Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae)

Maria J. Lombardero, Matthew P. Ayres, Richard W. Hofstetter, John C. Moser and Kier D. Lepzig

Lombardero, M. J., Ayres, M. P., Hofstetter, R. W., Moser, J. C. and Lepzig, K. D. 2003. Strong indirect interactions of *Tursonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). Oikos 102: 243-252.

Phoretic mites of bark beetles are classic examples of commensal ectosymbionts. However, many such miles appear to have mutualisms with fungi that could themselves interact with beetles. We tested for indirect effects of phoretic mites on *Dendroctonus frontalis*, which attacks and kills pine trees in North America. *Tarsonemus* mites are known to carry ascospores of *Ophiostoma minus*, which tends to outcompete the mutualistic fungi carried by *D. frontalis*. Experimental additions and removals of mites from beetles demonstrated that *Tursonemus* propagate 0. *minus* in beetle oviposition galleries. Furthermore, the abundance *of Tursonemus* and 0. *minus* tended to covary in nature. These results verified a strong mutualism between *Tursonemus* and 0. *minus*. Results also indicated that 0. *minus* is an antagonist of *D. frontalis*: beetle larvae seldom survived in the presence of 0. *minus* (compared to 83% survival elsewhere). Apparently, this is an indirect result *of 0. minus* outcompeting the two species of mycangial fungi that are critical to beetle nutrition. Thus, *Tursonemus* mites close a loop of species interactions that includes a commensalism (mites and beetles), a mutualism (mites and 0. *minus)*, asymmetric competition (0. *minus* and mycangial fungi), and another mutualism (mycangial fungi and beetles). This interaction system produces negative feedback that could contribute to the endogenous population dynamics of *D. frontalis*. Reproductive rate of *Tursonemus* was more temperature-sensitive than beetle generation time (which constrains the Lime for mite reproduction within a tree). This differential temperature sensitivity produces a narrow range of temperatures (centred at 27°C) in which mile reproduction per *D. frontalis* generation can attain its maximum of 100 mites/beetle. Consequently, seasonal oscillations in temperature are predicted to produce oscillations in the *D. frontalis* community, and climatic differences between regions could influence the community to dampen or exacerbate the cyclical outbreak dynamics of *D. frontalis*.

M. J. Lombardero, Dept de Producción Vegetal, Univ. de Santiago, ES-27002 Lugo, Spain. – M. P. Ayres and R. W. Hofstetter, Dept of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA (matthew.p.ayres@dartmouth.edu). – J. C. Moser and K. D. Lepzig, Southern Research Stn, USDA Forest Service, Pineville, LA 71360, USA.

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is arguably the most destructive forest pest species in North America (Price et al. 1997, Ayres and Lombardero 2000), but is also a keystone species for a diverse native community of arthropods and microbes. At least 57 species of mites (Moser and Roton 1971, Moser et al. 1974, Moser and Macias-Samano 2000) and 40 species of fungi and bacteria (Moore 1971, 1972, Bridges et al. 1984) are phoretic on the beetle. In addition, at least 167 species are known as predators and parasitoids of *D. frontulis* (Thatcher et al. 1980). A comparably diverse community of detritivores and their

Accepted 18 February 2003
Copyright © OIKOS 2003
ISSN 0030-1299

predators exploit pine logs after the departure of bark beetles (Savely 1939, Howden and Vogt 1951, Moser et al. 1971, Dajoz 1974). The closest associates of *D. frontalis* within this community are three species of mites, *Tarsonemus ips* Lindquist, *T. krantzi* Smiley and Moser and *T. fusarii* Cooreman (Acarina: Tarsonemidae), and three species of fungi. Two species of fungi, *Entomocorticium* sp. A (formerly referred as SJB122; Barras and Perry 1972, Happ et al. 1976, Hsiau 1996) and *Ceratocystiopsis ranaculosus* Perry and Bridges both serve as nourishment to the beetle larvae and travel between trees within specialised glandular invaginations of the beetle exoskeleton (mycangia; Barras and Perry 1972, Barras and Taylor 1973). The third fungus is a bluestaining fungus, *Ophiostoma minus* (Hedgcock) H. and P. Sydow, which travels on the exoskeleton of *D. frontalis* (Barras and Perry 1975) and is thought to be an antagonist of the beetle (Barras 1970, Bridges and Perry 1985, Goldhammer et al. 1991, Klepzig and Wilkens 1997, Ayres et al. 2000, Lombardero et al. *2000).* The *Tarsonemus* mites also appear to function in fungal dispersal by carrying spores of 0. *minus* and C. *ranaculosus* within specialised structures (sporothecae; Bridges and Moser 1983, Lombardero et al. 2000).

This heptad of species is linked by numerous direct interactions. *D. frontalis* larvae gain nutritional benefits from the two mycangial fungi (Payne 1983, Ayres et al. 2000). All mite and fungus species require *D. frontalis* to disperse from tree to tree (Bridges and Moser 1983). Mites feed upon *0. minus* and C. *ranaculosus* (Lombardero et al. 2000). Fungus species compete within the phloem (Klepzig and Wilkens 1997). Mites normally have little or no direct effect on the bark beetles that transport them (Moser 1976, Kinn and Witcosky 1978, Stephen et al. 1993). However, the structure of a community cannot be understood solely in terms of direct interactions. Accumulating evidence indicates that indirect interactions are common and important determinants of community properties (Sih et al. 1985, Abrams 1987, Strauss 1991, Wootton 1994, Callaway and Walker 1997, Abrams et al. 1998, Janssen et al. 1998, Martinsen et al. 1998).

Lombardero et al. (2000) and Klepzig et al. (2001a, b) hypothesized that indirect interactions involving *Tarsonemus* mites may produce a negative feedback loop that affects the population dynamics of *D. front&s:* increasing beetle abundance leads to increases in mite abundance, which leads to increases in 0. *minus,* which tends to decrease the colonization success of mycangial fungi within the phloem and thereby lower the survival of beetle larvae. However, this model requires that mites can enhance the dispersal of 0. *minus* enough that there are demographic consequences for beetles, which has not been tested. We know that mites carry ascospores and conidia of 0. *minus,* but beetles can also carry 0. *minus* inoculum (on their exoskeleton, not within mycangia), so it is possible that the mites have relatively little impact on the propagation of 0. *minus.* In this study, we conducted an experimental test for effects of *Tarsonemus* mites on the proliferation of *0. minus* within newly infested phloem. We also sampled replicate infested trees within multiple natural infestations to test for the predicted negative correlation between the abundance of *0. minus* and the survival of beetle larvae. Finally, we tested whether environmental conditions (specifically temperature) could influence this web of interactions by altering the relative development rates of mites and beetles.

