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Biology, demography and community interactions of *Tarsonemus* (Acarina: Tarsonemidae) mites phoretic on *Dendroctonus frontalis* (Coleoptera: Scolytidae)

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Abstract

1 *Dendroctonus frontalis*, the southern pine beetle, is associated with a diverse community of fungi and mites that are phoretic on the adult beetles. *Tarsonemus ips*, *T. kranzti* and *T. fusarii* (Acarina: Tarsonemidae) may interact within this community in ways that link the population dynamics of *D. frontalis*, the mites and three dominant species of fungi. We explored species associations by comparing the dietary suitability of different fungi for *Tarsonemus* spp.

2 All three mite species fed and reproduced at high rates when feeding on the bluestain fungus, *Ophiostoma minus,* which is an antagonist of *D. frontalis* larvae.

3 Mites also had positive population growth rates when feeding upon *Ceratocystiopsis ranaculosus,* one of the mycangial fungi, but could barely reproduce when feeding upon *Entomocorticium* sp. A, the mycangial fungus that is most suitable for *D. frontalis*.

4 During the time from colonization of a tree by *D. frontalis* adults until departure from the tree of their progeny (≈ 40 d at 30 °C), mite populations feeding upon *O. minus* can increase by factors of up to 209 (*T. fusarii*), 173 (*T. ips*) or 384 (*T. krantzi*). These high growth rates are allowed by rapid development (age of first reproduction = 8–9 d), high fecundity (≈ 1 egg/d) and high longevity (> 28 d).

5 Precocious mating increases the chance that females are mated prior to colonizing a new tree and arrhenotokous parthenogenesis permits reproduction by unmated females.

6 *Tarsonemus* mites may introduce negative feedback into *D. frontalis* population dynamics by generating indirect interactions between *D. frontalis* and *O. minus*.

Keywords Demography, indirect interactions, life-history, phoresy, southern pine beetle, trophic interactions.

Introduction

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is a major pest in coniferous forests of the south-eastern United States (Price *et al.*, 1997). This insect supports a diverse community of associated species by facilitating their access to the subcortical environment of the trees that they infest. Although *D. frontalis* may carry over 40 species of fungi and bacteria (Moore, 1971, 1972; Bridges *et al.*, 1984), three species of fungi have been studied extensively because of their strong interactions with *D. frontalis* (Paine *et al.*, 1997). Two of these species, *Ceratocystiopsis ranaculosus* Perry and Bridges and *Entomocorticium* sp. A (formerly SJB 122) are referred to as mycangial fungi because they are transported between trees within specialized glandular structures (mycangia) of adult female beetles (Barras & Perry, 1972; Hsiau, 1996). These fungi apparently serve as a crucial nutritional substrate for developing *D. frontalis* larvae (Barras, 1973; Bridges, 1983; Goldhammer *et al.*, 1990; Coppedge *et al.*, 1995). Most infestations of *D. frontalis* also involve a third fungal species, *Ophiostoma minus* (Hedgcock) H. and P. Sydow. *Ophiostoma minus* is sometimes referred to as a bluestain fungus for the distinctive blue-black coloration of infected wood. It is frequently carried on the beetle exoskeleton (phoresy) but is excluded from the mycangium (Barras & Perry, 1972). *Ophiostoma minus* is a

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strong antagonist of *D. frontalis* larvae. Bluestained areas of the phloem are characterized by inhibited egg production, reduced larval growth and very low larval survival (Barras, 1970; Franklin, 1970; Bridges, 1983) perhaps because *O. minus* competes for phloem with the beneficial mycangial fungi (Klepzig & Wilkens, 1997).

In addition to the fungi, there are at least 57 species of mites that are carried between trees by *D. frontalis* adults (Moser *et al.*, 1971; Moser *et al.*, 1974). This study focused on three species of *Tarsonemus* mites that are very abundant (carried by 24–75% of flying beetles; Moser, 1976a; Bridges & Moser, 1983) and of special ecological importance because they link species interactions between *D. frontalis*, the mycangial fungi and *O. minus* (Moser *et al.*, 1995). *Tarsonemus ips* Lindquist and *T. krantzi* Smiley and Moser are common associates of *D. frontalis* (Moser & Roton, 1971; Smiley & Moser, 1974; Moser, 1976a; Moser & Bridges, 1986). *Tarsonemus fusarii* Cooreman seems to be a less common associate of *D. frontalis* (Moser & Roton, 1971), but was relatively abundant during our study.

The relationship between adult females of *Tarsonemus* spp. and *D. frontalis* has been characterized as phoresy, a phenomenon in which an organism attaches to the outer surface of an animal for a limited time, during which it ceases feeding and ontogenesis (Lindquist, 1969; Smiley & Moser, 1974). This system allows dispersal, via movement of the host animal, away from habitat patches of declining suitability and into new patches of high suitability (Farish & Axtell, 1971). However, the relationship between *D. frontalis* and *Tarsonemus* is probably more complex. *Tarsonemus ips* and *T. krantzi* have specialized integumental structures (sporothecae) that are used to transport ascospores of both the beetle antagonist, *O. minus* (Bridges & Moser, 1983; Moser, 1985) and one of the beetle mutualists, *C. ranaculosus* (Moser *et al.*, 1995). The proportion of phoretic *Tarsonemus* individuals in wild populations that are carrying *O. minus* has been estimated at 59–93% (Bridges & Moser, 1983), 5–21% (Bridges & Moser, 1986) and 85–88% (Moser & Bridges, 1986). Rather extensive sampling indicates that *Tarsonemus* spp. are the mites associated with *D. frontalis* that most commonly transport ascospores between trees (Moser *et al.*, 1995).

