbiotic fungi (three species) on adult female beetles. (C) Mean percentage of beetles with *Tarsonemus* mites and mean percentage of mites carrying *O. minus* spores. Each point represents the mean and SE of five infestations. Infestations were measured in June after spring dispersal of beetles and resampled at intervals of ≈1 beetle generation until spring dispersal of following year.

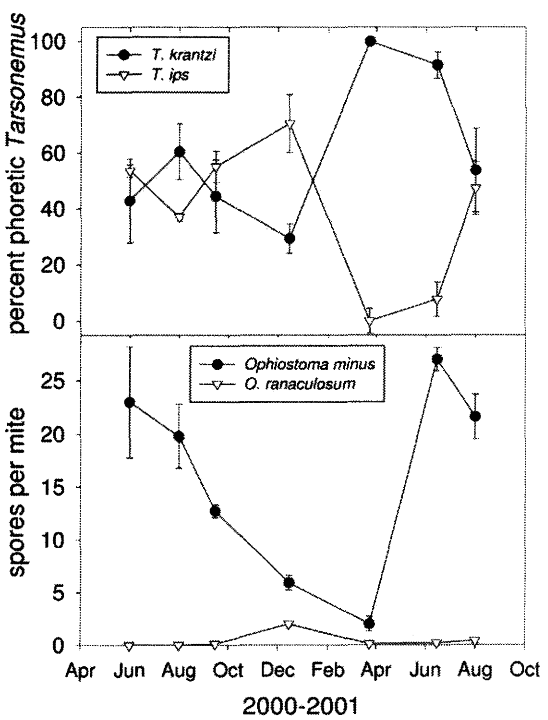

Fig. 6. Temporal dynamics of *Tarsonemus* mites on beetles and spore counts on mites in *D. frontalis* infestations Bankhead N. F. during 2000 and 2001. (A) Frequency (as a percentage of total in Fig. 5C) of phoretic *T. ips* and *krantzi* on beetles. (B) Mean number of *O. minus* and *O. ranaculosum* spores per phoretic *Tarsonemus* per infestation. Each point represents the mean and SE of mites from five infestations.

Three species of *Tarsonemus* (*krantzi*, *ips*, and *fusarii*) were collected from adult *D. frontalis* in flight traps. *T. fusarii* comprised <3% of the total mites collected but was present during each sample period. *T. krantzi* and *T. ips* were abundant but varied with season: *T. krantzi* was more abundant in spring and summer but less abundant in winter than *T. ips* ($\chi^2 = 450.3$, $P < 0.001$; Fig. 6A).

Percent of phoretic *Tarsonemus* that carried *O. minus* ascospores ranged from 22% in March 2001 to 81% in August 2001 ($\chi^2 = 411.7$, $P < 0.01$; Fig. 5C). Average number of *O. minus* spores per phoretic mite ranged from 2 in March 2001 to 27 in June 2001 (Fig. 6B). Overall, 62% of *Tarsonemus* carried *O. minus* ascospores, averaging 14.8 spores per mite. Also, on average, *T. krantzi* carried eight more *O. minus* spores per mite than *T. ips* ($t = 8.1$, $P < 0.01$). *O. ranaculosum* was carried during late summer and fall by some mites (Fig. 6B), more commonly by *T. ips* (11.7%) than *T. krantzi* (6.0%) ($\chi^2 = 19.3$, $P < 0.01$).

Discussion

Demographic Effects of Fungi and Mites on *D. frontalis*. Seasonal and annual variation in phoretic mites and *O. minus* in phloem coincides with fluctuations in *D. frontalis* populations (support of H1 and H2 for feedback from mites and *O. minus*). Relative abundance of each mycangial fungus appears unrelated to beetle population dynamics. During periods of low prevalence of *O. minus* within trees (below <35 bluestain/dm^2 bark) beetle population growth rates were constant and high (Fig. 2). Alternatively, prevalences of bluestain above this apparent threshold push beetle populations into a regimen dominated by interspecific competition between *O. minus* and mycangial fungi and intraspecific competition for remaining phloem space (support for H2) (Hofstetter et al.

2006). The greatest demographic effects of *O. minus* on beetles generally occurred late in the summer when *Tarsonemus* populations were high, apparently pushing bluestain levels above the threshold. In the absence of mites, the introduction of *O. minus* by beetles does not result in bluestain levels >40% (Hofstetter et al. 2006). High initial abundances of *Tarsonemus* and *O. minus* during infestation formation (during spring) appear to presage high *O. minus* prevalence within trees and phoretic *Tarsonemus* abundances late in the summer, coinciding with significant reduction in beetle per capita reproduction.

Temporal Dynamics of Beetles, Fungi, and Mites Across Multiple Infestations. Surveys of interacting species throughout the year revealed several patterns across all infestations that were not predicted a priori. (1) The ratio of mycangial fungi within infestations cycled seasonally (Fig. 5). *O. ranaculosum* was more prominent in late summer and fall, and *E.* sp. *A* was more abundant in the spring. Differences in the frequency of association of these fungi with *D. frontalis* seem to be driven by exogenous factors, although mites may contribute varying levels of *O. ranaculosum* by introducing spores into oviposition galleries. (2) The relative abundance of *Tarsonemus* species within infestations changed through time. *T. krantzi* was more abundant in the spring and summer, and *T. ips* was more abundant in fall and winter. (3) *Tarsonemus*–*O. minus* interactions seem to vary by species. *T. krantzi* carry more *O. minus* spores, on average, than *T. ips*, but *T. ips* carry more spores of *O. ranaculosum.* This suggests that mite species may differentially prefer or inhabit areas occupied by one or the other fungus. This also might help explain the frequent coexistence of two similar species that would presumably compete for the same niche (Lombardero et al. 2000). The strength of particular pathways within the web of interactions (Fig. 1) may depend strongly on the relative abundance of particular species (e.g., *kranzti* versus *ips*). (4) *Tarsonemus* carried greater numbers of *O. minus* spores during the summer than any other time of the year. This was true regardless of the abundance of mite species or prevalence of *O. minus* within trees.

Seasonal Effects on Community Interactions. Although climatic patterns have not been strongly correlated with yearly population dynamics of *D. frontalis* (Turchin et al. 1991, but see Kalkstein 1976, McClelland and Hain 1979, Miller and Parresol 1992), small changes in exogenous factors might indirectly affect *D. frontalis* populations by altering demographic processes and associations within the community (Fig. 1). For instance, the apparent seasonal rhythms in relative abundance of the two species of mycangial fungi could be caused by differential effects of temperature on fungal growth and development within trees (e.g., Voigt et al. 2003). Temperature alters *O. minus* growth relative to mycangial fungi (Klepzig et al. 2001a) and alters the growth of *Tarsonemus* populations relative to the development of beetles on which they depend (Lombardero et al. 2003). Similarly, the mutualism between *O. minus* and *Tarsonemus* could be influenced by differential responses to temperature, seasonal changes in tree physiology and phloem chemistry (Cook et al. 1986, Bernard-Dagan 1988), or seasonal changes in beetle physiology, survival, and behavior (Heddon and Billings 1979, Coppedge et al. 1994). Additionally, other insects associated with *D. frontalis* may introduce and alter the relative abundance of fungi within beetle-infested trees (Klepzig et al. 2001b, Hofstetter, 2004). For now, the mechanism(s) leading to seasonal variation in fungi and mites remain unknown. In any case, the relative abundance of symbionts associated with *D. frontalis* is dynamic on a time scale of months, with consequences for *D. frontalis* populations.

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