Methods

Experimental test for fungal propagation by mites

To test the role of *Tarsonemus* mites in propagating 0. *minus,* three trees of *Pinus taeda* L. were cut down and sectioned into seven logs each (ca 60 x 25 cm). The number of trees was a compromise between the desire for replication and a need to minimise forest impact. Subsequent analyses revealed no main effects or interactions involving trees. Ends of the logs were sealed with paraffin to limit unnatural desiccation. We inoculated each of the 21 logs with four pairs (male and female) of *D. frontalis* that had just emerged from naturally attacked trees within the Bankhead National Forest, Alabama, USA. Four pairs per log was enough to include each treatment in each log, while still retaining separation of their mites and fungi. Each pair was introduced by first using an increment borer (5 mm diameter) to remove a plug of bark, then placing one beetle pair on the exposed cambium, and affixing the bark back into place with tape. Each pair of beetles within each log represented one of four different experimental treatments: (1) natural, beetles carried natural loads (described below) of mites and fungi; (2) – mites, mites were carefully removed from beetles (0 to 5 mites/beetle) before beetle introduction into the logs; (3) – mites/ + 0. *minus,* mites were removed and then beetles were allowed to walk for 1 minute in a Petri dish with a growing culture of 0. *minus; (4)* + mites/ + *0. minus,* beetles were allowed to walk in a culture of *0. minus* as before, and then five mites were added to each beetle. Added mites were adult females drawn from a colony that had been grown in a culture of C. *ranaculosus* (which ensured that the mites themselves were not carrying 0. *minus* propagules). Natural densities of phoretic *Tarsonemus* mites in this forest at this time averaged 1.95 adult female mites/beetle; ~ 64% of beetles (including any phoretic mites) carried propagules of 0. *minus* that could be cultured in malt agar medium; and virtually all beetles (> 98%) carried one or the other of the two mycangial fungi (~ 7:3 *Entomocorticium* sp. A: *C. ranaculosus).* Each log also received one extra perforation without beetles to test for possi-

ble 0. minus contamination due to the experimental manipulation.

After inoculation, logs were held for 4 weeks at air temperature and protected from rain. Then, the bark was shaved from logs to expose the area around each point of inoculation that was occupied by the perithecia of 0. *minus* (bluestain). We sketched oviposition galleries and bluestain areas onto mylar acetate, the images from which were later digitised and analysed with Sigma Scan Pro 4. At the time of log dissection, we also examined each inoculation point for the presence of mites. In three logs, the bluestain area of two inoculations grew into contact with each other; these measurements were excluded from analysis. Bluestain area (log-transformed to reduce heteroscedasticity) was analysed with a one-way ANOVA. A complete model would have also included tree and logs nested trees, but this was intractable with the full data because of missing observations. Analyses of the data sub-sets that permitted tests for trees and logs indicated no significant effects from either source.

Sampling in natural infestations

We sampled trees within natural *D. frontulis* infestations in the Bankhead and Talladega (Oakmulgee Ranger District) National Forests, Alabama, USA during spring and summer of 1999. In late April (spring), five trees from each of two infestations were sampled within the Bankhead NF. During July and August (summer), we sampled an additional 5-7 trees (limited by availability of trees at a suitable stage of beetle colonization) from each of three different infestations in each of the two National Forests. Forests were separated by 150 km and infestations within forests were separated by 10–20 km. All sampled trees were *P. taeda* 25-35 years of age that were at the same stage of beetle colonization; i.e. contained pupae and callow adults of *D. frontulis*, which were the progeny of beetles that attacked the trees about 20 weeks earlier (spring samples) or 5 weeks earlier (summer samples). Two bark samples were removed from each tree at 1.5-2 m height (in the lower range of normal occupancy by *D. frontalis*, but high enough so that larval survival is representative of the tree; Coulson et al. 1977). Two samples per tree maximised the number of trees while still providing some replication within trees, and enough total area within trees (5.3 dm^2) to provide reasonable tree-specific estimates (Hain 1980). Each bark sample was 9.5 x 28 cm, which was large enough so that they included an average of $\sim$ 100 beetle larvae, usually including some both within and outside of bluestain patches. The rectangular shape matched the tendency of 0. *minus* to grow up and down through the vascular tissue more than it grows outward.

For each sample, we recorded the area occupied by 0. *minus* (evident as bluestain from hyphae and perithecia), number of pupation chambers (indicating successful larval development), and number of failed larval galleries (indicating larvae that died). At the time of our sampling (just after pupation), failed larval galleries were evident as small, frequently meandering, feeding galleries that did not produce a pupation chamber. Sections of each bark sample that were destroyed by buprestid or cerambycid borers (and could not be accurately measured) were subtracted from the sample area. Samples with borer damage exceeding 50% were discarded in the field and immediately replaced with another sample from the same tree. Areas of bluestain and borer damage were measured using Sigma Scan Pro 4 after tracing the areas onto mylar acetate (Bridges et al. 1985). Each larval gallery (successful or not) was scored for being inside or outside areas of bluestain. For each bark sample, we also estimated mite density by taking a census of replicate sub-plots within fresh samples using a dissecting scope at 25 x magnification: five randomly chosen subplots of 1 cm^2 stratified between areas with and without bluestain (3 samples in whichever class – bluestain or not – that was most abundant). We evaluated mite abundance with an ANOVA model that included season-forest (Bankhead spring, Bankhead summer, and Talladega summer) and trees nested within season-forest as a random effect. Mite abundance was transformed as $\log10(\text{mites} + 1)$.

Temperature response of mite population growth

Twenty mite colonies, each derived from a single wild-caught female, were initiated within Petri dishes containing cultures of 0. *minus* growing on 2.5% malt extract agar (25 g malt extract and 20 g agar per litre distilled water). The parental females were collected from the Bankhead N.F. Female mites were collected beneath the bark of *Pinus taeda* that were infested by *D. frontalis* and transferred individually to petri dishes. After two weeks, colonies originating from each female were identified to species (which can only be done by mounting on a slide) and the progeny (all reared in a controlled laboratory environment) were used in the two subsequent experiments.

We estimated population growth rates using life table analyses as in Lombardero et al. (2000). Fifty mite colonies, each derived from a different *T. fusurii* female were initiated in petri dishes of malt extract agar inoculated with 0. *minus*. This medium allowed easy monitoring of the colonies because mites remain visible while feeding in the upper layers of fungal hyphae. Age-specific schedules of mortality and natality were estimated from daily observations of each of 10 colonies at each of 5 temperatures (8, 15, 22, 28 and 32°C) during

48 d (75 d for mites at 8°C). Mothers were transferred weekly to fresh fungal cultures to ensure that diet quality and quantity remained uniformly high. Resulting data were used to construct a life table and calculate the potential population growth rate using Euler's equation.