This background suggests that *Tarsonemus* spp. may link species interactions in a way that influences *D. frontalis* and the rest of the community. However, evaluation of this hypothesis requires a better understanding of *Tarsonemus* biology. For example, little is known about feeding habits of these species, their demography, or their trophic relationships with various fungal species with which they are associated. This study addressed the following questions. Do *Tarsonemus* feed on the fungi that they transport, and if so, does their demography depend upon their fungal diet? Are the fungi that are most beneficial to *D. frontalis* also most beneficial to *Tarsonemus*? Do the three *Tarsonemus* species differ in their demography, feeding habits and fungal relationships?

Methods

Mite colonies were initiated from wild populations in the Kisatchie National Forest in Louisiana, U.S.A. Female mites were collected beneath the bark of *Pinus taeda* L. that were infested by *D. frontalis*, and were transferred individually to Petri dishes containing cultures of *O. minus* growing on 2.5% malt extract agar (25 g malt extract and 20 g agar/L distilled water). After a week, colonies originated by each original female were identified to species and their progeny, which were all reared in a common laboratory environment, were used in subsequent experiments.

Replicated, experimental cultures of *T. ips*, *T. krantzi* and *T. fusarii* were initiated (12–28 cultures per species), each with a single pair of recently eclosed adults, and monitored daily for 28 d (at 25 °C). We recorded age of first reproduction, rate of egg production per day and adult longevity. Eggs and larvae were monitored to determine time to egg hatch and duration of larval development (and then removed from the colony when they became pharate adults). From these data, we constructed life tables describing the demography of *Tarsonemus* spp. when feeding on *O. minus*. To test for parthenogenesis, similar studies were conducted with unmated females, separated from their colony as larvae. The potential rate of population increase (r), was calculated using Euler's equation (Gotelli, 1998):

$$1 = \sum_{x=0}^{\infty} e^{-rx} l(x) b(x) \qquad (1)$$

where $l(x)$ is the proportion of the original cohort that survived to the start of age x and $b(x)$ is the average number of offspring per female of age x. For the purposes of these calculations, the sex ratio of offspring was assumed to be 1 : 1; in fact, the sex ratios in this group are often skewed toward females (Lindquist, 1986), but this simplifying assumption does not affect species comparisons unless there are differences in sex ratios between species. Net reproductive rate (R_0) and generation time (G) were calculated as:

$$R_0 = \sum_{x=0}^{\infty} l(x) b(x) \qquad (2)$$

$$G = \frac{\ln(R_0)}{r} \qquad (3)$$

In another set of studies, we compared the realized growth rate of mite colonies that were initiated on five different species of fungi: the three *D. frontalis* associates (*Ophiostoma minus, Ceratocystiopsis ranaculosus* and *Entomocorticium* sp. A), plus *O. ips* and *Leptographium terebrantis*, which are commonly associated with other bark beetles and occasionally associated with *D. frontalis* (Yearian *et al.*, 1972; authors unpublished observations). Fungi were grown in 96-well tissue culture plates with a sterile medium containing water, ground freeze-dried *Pinus taeda* phloem and agar (50 : 15 : 1). Each of 5–15 mite colonies per treatment were initiated with one to three mated females. After 40 days at 30 °C (≈ one *D. frontalis* generation), we counted the mites and calculated population growth rate (r) for each colony as:

$$r = \frac{\ln(N_t) - \ln(N_0)}{t} \qquad (4)$$

where N_t = mites after 40 d, $N_0 = 1$ and $t = 40$ d. The parental stock for these studies were the first generation progeny of adult

mites that were collected from nature within 14 d of the start the experiment; this minimized the possibility that selection or habituation within the laboratory could have influenced their growth and reproduction during our experiments. Because these experiments were time-intensive, and because all species of mites and fungi were not continuously available, it was not possible to test all mite species on all fungal species.

To determine the distribution and abundance of the mites in nature, we sampled wild populations in six natural infestations in Alabama U.S.A. during the summer of 1999. Thirty trees were sampled in three infestations within Talladega National Forest, and 20 trees in three other infestations within Bankhead National Forest (infestations within forests were separated by 10–20 km and forests were separated by 150 km). All trees were *P. taeda*, 25–35 years of age. Two bark samples of 9.5 × 28 cm were removed from each tree at 1.5–2 m height. Mite density within the inner bark of each sample was estimated from five randomly chosen subplots of 1 cm^2 within areas with *O. minus* perithecia (bluestain) and areas without *O. minus* perithecia. All trees were at a similar stage in the colonization process (*D. frontalis* progeny were late larvae and pupa). Abundances were log-transformed to correct for heteroscedasticy. We used a paired *t*-test to compare mites/cm^2 in patches within trees containing bluestain vs. patches without bluestain and a nested ANOVA to partition sources of variation. The nested ANOVA treated infestations within forests, trees within infestations, bark samples within trees, and subplots within bark samples as random effects (and was restricted to bluestain subplots because these accounted for nearly all the mites).

Results

Life history

In all three species of *Tarsonemus*, larvae moved and fed like adults. During 2–3 d of feeding, larvae increased by about two-fold in their linear dimensions (without moulting). This was followed by ≈ 24 h in a distinctive inactive stage during which larvae transform into active adults. This state has also been referred to as 'pupa', 'quiescent nymphs' and 'quiescent larva' (Lindquist, 1986). Female adults laid their first egg 2–3 d after eclosion and continued to produce a single egg every 1–2 d throughout the 28 d trial (somewhat higher rates for *T. krantzi* compared to other species; Table 1). Eggs were more than half as long as adult females, so the idiosoma was conspicuously distended in gravid females. Females were all still alive after 28 d, whereas males lived less than one week as adults (mean ± SE = 5.09 ± 0.21 d for *T. krantzi*).

Sex determination and mating biology

Sampling of natural populations suggested a female biased sex ratio (authors unpublished data), probably because the females live longer (> 28 d vs. ≈ 5 d) and because only females colonize new trees (Lindquist, 1986). Arrhenotokous parthenogenesis was observed in all three species (i.e. unfertilized females gave rise to all-male progeny). After the new progeny became adults, females started producing new females, presumably after mating with one of their male progeny. This system has been observed in other mites, e.g. *Polyphagotarsonemus latus* (Banks) (Flechtmann & Flechtmann, 1984). Our observations of *T. ips*, *T. krantzi* and *T. fusarii* are consistent with a system of haplodiploid sex determination, as has been indicated for other species of *Tarsonemus* (Helle *et al.*, 1986; Flechtmann & Flechtmann, 1984).

Male adults are only about 70% as long as females and the last pair of legs are modified into robust claspers for mating. Prior to copulation, males search for immobile pharate females, still within the larval cuticula, and several males may compete for the same female. A successful male attaches to a pharate female by the opisthosoma, affixing his genital capsule to the posterior of the female body, and carries her to a protected place using his fourth pair of legs to help support the female. Although copulation has been observed among *Tarsonemus* adults (Lindquist, 1986), we only saw this happen once, and three of six colonies initiated with single pharate females of *T. fusarii* that we separated from males produced fertile, diploid female eggs. Apparently, copulation and seminal transfer in our study species frequently occur while females are still in the pharate stage.

Life tables

Life table data are summarized in Table 1. Survival to first reproduction was estimated at 90% for all three species (this was conservative in that we never observed larval mortality in growing cultures of *O. minus*). Adult reproductive rate was estimated at 0.46 ± 0.06, 0.43 ± 0.03 and 0.66 ± 0.08 female eggs/d for *T. ips, T. fusarii* and *T. krantzi*, respectively (assumes sex ratio of 1 : 1). Adult longevity for all species was estimated at 28 d. (This was also conservative in that 100% of female adults survived > 28 d, but because the age of first reproduction is so early, truncation of adult longevity at 28 vs. 40 d changed our estimate of population growth rate by only 0.9%; 40 d is the approximate residence time of *D. frontalis* within a tree at these temperatures, which sets an upper limit on the longevity of most females in nature). Estimated generation times were 18.5 d for *T. ips* and *T. fusarii* and 19 d for *T. krantzi*. Estimated net reproductive rates (R_0) were 8.69, 8.13 and 11.97 females/female/lifetime for *T. ips, T. fusarii* and *T. krantzi*, respectively. With these rates of natality and mortality the population growth rate at 30 °C, under a stable age distribution, would be 0.133, 0.128 and 0.149 mites/mite/d for *T. ips, T. fusarii* and *T. krantzi*, respectively. Given these growth rates, mite population size would increase by factors of 209, 173 and 384 during 40 d (the approximate time from tree colonization until departure of *D. frontalis* adults) for *T. ips, T. fusarii* and *T. krantzi*, respectively. Thus, a colonizing population of 10 mites (a typical number accompanying one pair of colonizing *D. frontalis*; Moser & Bridges, 1986) could potentially multiply to 2043, 1673 or 3876 during the time available until the next inter-tree dispersal phase.

Growth of mite colonies feeding on different fungi

Colonies of all three mite species had positive growth rates when feeding upon new hyphal growth of the fungal species that they transport (*O. minus* and *C. ranaculosus*) (Table 2). None of the

Table 1 Demographic parameters for three species of *Tarsonemus* feeding on *Ophiostoma minus*.