We also measured realized population growth rates across the same temperatures. Seventy-five colonies were started using 5 mated females of *T. fusarii* in petri dishes previously inoculated with 0. minus growing in a sterile medium containing water, ground freeze-dried *Pinus taeda* phloem and agar (50:15:1). Fungi in the petri dishes had well developed hyphae at the start of the experiment to ensure that all mites had an abundance of high quality food throughout the measurement period. Individual colonies (15 per temperature) were randomly allocated to dark growth chambers at constant temperature of 8, 15, 22, 28 or 32°C. Colonies were allowed to develop, untouched, in the fungal cultures for 65, 65, 30, 22, or 22 d, respectively (longer durations at cooler temperatures). Then, colonies were opened and all mites counted. Sixty-five days is 1/10 of the theoretical developmental time of *D. frontalis* at 8°C, while the other durations were set at half of the generation time of *D. frontalis* at those temperatures (Ungerer et al. 1999). Population growth rate for each colony was calculated as $[\ln(N_{final}) - \ln(N_{initial})]/t$.

Results

Experimental test for fungal propagation by mites

Bluestain area within inoculated logs was strongly affected by experimental manipulations of mites and/or fungi (Fig. 1; $F_{4,68} = 12.79$; $P < 0.0001$). The presence of mites clearly contributed to the propagation of 0. *minus* within the phloem. The surface colonised by 0. *minus* was halved by the removal of natural densities of mites (2.8 vs 1.4 cm^2 for natural vs -mites) and quadrupled by the addition of mites (8.5 vs 32.3 cm^2 for + 0. *minus vs* + 0. *minus*/ + mites). The latter effect is notable in that the mites did not carry 0. *minus* when they were introduced. Increasing the amount of inoculum directly on the surface of the beetles tripled the area subsequently occupied by *0. minus* (natural vs + *0. minus*, Fig. 1). In the absence of mites, the area of *0. minus* colonization from naturally inoculated beetles was very low and indistinguishable from control punctures that lacked beetles or mites (P = 0.44 for a priori comparison).

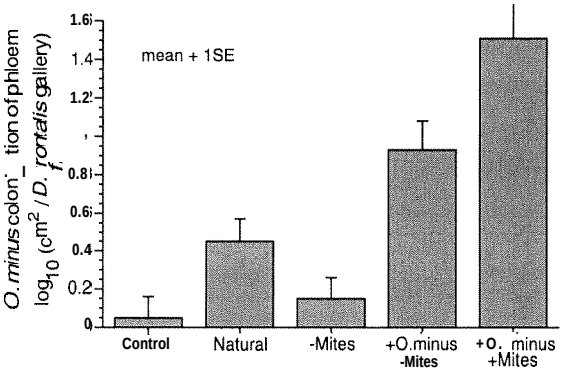

Fig. 1. The area of phloem colonised by 0. *minus* (bluestain) around galleries initiated by *D. frontalis* adults carrying natural loads of mites and 0. minus (natural), with mites removed (mites), with supplemental exposure of beetles to 0. minus (+ 0. minus), or with supplemental exposure of beetles to 0. *minus* plus the addition of 5 *Tarsonemus* mites (+ 0. *minus*/ + mites). Data are log transformed.

Sampling in natural infestations

In natural infestations, larval survival of *D. frontalis* was dramatically different inside and outside of phloem patches that were occupied by 0. *minus:* usually < 20% survival with 0. *minus* vs > 80% without 0. *minus* (Fig. 2). Larval movements, as revealed by their galleries, were small (usually < 2 cm) compared to the patch sizes of 0. *minus*, and seldom crossed into or out of 0. *minus* patches. In the Bankhead N.F., the area of bluestain was only half as high in spring vs summer, and larval survival was more than twice as high in spring vs summer (Fig. 3; $F_{1,52}$ -4.76; P = 0.03, and $F_{1,52}$ = 40.20, P < 0.0001, respectively). Abundance of *Tarsonemus* mites in the Bankhead N.F. was markedly higher in spring than summer, and similar to the Talladega N.F. during summer (back-transformed means = 3139 vs 78 vs 115 mites/264 cm', respectively; $F_{2,35} = 5.66$, P = 0.008). Average mite abundance in the Talladega N.F. increased from 0 to 6000 mites/264 cm^2 as 0.

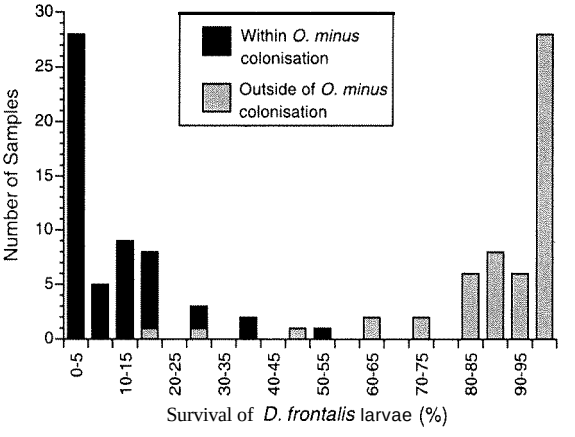

Fig. 2. Frequency distributions of survival of *D. frontalis* larvae within and outside areas of 0. *minus* colonisation (bluestain) within the phloem.

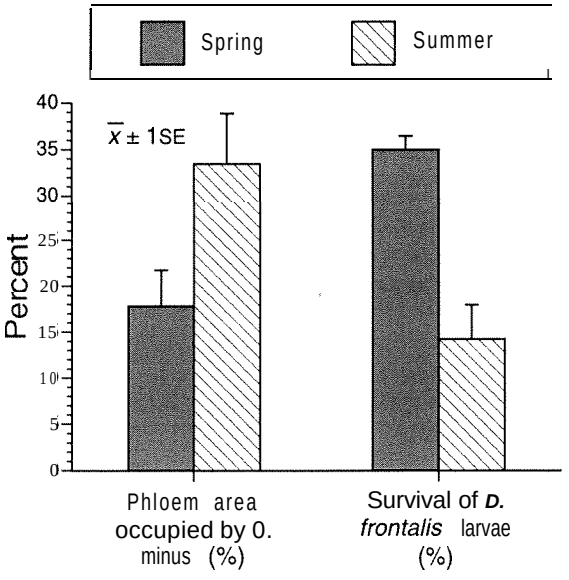

Fig. 3. Seasonal change in the amount of *O. minus* colonisation (bluestain) and the survival of *D. frontalis* larvae in the Bankhead National Forest during 1999.

minus colonization increased from 5 to 45% of the phloem surface (P = 0.0006 and r^2 = 0.35 for linear regression, Fig. 4). In the Bankhead N.F., mite abundance was strongly related to 0. *minus* in the spring: Log(mites) = 2.85 + 0.036 x %bluestain, $r^2 = 0.65$, P = 0.0003, Fig. 4), but not during the summer (P = 0.68).