	T. ips	*T. fusarii*	*T. krantzi*	*F* statistic (d.f.)
Time to egg hatch (d)	2.20 ± 0.23^{ab}	1.81 ± 0.13^{a}	2.70 ± 0.16^{b}	9.26** (2, 28)
Larval to adult (d)	3.90 ± 0.10^{a}	5.00 ± 0.19^{b}	4.87 ± 0.09^{b}	27.22*** (2, 47)
Age of 1st reproduction (d)	8.10 ± 0.10^{a}	8.81 ± 0.19^{b}	9.57 ± 0.09^{c}	53.61*** (2, 47)
Survival: egg to adult	>90%	>90%	>90%	
Adult female longevity (d)	>28	>28	>28	
Fecundity (eggs/d)	0.92 ± 0.11	0.87 ± 0.19	1.33 ± 0.13	3.36+ (2, 14)
Population growth rate*, *r*	0.133	0.128	0.149	
Mites/mite after 40 d	209	173	384	

* $P<0.05$; ** $P<0.01$; *** $P<0.001$ (one-way ANOVA comparing species). + $P=0.06$.
[a, b, c] Different letters within rows indicate significant differences among mite species (Tukey–Kramer HSD, $P<0.05$).
*Based on life table analyses (mites/mite/d).

Table 2 Realized population growth rates* (mean ± SE) for colonies of three *Tarsonemus* mite species feeding on five fungal species. *Ophiostoma minus, Ceratocystiopsis ranaculosus* and *Entomocorticium* sp. A are all associated with the focal bark beetle, *Dendroctonus frontalis. Leptographium terebrantis* and *O. ips* are associated with other bark beetles in the same forest.

	T. ips			*T. krantzi*			*T. fusarii*		
	r (mites/mite/d)	Colonies surviving (%)	*n*	*r* (mites/mite/d)	Colonies surviving (%)	*n*	*r* (mites/mite/d)	Colonies surviving (%)	*n*
O. minus				0.044 ± 0.014^{a}	47	15	0.045 ± 0.012^{a}	100	9
C. ranaculosus				0.022 ± 0.009^{ab}	53	15	0.062 ± 0.004^{a}	100	7
E. sp. A	0.012 ± 0.012	16	6	0.002 ± 0.002^{b}	10	10	0.014 ± 0.015^{b}	80	5
L. terebrantis							0.044 ± 0.015^{a}	100	5
O. ips							-0.003 ± 0.004^{b}	60	5

*Equation (4).
[a, b, c] Different letters within rows indicate significant differences among fungal species (Tukey-Kramer HSD, $P<0.05$).

mite species realized meaningful population growth when feeding upon *Entomocorticium* sp. A, the mycangial fungus of *D. frontalis* that is not phoretic on the mites (Table 2). Experiments also included two fungal species, *L. terebrantis* and *O. ips*, that are only occasional associates of *D. frontalis* but are commonly vectored by other bark beetles (usually *Ips* spp.) in the same forests. *Tarsonemus fusarii* colonies reproduced successfully when feeding upon *L. terebrantis* but not *O. ips*.

Natural infestations

Sampling in natural infestations showed that *Tarsonemus* mites occur primarily within patches of phloem infested with *O. minus*: back-transformed mean = 3.16 *Tarsonemus*/cm^2 (95% CI = 1.96–4.86) within areas of *O. minus* perithecia (bluestain) vs. 0.026 *Tarsonemus*/cm^2 (95% CI = 0.008–0.044) in no bluestain areas for a total of 50 trees from six infestations in two National Forest. There was dramatic variation in mite density among trees, which accounted for 44% of the total random variance (range in tree means = 0–76 *Tarsonemus*/cm^2 of *O. minus*; $F_{44,39} = 3.61$, $P<0.0001$). There was no significant variation among forests ($F_{1,4} = 0.89$, $P = 0.39$), infestations within forests ($F_{4,44} = 1.00$, $P = 0.44$) or bark samples within trees ($F_{39,97} = 1.17$, $P = 0.27$)

Discussion

Life history adaptations

The three *Tarsonemus* species are similar in their morphology, behaviour and life history attributes. All have very early age of first reproduction and are capable of rapid population growth. In this sense, they are well adapted for coexistence with *D. frontalis*. The window of opportunity for mite reproduction is set by the time for *D. frontalis* to complete a generation, which is usually 40–100 d depending upon temperature (Ungerer *et al.*, 1999). Soon after *D. frontalis* progeny vacate a tree, the phloem becomes unsuitable for *Tarsonemus* spp. and the mite populations that remain are destined for extinction unless there are still *Ips* bark beetles within the tree (Moser & Bridges, 1983). Although the mite species are similar in many ways, there are differences in demographic attributes (Table 1) that could influence their reproductive rate and therefore their relative success in colonizing the next tree. *Tarsonemus krantzi*, by virtue of having the highest fecundity, has a higher rate of potential population growth than its congeners. Given this difference in growth rate, and in the absence of resource limitations, the relative abundance of *T. krantzi* could increase from 33% to >90% of the total *Tarsonemus* individuals within five generations of *D. frontalis* (assuming 40 d as the time for

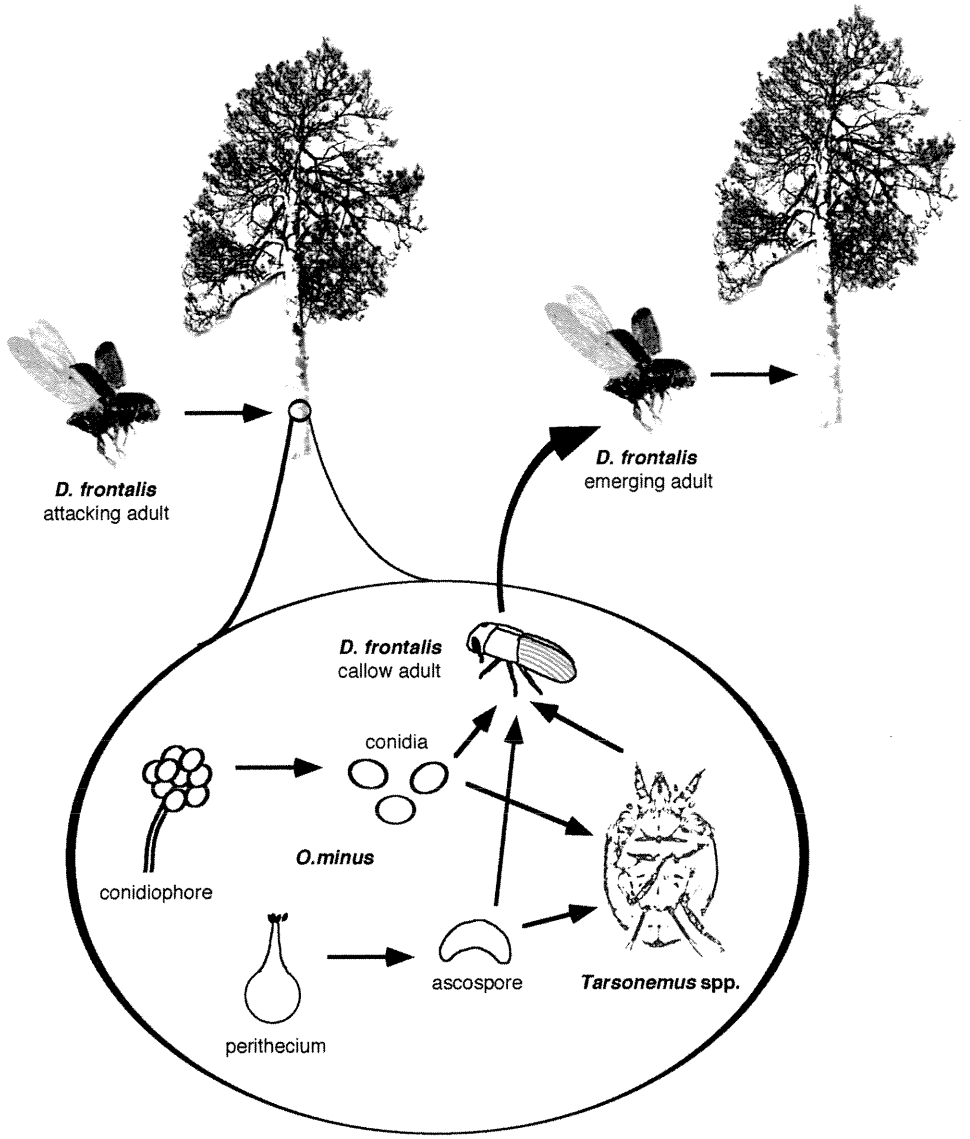

Figure 1 Life history diagram for *Ophiostoma minus*. Fungal propagules are introduced into the phloem of a tree by the attacking adults of *Dendroctonus frontalis*. Within the phloem (enlargement), fungal tissue grows and differentiates to produce new propagules: conidiophores → conidia (asexual) and/or perithecia → ascospores (sexual). *Ophiostoma minus* is homothallic, so ascospores are potentially produced by any colony. Ascospores and conidia can be transported to the next tree either by *D. frontalis* directly, or by *Tarsonemus*, which themselves are transported by *D. frontalis*. The cycle from arrival of attacking *D. frontalis* until the departure of their progeny is ≈ 40 d at 28–30 °C.

D. frontalis complete a generation). The high variation among trees in mite density within apparently suitable habitat (bluestain patches) is apparently due to differences in the number of colonizing mites. This indicates that food resources are commonly not limiting in nature and that potential population growth rate is ecologically relevant for this species. Presumably the advantage of *T. krantzi* in potential growth rate is compensated by other differences between the species that allow coexistence upon the resource base. For example, relatively subtle differences in the success of mites in attaching to *D. frontalis* adults or the temperature responses of mite development, could be enough to compensate for the higher intrinsic growth rate of *T. krantzi*.

The mating system of these *Tarsonemus* species further promotes their coexistence with *D. frontalis*. Males inseminate pharate adult females, so most dispersing female adults are probably already mated. In the event that females are not mated when they disperse, they can produce male progeny by parthenogenesis and mate with their progeny. These attributes are especially important because female adults are the only life stage of *Tarsonemus* spp. that are phoretic (Lindquist, 1986).