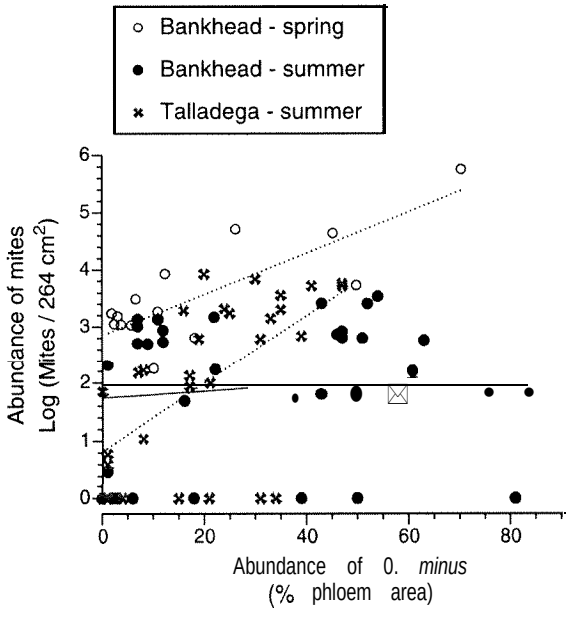

Fig. 4. Density of Tursonemus mites as a function of phloem area occupied by 0. *minus* (bluestain) in the Bankhead and Talladega National Forests during 1999.

Temperature response of mite population growth

Reproduction of *Tursonemus* mites was highly sensitive to temperature (Table 1). At 8°C, adult females in the malt agar medium rarely moved or fed; only 3 of 10 females had laid even a single egg after 71 days, and none of the eggs had hatched after 30 d. From 15 to 28°C, age of first reproduction decreased from 36 to 8 d, and natality increased from 1 egg/5 d to 1 egg/d (Table 1). At 32°C, adult female mites were very active but only 3 of 10 females were able to lay eggs before dying within 1 to 9 days, and no larvae completed development.

Similar temperature responses were observed in the colonies that were allowed to grow undisturbed in phloem-based medium (Fig. 5). Again, population growth rates were < 0 at 8°C, increased to very high rates at 28°C (doubling time of 6 d), and declined sharply at 32°C. Population growth rates estimated from life table analyses and colony growth rates were very similar from 8 to 28°C (compare r in Table 1 and Fig. 5). However, at 32°C. growth rates were 0.061 ± 0.021 mites x mite-' x d^{-1} in the phloem medium vs 0 in the agar medium. This was probably an artefact of the agar medium, which became soft at 32°C and appeared to interfere with the movement of females.

Discussion

Effects of mites on 0. minus

Tursonemus mites are clearly important in the propagation of 0. *minus* within beetle-infested trees (Fig. 1). It was already known that phoretic female mites commonly transport ascospores of 0. *minus* from one tree to another (Moser 1985), but it was not known whether this process was quantitatively important compared to the transport of conidia directly on beetle exoskeletons (Bridges and Moser 1983). In fact, it appears to be very important. We found 0. *minus* colonization in 41% of the galleries excavated by wild-caught beetles, compared to only 10% of the galleries excavated by wild-caught beetles from which the mites had been removed. The extent of 0. *minus* colonization associated with beetles that lacked mites can be enhanced by increasing the inoculum carried by beetles directly *(+ 0. minus* in Fig. 1), indicating that direct propagation by beetles can also occur (90% of such galleries had some 0. *minus),* at least with high loading of inoculum. However, 0. *minus* colonization in these samples was generally restricted to within l-4 cm of the point of entry by the beetles. The addition of mites (which themselves lacked 0. *minus)* to these beetles resulted in a 4-fold increase in the average area colonised by 0. *minus* (Fig. 1), and, in most cases, there was 0. *minus* development along the full length of the oviposition gallery. Appar-

Table 1. Demographic parameters (mean ± SE) of *Tursonemus fusarii* feeding on *Ophiostoma* minus in malt agar cultures at different temperatures.

	8°C	15°C	22°C	28°C	32°C
Time to egg hatch (d)	> 30 d	14.7 ± 1.08	5.5 ± 0.16	3.0 ± 0.14	1.6 ± 0.28
Larval to adult (d)		13.8 ± 0.74	5.0 ± 0.27	3.8 ± 0.15	
Age of 1st reproduction (d)		36.12 ± 2.42	12.44 ± 0.82	8.33 ± 0.33	
Surviving colonies after 50 d	50%	80%	90%	100%	0%
Adult longevity (d)	> 57	> 48	> 48	> 48	< 5
Fecundity (eggs × ♀ adult^{-1} × d^{-1})	0.01 ± 0.01	0.23 ± 0.04	0.70 ± 0.06	0.97 ± 1.17	0.12 ± 0.06
Population growth rate[a], r	0	0.009	0.096	0.140	0
Population doubling time (d)	∞	77	7	5	∞

[a] Based on Euler's equation.

ently, *Tarsonemus* not only transport fungal propagules between trees, but also actively spread inoculum throughout the beetle gallery system. This could be a passive consequence of mites walking to and fro through the beetle galleries, but might also involve specialised behaviours of the mites, such as actively picking up fungal propagules and/or sowing them in suitable microsites (e.g. areas of unoccupied phioem with little or no oleoresin). Natural selection should favour mite behaviours that promote 0. *minus* development because their own growth and reproduction is maximised when they are grazing on 0. minus (Lombardero et al. 2000).

Beetles with natural inoculations of 0. *minus*, but lacking mites, produced such low levels of 0. minus colonization that they were statistically indistinguishable from control treatments (Fig. 1). 0. *minus* inoculum on beetle exoskeletons is even less likely to be viable in wild populations than it was in our experimental arena because wild beetles are attacking live trees instead of freshly cut logs, and are frequently immersed in oleoresin that flows into the points of beetle attack from the resin duct system (Dunn and Lorio 1993, Reeve et al. 1995). The oleoresin has broad-spectrum toxicity (Hemingway et al. 1977, DeAngelis et al. 1986, Bridges 1987), and beetles that have been exposed to oleoresin carry dramatically reduced populations of viable fungal propagules on their exoskeleton (Veysey et al., in press). In contrast, many of the fungal spores carried by *Tarsonemus* are protected within the sporothecae (Moser 1985). *Tursonemus* mites appear to be a dominant agent in the dispersal of *0. minus* within and among trees. Indeed, 0. *minus* was most abundant in the spring, at the same time as *Tursonemus* were most abundant. Similarly, Bridges and Moser (1986) reported a positive correlation between the abundance of *T. kruntzi* and 0. *minus*. Presumably, high abundance of *Tursonemus* is partly the cause (mites transporting fungus) and partly the effect (mites consuming fungus) of high abundance of *0. minus*. *Tursonemus* may have additional importance in the evolutionary *ecology* of 0. *minus* because mites are the main way in which ascospores, which are the product of sexual reproduction, are transported (Moser 1985, Lombardero et al. 2000). Recent work has identified the existence of, and variability within, multiple mating types of 0. *minus* (Uzonovic 1997, Gorton and Webber 2000). Mites may be especially important in bringing together compatible mating types of 0. *minus* and thus perpetuating outcrossing and variability within this fungus. Diverse communities of phoretic mites are associated with many bark beetle species, and are probably of general importance in propagating fungi in dying trees (Blackwell et al. 1986, Levieux et al. 1989, Moser et al. 1989, 1997).

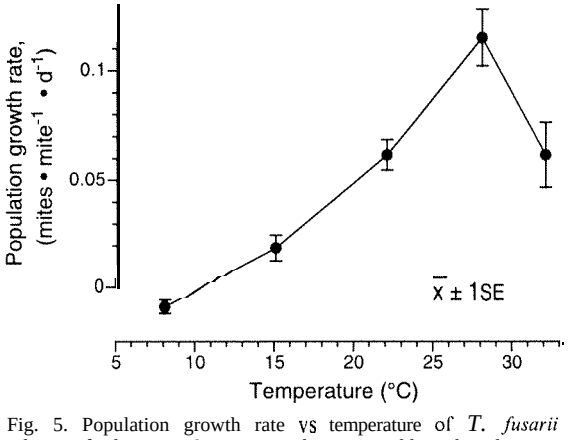

Fig. 5. Population growth rate vs temperature of *T. fusarii* colonies feeding on 0. minus cultures in phloem-based agar. Compare to independent estimates of population growth rates from life table analyses (Table I).

Effects of 0. *minus on* beetles

Sampling of natural infestations indicated strong negative effects of 0. *minus* on the larval survival of *D. frontalis* (Fig. 2). Larvae within bluestain areas had abnormal meandering feeding galleries, and usually died prior to completing development (see also laboratory studies by Barras 1970, Bridges and Perry 1985 and Goldhammer et al. 1991). Our sampling indicated that the negative effects of 0. *minus* on *D. frontalis* are enough to have strong demographic impacts on *D. frontalis*. The average larval survival (± SE) was only

10 ± 2% in bluestain vs 83 ± 3% outside of bluestain (Fig. 2). If other things remain equal, a population of *D. frontalis* that was at replacement reproduction ($R_o = 1$) with 35% of the phloem occupied by *0. minus,* would grow at the very rapid rate of 26% per generation if bluestain decreased to 10% of the phloem. Accordingly, the growth rate of local *D. frontalis* infestations tends to be inversely related to the abundance of *0. minus* (Bridges 1983, 1985, Bridges and Moser 1986), and we found that average larval survival increased from 18% to 35% as bluestain decreased from 35% in the spring to 15% in the summer (Fig. 3). The mechanisms for this antagonism remain unclear. It could be due to direct competition for phloem nutrients between *D. frontalis* larvae and *0. minus* hyphae (Barras and Hodges 1969) or to allelopathic effects on *D. frontalis* larvae of the isocoumarins and phenols that are synthesised by 0. *minus* (Hemingway et al. 1977, DeAngelis et al. 1986, Bridges 1987). However, sympatric species of bark beetles that lack mutualistic relations with mycangial fungi, such as *Ips grandicollis* (Ayres et al. 2000) appear to be unaffected by the presence or absence of *0. minus* (Yearian et al. 1972). This suggests that the detrimental effects of *0. minus* on *D. frontalis* larvae are an indirect result of 0. *minus* outcompeting the mycangial fungi on which larvae depend (Bridges and Perry 1985, Klepzig and Wilkens 1997, Klepzig et al. 2001a, b).

Regardless of the mechanisms, it appears that any factor that increases the amount of 0. *minus* will tend to depress population growth rates of *D. frontalis.* In combination with the experimental evidence that *Tarsonemus* mites propagate 0. *minus* (Fig. 1), it seems probable that mites can influence the population dynamics of *D. frontalis* through an indirect pathway that involves a mutualism between mites and 0. *minus,* and asymmetric competition between *0. minus* and the mycangial fungi (Lombardero et al. 2000, Klepzig et al. 2001a, b). Because the mites are themselves dependent upon *D. frontalis* for dispersal between trees, this produces a negative feedback loop of community interactions that could influence the endogenous dynamics of beetle populations (increases in beetles lead to increases in mites, which promote increases in 0. *minus,* which limit the colonization success of mycangial fungi, which lowers the reproductive success of beetles). If there is a delay in the feedback, as seems probable given the number of community interactions that are involved (Turchin 1991), this pathway could contribute to the delayed density-dependence that characterises time series of *D. frontalis* abundance (Turchin et al. 1991), and which have thus far been attributed to a specialist predator (Turchin et al. 1999, Reeve and Turchin 2002). This adds to other known cases in which indirect interactions can influence population dynamics and community structure (Callaway and Walker 1997, Gaume et al. 1998). Mites have previously been discounted in studies of bark beetle population dynamics because they are commensals that have little or no direct effects on the beetles (Moser 1976). Indeed, we would still expect this to be the case for beetle species that lack mutualistic associations with fungi (Ayres et al. 2000), because there would then be no feedback loop of community interactions. Mutualisms, which have received far less attention by community ecologists than predation or competition (Christian 2001, Stachowicz 2001), might have general importance in linking direct community interactions into chains, webs, or even loops, of indirect interactions,

Environmental mediation of indirect interactions?

Comparisons of temperature effects on mite reproductive rates and beetle development time support the hypothesis that the abiotic environment can influence community structure. The growth of phoretic mite populations must depend in part upon the time that is available for reproduction by initially colonizing mites until the departure of adult progeny of the colonizing beetles. That is, the window of opportunity for mite reproduction is set by the generation time of *D. frontalis. (Tarsonrmus* that remain within a tree after the departure of *D. frontalis* are functionally extinct.) *T. fusarii* is more sensitive to temperature than *D. frontalis. D. frontalis* larvae can continue development even during the winter (Thatcher 1967), and adult beetles may be flying at temperatures as low as 7°C (Moser and Thompson 1986). At the same temperatures, *T. fusarii* is barely able to move, feed, or lay eggs (Table 1, Fig. 5). *D. frontalis* development rates as a function of temperature have previously been summarised by Ungerer et al. (1999) using empirical data (Gagne et al. 1982, Wagner et al. 1984) applied to a general biophysical model of poikilotherm development (Sharpe and DeMichele 1977, Schoolfield et al. 1981). This permitted a comparison of mite reproductive potential with beetle development rate (Fig. 6). Both species minimise their development time at 27–30°C, but the generation time of *D. frontalis* increases more slowly on either side of those temperatures than the time required for *T. fusurii* abundance to increase by 100-fold (Fig. 6, top panel). This difference in temperature sensitivity produces a surprisingly narrow range of temperatures (centred at 27°C) in which mite reproduction per *D. frontalis* generation can be very high (up to 100-fold, Fig. 6, bottom panel). At temperatures < 23°C or > 30°C, mite reproductive potential is less than half it's maximum.