Trophic interactions between *Tarsonemus* mites and fungi

The three fungi associated with *D. frontalis* differ greatly in their suitability for *Tarsonemus* mites. All three mite species had high

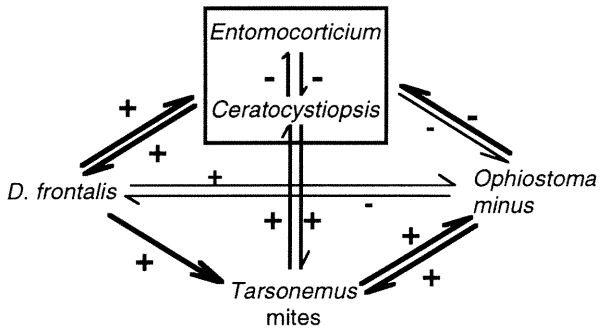

Figure 2 Summary of community interactions among *D. frontalis*, *Tarsonemus* mites and three species of fungi. Arrow size indicates hypothesized effects. Indirect interactions are represented by sequences of arrows. *Dendroctonus frontalis* benefits *Tarsonemus* spp. by transporting them between trees, but experiences no direct effects from *Tarsonemus*. *Tarsonemus* transport *Ophiostoma minus* and *Ceratocystiopsis ranaculosus* between trees and feed on them within trees. *Ophiostoma minus* is a strong competitor of the mycangial fungi, *Entomocorticium* and *C. ranaculosus*, and experiences some (but weaker) reciprocal competition. *Entomocorticium* and *C. ranaculosus* are transported between trees by *D. frontalis* and fed upon by *D. frontalis* within trees. *Entomocorticium* and *C. ranaculosus* compete within the beetle mycangium and within the phloem. *Dendroctonus frontalis* adults transport *O. minus* propogules between trees and *D. frontalis* larvae have reduced survival in the presence of *O. minus*.

reproductive rates when feeding upon *O. minus* (Tables 1 and 2). By contrast, the mycangial fungus *Entomocorticium* sp. A was a very poor nutritional substrate and was effectively unsuitable for growth of any *Tarsonemus* species (Table 2). The other mycangial fungus, *C. ranaculosus*, was of intermediate quality for *T. krantzi* and comparable to *O. minus* for *T. fusarii* (Table 2). Laboratory colonies of *T. ips* also reproduced successfully on *C. ranaculosus*, although we did not record their population growth rates. The two fungal species that are phoretic on *Tarsonemus* mites, *O. minus* and *C. ranaculosus*, are both apparently suitable diets for *Tarsonemus* mites. Sampling of natural infestations indicates that *O. minus* provides the primary diet for wild populations. Thus, the symbiosis between *O. minus* and *Tarsonemus* spp. seems to be a clear case of mutualism. However, *C. ranaculosus* is also nutritionally suitable for *Tarsonemus* spp. and could sometimes be an important food source, especially during early colonization of a tree. *Tarsonemus* only reproduce when they have access to growing hyphae. *Ophiostoma minus* colonization of the phloem begins with dormant conidia and/or dormant ascospores but *C. ranaculosus* is already growing inside of the mycangia when beetles reach the phloem (Barras & Perry, 1972; Happ *et al.*, 1976; Bridges & Perry, 1985). The number of days when mites are reproducing would have a strong effect on their population size when *D. frontalis* adults leave the tree to colonize another. For example, a 10 day difference in beetle development time (from 40 to 30 d) could change the population growth of *T. krantzi* from 188 mites/mite to only 55 mites/mite (based on *r* in Table 1).

Community interactions

It is usually thought that mites have little direct effect on the bark beetles that transport them (Stephen *et al.*, 1993), although there may be some decrease in flight capacity when the number of mites becomes very high (Moser, 1976b; Kinn & Witcosky, 1978). However, indirect interactions can be important in many biological communities (Callaway & Walker, 1997; Abrams *et al.*, 1998; Janssen *et al.*, 1998; Martinsen *et al.*, 1998). Our understanding of the full effects of phoresy requires consideration of indirect interactions.

Tarsonemus mites are apparently very important in the dispersal of *O. minus* among trees. *Ophiostoma minus* abundance within a tree is positively correlated with the number of *T. krantzi* per colonizing beetle (Bridges & Moser, 1986; authors unpublished data). Larvae of *D. frontalis* move to the outer bark to pupate, which probably reduces the chance of acquiring propagules of fungi that are growing within the phloem. Mites moving within the beetle galleries may be especially important in transporting fungi to callow adult beetles prior to dispersal (Roton, 1978; Bridges & Moser, 1983). Mites may have further importance in the propagation of fungi within trees during the early attack phase by beetles. In the absence of mites, *O. minus* can still travel between trees directly on the exoskeleton of dispersing beetles, but many of these propagules are likely to be killed by exposure to oleoresin (through which adult beetles must frequently tunnel when they attack a pine tree; Lorio, 1988). Viable fungal spores may be more likely to reach the phloem when they are transported within the sporothecae of mites. Figure 1 summarizes the possible means by which *O. minus* can reach its host plant.

Dispersion of *O. minus* by *Tarsonemus* could have strong deleterious effects on the larval survival of *D. frontalis* and thereby contribute to the collapse of *D. frontalis* outbreaks. Larvae growing in bluestain areas have long, abnormal feeding galleries and usually do not complete development (Barras, 1970; Bridges & Perry, 1985; Goldhammer *et al.*, 1990). The mechanisms for this antagonism remain unclear. Figure 2 summarizes our working hypothesis of community interactions involving *D. frontalis*, its mycangial fungi, *O. minus* and *Tarsonemus* spp. With the new finding that *O. minus* is a high quality diet for *Tarsonemus* spp., there is evidence for all of the interactions depicted in Fig. 2. *Dendroctonus frontalis* populations could be regulated by this web of community interactions if increased abundance of *D. frontalis* leads to increased abundance of *Tarsonemus* spp., which leads to increased abundance of *O. minus* and subsequently reduces the abundance of *D. frontalis*. Because this hypothesized feedback to *D. frontalis* populations involves a sequence of demographic interactions among species, some delay would be expected and population abundances within the community would tend to cycle. *Dendroctonus frontalis* populations do cycle (Turchin *et al.*, 1991; Turchin *et al.*, 1999) and the source of the delayed density dependence has not yet been resolved (Reeve *et al.*, 1995). If the interaction loop in Fig. 2 is important, then *D. frontalis* should have different population dynamics in forests that lack *Tarsonemus* spp.

Tarsonemus spp., like *D. frontalis*, regularly transport propagules of *C. ranaculosus* among trees, so may also influence the relative abundance of the two species of mycangial fungi. This has consequences for *D. frontalis* because *Entomocorticium* sp. A and *C. ranaculosus* are not equally beneficial for *D. frontalis* (Barras, 1973; Bridges & Perry, 1985;