This model predicts that the growth rate of mite populations, and therefore the abundance of mites and propagation of *0. minus,* will vary with seasonal and regional patterns in temperature. There is evidence of seasonal changes in the abundance of *Tarsonemus* and

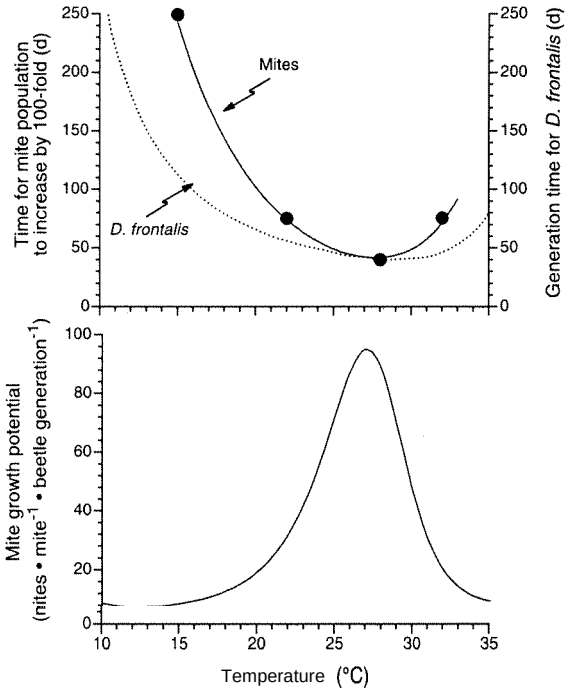

Fig. 6. Comparison of temperature responses of *T. fusarii* and *D. frontalis*. Top panel compares the time required for mite populations to increase by 100-fold with the generation time of *D. frontalis*. *T. fusarii* data points were calculated from Fig. 5 and interpolated with the biophysical kinetics model of Sharpe and DeMichele (1977). *D. frontalis* function is from the same biophysical model fit to empirical measurements (Ungerer et al. 1999). Bottom panel (calculated from functions in the top panel) shows the theoretical factor of increase for mites during the window of opportunity from when they arrive on colonizing beetles until the opportunity to depart on emerging beetle progeny (one *D. frontalis* generation).

0. *minus,* but at present the data are few and the patterns unclear. The abundance of phoretic *Tarsonemus* increased from spring to summer in the Kisatchie National Forest, Louisiana (*T. krantzi*/flying beetle averaged < 1 in May vs > 7 in July; Kinn 1982). This is the general seasonal pattern predicted by Fig. 6. For example, the potential growth of mite populations in the Bankhead Forest during 1999, based on environmental temperatures, was less during the spring than summer: mean $\pm$ SD = 10.4 $\pm$ 8.6 vs 25.3 $\pm$ 5.8°C (1 hour temperatures interpolated with a sin function from daily maximum and minimum air temperatures for 20 November 1998 to 15 April 1999 vs 15 June to 1 August 1999, respectively; both time periods correspond to the development times predicted from the model in Ungerer et al. 1999 for the generation of *D. frontalis* emerging at the time of our sampling; based on NOAA data for Bankhead Lock and Dam site). In contrast, we found higher abundance of mites (in phloem) in spring vs summer. This could be reconciled with the model in Fig. 6 if food was limiting for mites during the summer (as suggested by the decrease in 0. *minus,* Fig. 3), and/or if there were more colonizing mites that initiated the spring infestations. More data are required to test the hypothesis that seasonal temperature oscillations produce seasonal dynamics in mite reproduction, which influences the proliferation of 0. *minus* (Fig. 1), which feeds back to influence the realized growth of mite populations (Lombardero et al. 2000, Fig. 4). Given the strong antagonistic effects of *0. minus* on *D. frontalis* (Fig. 2), such seasonal oscillations would probably have consequences for beetle population dynamics. A satisfying model of this system might need to incorporate temperature responses in the three dominant fungal species and the two other species of *Tarsonemus.* However, it might remain relatively simple because the three *Tarsonemus* species have proven to be very similar in other aspects of their biology (e.g. life history attributes and nutritional ecology; Lombardero et al. 2000), and the three fungal species appear to have similar growth-temperature responses (Klepzig et al. 2001a).

Differences in the temperature responses of interacting species can have dramatic effects in some other ecological systems. For example, temperature can alter the outcome of a developmental race between maturing foliage and caterpillars that feed on immature foliage (Ayres 1993), influence whether or not parasitoids regulate their host population (Burnett 1949), modulate the community impacts of starfish predator (Sanford 1999), entrain predator-prey dynamics in a polychaete community (Beukema et al. 2000), and alter trophic structure and ecosystem function in aquatic microcosms (Petchey et al. 1999). Similarly, strong interactions between mycophagous *Drosophila* and their nematode parasites are influenced by rainfall patterns (Jaenike 2002), and communities of pine, ectomycorrhizae, and soil fauna are influenced by soil type (Setala et al. 1997). The *D. frontalis* community may be another case in which the abiotic environment can alter a system of species interactions.

Acknowledgements – We thank Jonny Fryar, Alyson Santoro, Erich Vallery, and Jessica Veysey for lab and field assistance, and personnel of the Bankhead National Forest for their cooperation. The manuscript benefited from comments by Bruce Ayres, Tom Dempsey, Sharon Martinson and Tiina Ylioja. Research was supported by NRI CGPs # 9835302, # 2001-35302-09921.

References

Abrams, P. A. 1987. On classifying interactions between populations. – Oecologia 73: 272-281.

Abrams, P. A., Holt, R. D. and Roth, J. D. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. – Ecology 79: 201–212.

Ayres, M. P. 1993. Global change, plant defense, and herbivory. – In: Kareiva, P. M., Kingsolver, J. G. and Huey, R. B. (eds), Biotic interactions and global change. Sinauer Associates, pp. 75-94.

Ayres, M. P. and Lombardero, M. J. 2000. Assessing the consequences of climate change for forest herbivore and pathogens. – Sci. Total Environ. 262: 2633286.

Ayres, M. P., Wilkens, R. T., Ruel, J. J. et al. 2000. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. – Ecology 81: 2198-2210.

Barras, S. J. 1970. Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis* minor. – Ann. Entomol. Soc. Am. 63: 1187-1190.

Barras, S. J. and Hodges, J. D. 1969. Carbohydrates of inner bark of *Pinus taeda* as affected by *Dendrocronus frontalis* and associated microorganisms. – Can. Entomol. 101: 489-493.

Barras, S. J. and Perry, T. 1972. Fungal symbionts in the prothoracic mycangium of *Dendrocronus frontalis* (Coleopt.: Scolytidae). – Z. Anegw. Entomol. 71: 95-104.

Barras, S. J. and' Taylor, J. J. 1973. Varietal Ceratocystis minor identified from mycangium of *Dendroctonus frontalis*. – Mycopathol. Mycol. Appl. 50: 293–305.

Barras, S. J. and Perry, T. J. 1975. Interrelationships among microorganisms, bark or ambrosia beetles, and woody plant tissue: an annotated bibliography, 1965– 1974. U S Dept of Agric. Forest Service, Southern Forest Exp. Stn, General Technical Report SO-IO.

Beukema, J. J., Essink, K. and Dekker, R. 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the wadden seathe role of weather and predator-prey interactions. – J. Anim. Ecol. 69: 31–44.

Blackwell, M., Bridges, J. R., Moser, J. C. and Perry, T. J. 1986. Hyperphoretic dispersal of a *Pyxidiophora anamorph*. – Science 232: 993-995.

Bridges, J. R. 1983. Mycangial fungi of *Dendroctonus frontalis* (Coleoptera: Scolytidae) and their relationship to beetle aoqulation trends. – Environ. Entomol. 12: 858–861.

Bridges, J. R. 1985. Relationship of symbiotic fungi to southern pine beetle population trends. – In: Branhan, S. J. and Thatcher, R. C. (eds), lnlegrdled pest management research symposium: the proceedings. U S Dept of Agric. Forest Service, Southern Forest Exp. Stn, General Technical Report SO-56., pp. 127–135.

Bridges, J. R. 1987. Effects of terpenoid compounds on growth of symbiotic fungi associated with the southern pine beetle. – Phytopathology 77: 83-85.

Bridges, J. R. and Moser, J. C. 1983. Role of two phoretic mites in transmission of bluestain fungus, *Ceratocystis minor*. – Ecol. Entomol. 8: 9–12.

Bridges, J. R. and Perry, T. J. 1985. Effects of mycangial fungi on gallery construction and distribution of bluestain in southern pine beetle-infested pine bolts. J. Entomol. Sci. 20: 271–275.

Bridges, J. R. and Moser. J. C. 1986. Relationship of nhoretic mites (Acari: Tarsonemidae) to the bluestaining 'fungus, *Ceratocystis minor*, in trees infested by southern pine beetle (Coleoptera: Scolytidae). – Environ. Entomol. 15: 951–953.

Bridges, J. R., Marler, J. E. and McSparrin, B. H. 1984. A quantitative study of the yeasts and bacteria associated with laboratory-reared *Dendroctonus frontalis* Zimm. (Coleoptera: Scolytidae). – Z. Angew. Entomol. 97: 261–267.

Bridges, J. R., Nettleton, W. A. and Connor, M. D. 1985. Southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae) infestations without the bluestain fungus *Ceratocystis minor*. – J. Econ. Entomol. 78: 325-327.

Burnett, T. 1949. The effect of temperature on an insect host-parasite population. – Ecology 30: 113– 134.

Callaway, R. M. and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – Ecology 78: 1958– 1965.

Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. – Nature 413: 635-639.

Coulson, R. N., Pulley, P. E., Foltz, J. L. et al. 1977. Survival models for within-tree populations of *Dendroctonus frontalis* (Coleoptera: Scolytidae). – Can. Entomol. 109: 1071–1077.

Dajoz, R. 1974. Les insectes xylophages et leur role dans la degradation du bois mort. – In: Pesson, P. (ed.), Ecologie forestiere. Gautiers-Villars, Paris, pp. 257–307.

DeAngelis, J. D., Hodges, J. D. and Nebeker, T. E. 1986. Phenolic metabolites of *Ceratocystis minor* from laboratory cultures and their effects on transpiration in loblolly pine *Pinus taeda* seedlings. – Can. J. Bot. 64: 151–155.

Dunn, J. P. and Lorio, P. L., J.r. 1993. Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). Environ. Entomol. 22: 948-957.

Gagne, J. A., Wagner, T. L., Sharpe, P. J. H., Coulson, R. N. and Fargo, W. S. 1982. Reemergence of *Dendrocronus frontalis* (Coleoptera: Scolytidae) at constant temperatures. Environ. Entomol. 11: 1216–1222.

Gaume, L., McKey, D. and Terrin, S. 1998. Ant-plant-homonteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. Proc. R. Soc. Lond. (Biol.) 265: 569–575.

Coldhammer, D. S., Stephen, F. M. and Paine, T. D. 1991. The effect of the fungi *Ceratocystis minor* (Hedgecock) Hunt, *Ceratocystis minor* (Hedgecock) Hunt var. *barrasii* Taylor, and SJB 122 on reproduction of the southern pine beetle. *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). – Can. Entomol. 122: 407–418.

Gorton, C. and Webber, J. F. 2000. Reevaluation of the status of the bluestain fungus and bark beetle associate *Ophiostoma minus*. – Mycologia 92: 1071-1079.

Hain, F. P. 1980. Sampling and predicting population trends. -- In: Thatcher, R. C., Searcy, J. L., Coster, J. E. and Hertel, G. D. (eds), The southern pine beetle. U S Dept of Agric. Forest Service, Combined Forest Pest Research and Development Program, Pineville, LA, Technical Bulletin 1631., pp. 107–136.

Happ, G. M., Happ, C. M. and Barras, S. J. 1976. Bark beetle-fungal symbiosis. II. Fine structure of a basidiomycetous ectosymbiont of the southern pine beetle. Can. J. Bot. 54: 1049-1062.

Hemingway, R. W., McGraw, G. W. and Barras, S. J. 1977. Polyphenols in *Ceratocystis* minor infected *Pinus taeda*: fungal metabolites, phloem and xylem phenols. J. Agr. Food Chem. 25: 717-722.

Howden, H. F. and Vogt, G. B. 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill.). Ann. Entomol. Soc. Am. 44: 581–585.

Hsiau, 0. T. H. 1996. The taxonomy and phylogeny of the mycanaial fungi from Dendroctonus brevicomus and Dendroctonus frontalis (Coleoptera: Scolytidae). PhD thesis. Iowa State Univ.

Janssen, A., Pallini, A., Venzon, M. and Sabelis, M. W. 1998. Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. – Exp. Appl. Acarol. 22: 497–521.

Jaenike, J. 2002. Time-delayed effects of climate variation on host-parasite dynamics. – Ecology 83: 917-924.

Kinn, D. N. 1982. Seasonal distribution of three common mite associates of the southern pine beetle (Coleoptera: Scolytidae) in central Louisiana. – Fla. Entomol. 65: 185–187.

Kinn, D. N. and Witcosky, J. J. 1978. Variation in southern pine beetle attack height associated with phoretic uropodid mites. – Can. Entomol. 110: 249-252.

Klepzig, K. D. and Wilkens. R. T. 1997. Comoetitive interactions among symbiotic fungi of the southern pine beetle. Appl. Environ. Microbiol. 63: 621–627.

Klepzig, K. D., Moser, J. C., Lombardero, M. J. et al. 2001a. Mutualism and antagonism: ecological interactions among bark beetles, mites, and fungi. – In: Jeger, M. J. and Spence, N. J. (eds), Biotic interactions in plant-pathogen associations. CABI Publishing, New York, pp. 237-269.

Klepzig, K. D., Moser, J. C., Lombardero, M. J. et al. 2001b. Symbiosis and competition: complex interactions among beetles, fungi and mites. – Symbiosis 30: 83-96.

Levieux, J., Lieutier, F., Moser, J. C. and Perry, T. J. 1989. Transportation of phytopathogenic fungi by the bark beetle *Ips sexdentatus* Boerner and associated mites. – J. Appl. Entomol. 108: l-l 1.