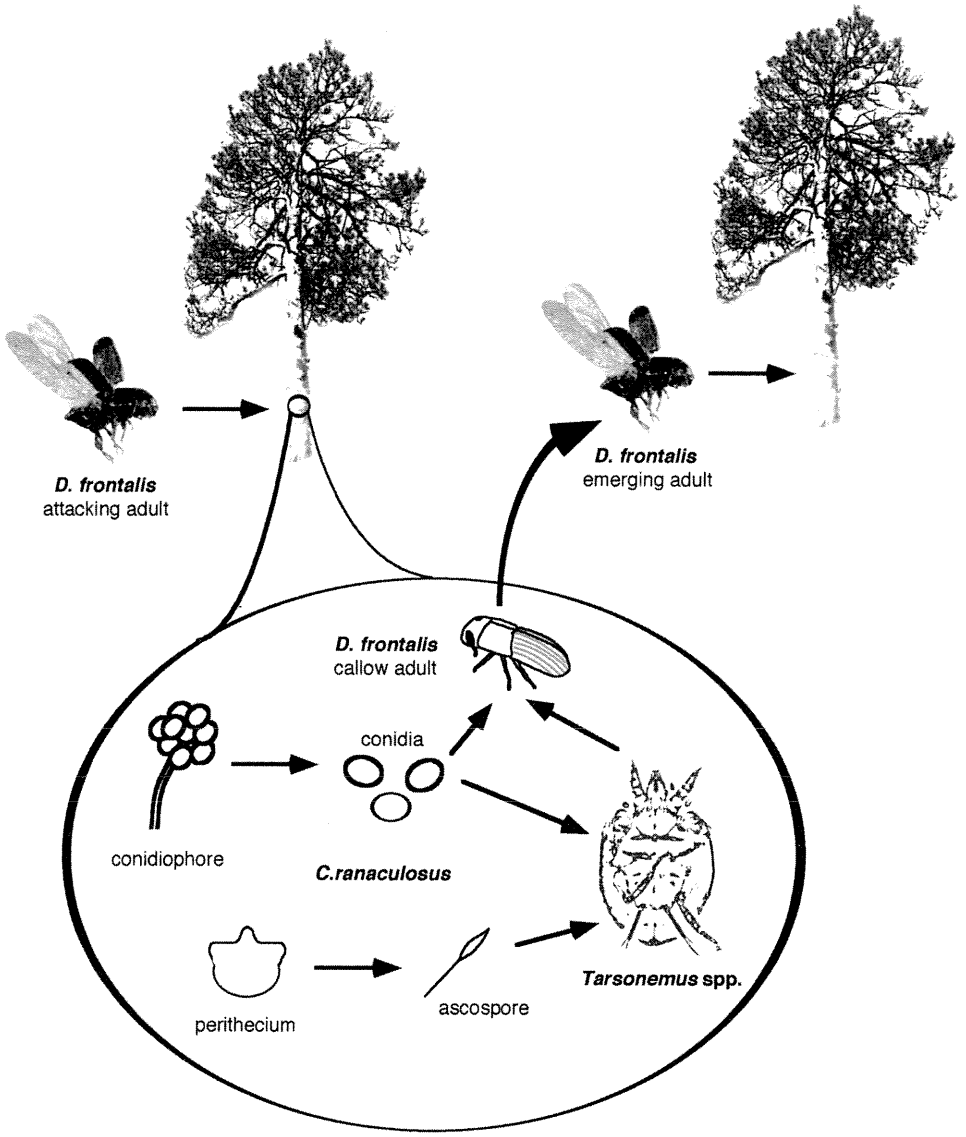

Figure 3 Life history diagram for *Ceratocystiopsis ranaculosus*. Fungal propagules are introduced into the phloem of a tree by the attacking adults of *Dendroctonus frontalis*. Within the phloem (enlargement), fungal tissue grows and differentiates to produce new propagules: conidiophores → conidia (asexual) and/or perithecia → ascospores (sexual). *C. ranaculosus* is heterothallic, so the production of ascospores requires the union of different mating types. Ascospores can be transported to the next tree by *Tarsonemus*, which themselves are transported by *D. frontalis*. Conidia can be transported to the next tree either by *Tarsonemus* or directly by *D. frontalis*. Conidia that reach the mycangium of a *D. frontalis* female can grow within the mycangium as a budding yeast-like colony while dispersing to the next tree. The cycle from arrival of attacking *D. frontalis* until the departure of their progeny is ≈ 40 d at 28–30 °C.

Goldhammer *et al.*, 1990). High abundance of *Entomocorticium* sp. A relative to *C. ranaculosus* is correlated with high rates of population growth in *D. frontalis* and high lipid contents of *D. frontalis* adults (Bridges, 1983; Goldhammer *et al.*, 1990; Coppedge *et al.*, 1995). There is some antagonism between the two mycangial fungi because they do not usually coexist within the same mycangium (Barras & Taylor, 1973; Bridges, 1983). *Ceratocystiopsis ranaculosus* tends to outcompete *Entomocorticium* sp. A in culture (Klepzig & Wilkens, 1997). Also, *C. ranaculosus* colonies are less able to exclude *O. minus* (Klepzig & Wilkens, 1997), which is an antagonist of *D. frontalis* larvae (Barras, 1970; Goldhammer *et al.*, 1990). Thus, there is an indirect antagonism between *Tarsonemus* and *D. frontalis* because the mycangial fungus that provides the greatest benefits to *D. frontalis* (*Entomocorticium* sp. A) is the least suitable as a diet for the mites (Table 2). *Ceratocystiopsis ranaculosus* may be maintained as a mycangial fungus partly as a result of its continued introduction by *Tarsonemus* spp. into the feeding habitats of *D. frontalis*. If initial *Tarsonemus* population growth depends in part upon *C. ranaculosus* cultures that have been

transported and inoculated by *D. frontalis*, this creates an indirect positive effect of *D. frontalis* on *Tarsonemus* spp. (Fig. 2).

The ecological benefits of *Tarsonemus* spp. for *C. ranaculosus* seems to be less important than the benefits from *D. frontalis*. The sporothecae of *Tarsonemus* species, unlike the mycangia of *D. frontalis*, do not have any glandular secretions to promote fungal growth. In the absence of mycangial secretions, the growth rate of *C. ranaculosus* is dramatically lower than that of *O. minus* (Ross *et al.*, 1992; Klepzig & Wilkens, 1997). However, there are probably strong evolutionary benefits for *C. ranaculosus*. This fungus is a heterothallic species and therefore requires that opposite mating types be present for sexual reproduction. *Tarsonemus* spp., by introducing additional mating types of *C. ranaculosus* into the galleries of *D. frontalis*, may be critical for establishing sexually compatible colonies of the fungus (Fig. 3; Moser *et al.*, 1995).

Community interactions may be even more complex if *O. minus* aids *D. frontalis* in killing the host tree, as has been suggested (Nelson & Beal, 1929; Nelson, 1934; Caird, 1935; Bramble & Holst, 1940; Craighead & St. George, 1940; Mathre, 1964; Basham, 1970). This form of mutualism with fungal pathogens is well known for some species of bark beetles (Paine *et al.*, 1997). However, there are numerous reports of *D. frontalis* killing trees in the absence of *O. minus* (Hetrick, 1949; Barras, 1970; Franklin, 1970; Whitney & Cobb, 1972; Bridges *et al.*, 1985). It remains possible that antagonistic effects of *O. minus* on *D. frontalis* are sometimes mitigated by benefits to attacking adults. In some communities, species interactions can switch between positive to negative depending upon environmental conditions (Hobbs, 1996; Callaway & Walker, 1997; Callaway, 1997; Hamback & Ekerholm, 1997).

Dendroctonus frontalis infestations create ephemeral habitats within attacked trees that are occupied by predictable communities of beetles, mites and fungi. These species interact with each other and the host tree in ways that modify the phloem resources on which they all depend. The strongest species interactions form a loop that links, and potentially regulates, the population dynamics of the beetle, three species of *Tarsonemus* mites, and three species of fungi (Fig. 2). More studies are needed to evaluate how these interactions may change over space and time and how the system of interactions influences the community. The ecological and evolutionary dynamics produced by this web of interactions may have ramifications for several hundred other species that inhabit pine forests of the southern United States. Impacts extend to at least 97 species of mites and microorganisms that are phoretic on *D. frontalis*, at least 167 predators and parasitoids of *D. frontalis* (Thatcher *et al.*, 1980) and a comparably diverse community of detritivores and their predators that exploit pine logs after the departure of bark beetles (Savely, 1939; Howden & Vogt, 1951; Dajoz, 1974).

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