Lombardero, M. J., Klepzig, K. D., Moser, J. C. and Ayres, M. P. 2000. Biology, demography, and community interactions of *Tarsonrmus* (Acarina: Tarsonemidae) mites phoretic on *Dendroctonus frontalis* (Coleoptera: Scolytidae). – Agric. Forest Entomol. 2: 193–202.

Martinsen, G. D., Driebe, E. M. and Whitham, T. G. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. – Ecology 79: 192–200.

Moore, G. E. 1971. Mortality factors caused by pathogenic bacteria and fungi of southern pine beetle in North Carolina. – J. lnvertebr. Pathol. 17: 28-37.

Moore, G. E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environ. Entomol. 1: 58–65.

Moser, J. C. 1976. Phoretic carrying capacity of flying southern pine beetle (Coleoptera: Scolytidae). – Can. Entomol. 108: 807–808.

Moser, J. C. 1985. Use of sporothecae by phoretic *Tarsonrmus* mites to transport ascospores of coniferous bluestain fungi. – Trans. Br. Mycol. Soc. 84: 750–753.

Moser, J. C. and Roton, L. M. 1971. Mites associated with southern pine bark beetles in Allen Parish, Louisiana. – Can. Entomol. 103: 1775–1798.

Moser, J. C. and Thompson, W. A. 1986. Temperature thresholds related to flight of *Dendroctonus frontalis* Zimm. (Col.: Scolytidae). – Agronomie 6: 905–910.

Moser, J. C. and Macias-Samano, J. E. 2000. Tarsonemid mite associates *of Dendroctonus frontalis* (Coleoptera: Scolytidae): implications for the historical biogeography of *D. frontalis*. – Can. Entomol. 132: 765–771.

Moser, J. C., Thatcher, R. C. and Pickard, L. S. 1971. Relative abundance of southern pine beetle associates in East Texas. Ann. Entomol. Soc. Am. 64: 72-77.

Moser, J. C., Wilkinson, R. C. and Clark, E. W. 1974. Mites associated with *Dendroctonus frontalis* Zimmermann (Scolytidae: Coleoptera) in Central America and Mexico. Turrialba 24: 379-381.

Moser, J. C., Perry, T. J. and Solheim, H. 1989. Ascospores hyperphoretic on mites associated with *Ips typographus*. – Mycol. Res. 93: 513–517.

Moser, J. C., Perry, T. J. and Furuta, K. 1997. Phoretic mites and their hyperphoretic fungi associated with flying *Ips typographus* Japonicus Niijima (Col., Scolytidae) in Japan. J. Appl. Entomol. 121: 425–428.

Payne, T. L. 1983. Behavior. – In: History, status and future needs for entomology research in southern forests. 'Proc. 10th anniversary of the East Texas Forest Entomol. Sem. Texas Agric. Exp. Stn, Texas A&M Univ. System, College Station, TX USA. 72 pp.

Petchey, 0. L., McPhearson, P. T., Casey, T. M. and Morin, P. J. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402: 69-72.

Price, T. S., Dogget, H. C., Pye, J. M. and Smith, B. 1997. A history of southern pine beetle outbreaks in the southeastern United States. – Georgia Forestry Commission, Macon, Georgia.

Reeve, J. R. and Turchin, P. 2002. Evidence for predator-prey cycles in a bark beetle. – In: Berryman, A. (ed.), Population cycles: the case for trophic interactions. Oxford Press, pp. 92– 108.

Reeve, J. R., Ayres, M. P. and Lorio, P. L., J.r. 1995. Host suitability, predation, and bark beetle population dynamics. – In: Cappuccino, N. and Price, P. W. (eds), Population dynamics: new approaches and synthesis. Academic Press, pp. 339-357.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. – Science 283: 2095–2097.

Savely, H. E. 1939. Ecological relations of certain animals in dead pine and oak logs. – Ecol. Monogr. 9: 321-385.

Schoolfield, R. M., Sharpe, P. J. H. and Magnuson, C. E. 1981. Nonlinear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. – J. Theor. Biol. 88: 717-731.

Setala, H., Rissanen, J. and Markkola, A. M. 1997. Conditional outcome in the relationship between pine and ectomycorrhizal fungi in relation to biotic and abiotic environment. – Oikos 80: 112-122.

Sharpe, P. J. H. and DeMichele, D. W. 1977. Reaction kinetics of poikilotherm development. – J. Theor. Biol. 64: 649-670.

Sih, A., Crowley, P., McPeek, M. et al. 1985. Predation, competition and prey communities: a review of field experiments. Annu. Rev. Ecol. Syst. 16: 269–311.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51: 235-246.

Stephen, F. M., Berisford, C. W., Dahlstein, D. L. et al. 1993. Invertebrate and microbial associates. – In: Schowalter, T. D. and Filip, G. M. (eds), Beetle-pathogen interactions in conifer forests. Academic Press, pp. 129– 147.

Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study, and importance. – Trends Ecol. Evol. 6: 206–210.

Thatcher, R. C. 1967. Winter brood development of southern pine beetle in southeast Texas. – J. Econ. Entomol. 60: 599–600.

Thatcher, R. C., Searcy, J. L., Coster, J. E. and Hertel, G. D. 1980. The southern pine beetle. Technical Bulletin 1631, U S Dept of Agric. Forest Service, Combined Forest Pest Research and Development Program, Pineville, LA.

Turchin, P. 1991. Nonlinear modeling of time series data: limit cycles and chaos in forest insects, voles and epidemics. – In: Logan, J. A. and Hain, F. P. (eds), Chaos and insect ecology. Virginia Polytechnic Inst. and State Univ., Blacksburg, Virginia, pp. 39-62.

Turchin, P., Lorio, P. L. J.r. Tavlor. A. D. and Billings, R. F. 1991. Why do populations of southern pine- beetles (Coleoptera: Scolytidae) fluctuate? – Environ. Entomol. 20: 401–409.

Turchin, P., Taylor, A. D. and Reeve, J. D. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. – Science 285: 1068–1071.

Ungerer, M. J., Ayres, M. P. and Lombardero, M. J. 1999. Climate and the northern distribution limits *of Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). – J. Biogeogr. 26: 1133–1145.

Uzonovic, A. 1997. Biology of bluestain in the context of modern forestry. PhD thesis. Imperial College, London.

Veysey, J. S., Ayres, M. P., Lombardero, M. J. et al. 2003. Relative suitability of Virginia pine and loblolly pine as host species for Dendroctonus frontalis (Coleoptera: Scolytidae). – Environmental Entomology 32 (3): (in press).

Wagner, T. L., Gagne, J. A., Sharpe, P. J. H. and Coulson, R. N. 1984. A biophysical model of southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae) development. – Ecol. Model. 21: 125–147.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75: 151–165.

Yearian, W. C., Gouger, R. J. and Wilkinson, R. C. 1972. Effects of the bluestain fungus, *Ceratocystis ips*, on development of *Ips* bark beetles in pine bolts. – Ann. Entomol. Soc. Am. 65: 481–487.