

Is the outbreak status of *Thrips calcaratus* Uzel in North America due to altered host relationships?

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Abstract

The introduced basswood thrips, *Thrips calcaratus*, undergoes outbreaks on and damages American basswood, *Tilia americana*, in North America, but is less common on and does not cause significant damage to little-leaf linden, *Tilia cordata*, in its native European range. A possible explanation is that altered host relationships in North America allow increased exploitation of *T. americana*. Three experiments were conducted to compare host associations of *T. calcaratus* between *T. americana* and *T. cordata*. In a laboratory choice bioassay, *T. calcaratus* occupied foliage of both tree species with equal frequency. A field assay conducted in North America revealed an identical trend on planted *T. americana* and *T. cordata* seedlings planted in a paired design. In a separate field experiment bud break phenology, peak *T. calcaratus* emergence, and foliar development showed similar temporal patterns in 10 *T. cordata* and *T. americana* sites distributed across the insect's native range of Europe and introduced range of North America. These results suggest that physiological and phenological differences between native and newly acquired *Tilia* hosts are not likely responsible for the increased impact of *T. calcaratus* in its introduced range. Rather, temporal escape from natural enemies seems to be the more likely explanation. This is evidenced by the stronger synchrony of the North American predator, *Leptothrips mali*, with the native basswood thrips, *Neohydatothrips tiliae*, than with *T. calcaratus*. Understanding the basis for increased success of *T. calcaratus* in its introduced range may provide insight into managing this insect in basswood forests in the Great Lakes region.

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1. Introduction

Biological invasions comprise an increasing global threat to forest ecosystems. Over 400 species of insects and 20 species of

pathogens associated with trees or shrubs have been introduced into the United States, and about 30% of these pose serious economic or ecological threats (Haack and Byler, 1993). Sources of invasion include solid wood packing material, nursery stock, and intentional introduction.

There are many examples of species being highly injurious to ecosystems and economies in an introduced area, yet causing no significant damage in their native range. Some possible explanations include altered host plant relationships, release from competition, release from natural enemies, and genetic

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adaptations of invaders (Elton, 1958; Settle and Wilson, 1990; Porter et al., 1997; Suarez et al., 1999). Understanding why a species becomes injurious in a new area can provide important insights for effective management. Unfortunately, few empirical studies comparing the ecological interactions of invasive species in their introduced versus native ranges have been conducted (but see Edwards et al., 1999; Suarez et al., 1999; Torchin et al., 2001).

The order Thysanoptera, thrips, contains approximately 5000 species, 1% of which are considered serious pests (Mound and Teulon, 1995). Thrips are characterized by their small size, fringed wings, and asymmetric, rasping–sucking mouthparts. Many species reproduce asexually (Lewis, 1973), which increases their chances of survival if introduced to a new area.

The introduced basswood thrips, *Thrips calcaratus* Uzel, is native to Europe, where it is primarily associated with little-leaf linden, *Tilia cordata* P. Mill. (Jacot-Guillarmod, 1975). *T. cordata* occurs throughout Europe in mixed-species stands. It has few known pathogens, but 57 insects feed on *T. cordata*, including *T. calcaratus*, *Thrips minutissimus* Linnaeus, *Dendrothrips degeeri* (Uzel), and *Dendrothrips ornatus* (Jablonowski) (Morison, 1970; Pitkin, 1976; Kucharczyk and Seczkowska, 1991; Pigott, 1991). *T. minutissimus* has been recorded on *T. cordata* in Spain, Italy, Hungary, and Poland (Kucharczyk and Seczkowska, 1991; Szenasi et al., 2002), and has also been associated with damage to nectarine and peach trees in Italy (Gargani, 1996). *D. ornatus* is a pest of lilac and privet (Veselinov, 1976).

First observed in New York during the 1930's, *T. calcaratus* has been recorded from Illinois, Iowa, Michigan, Ontario, New York, and Wisconsin in North America (Rieske and Raffa, 1995). *T. calcaratus* now vastly outnumbers native Thysanoptera on American basswood, *Tilia americana* Linnaeus in the Great Lakes region (Werner et al., 2005), where it has been associated with damage to this tree species for the past two decades (Raffa and Hall, 1989; Raffa, 1991; Nakahara, 1994). Although *T. calcaratus* feeding rarely leads to basswood mortality on its own, repeated defoliation by this insect can lead to increases in dieback, growth reductions, and decline in combination with other site factors (Raffa et al., 1992; Werner et al., 2005).

T. americana is a major component of northern hardwood forests throughout the northeastern United States and southeastern Canada (Neelands, 1968). It usually occurs in mixed stands with *Acer*, *Quercus*, *Tsuga*, and *Betula* species. Foliage that has been damaged by *T. calcaratus* feeding initially appears silvery due to air that remains in empty cells (Lewis, 1973), and later becomes chlorotic, dry, and shriveled (Rieske and Raffa, 1995, 1996). Damage sometimes causes early leaf drop, necessitating energetically costly refoliation within the same season (Rieske and Raffa, 1995). Investigators have hypothesized that *T. calcaratus* may cause more damage to *T. americana* than native herbivores due to differential host relationships. This could occur through several mechanisms, such as a lack of chemical defenses in *T. americana*, or phenological differences that could lead to feeding on the more sensitive bud tissue of *T. americana* in North America,

compared to foliar tissue of *T. cordata* in Europe (Raffa et al., 1992).

At least two other herbivorous thrips, *Neohydatothrips tiliae* (Hood) (native basswood thrips), *Taeniothrips inconsequens* (Uzel) (pear thrips), and two predaceous thrips, *Leptothrips mali* (Fitch) (black hunter thrips) and *Aeolothrips melaleucus* Haliday (banded-winged thrips) occur on *T. americana* in North America (Raffa et al., 1992; Rieske and Raffa, 1996). *T. inconsequens* has recently been linked to serious injury of sugar maple, and has also been associated with damage to Rosaceae in orchards, following its introduction from Europe (Stannard, 1968; Parker et al., 1988; Kolb and Teulon, 1991, 1992; Schultz, 1991). The occurrence of *T. inconsequens* on *T. americana* is uncommon and appears largely incidental (Werner et al., 2005). *A. melaleucus* is a predatory species that is also native to Europe (Stannard, 1968).

The objective of this study was to evaluate whether altered host plant relationships explain the different levels of damage caused by *T. calcaratus* between its introduced North American versus native European ranges. Specifically, we tested whether (1) *T. calcaratus* preferred *T. americana* or *T. cordata* foliage in a laboratory choice bioassay, (2) *T. calcaratus* occurred in similar numbers on *T. americana* and *T. cordata* seedlings planted in a North American site with high *T. calcaratus* populations, and (3) there were phenological differences between synchrony of *T. calcaratus* emergence and bud break with *T. americana* in North America versus *T. cordata* in Europe.

2. Materials and methods

2.1. Host choice bioassay

Foliage was collected from 24 *T. cordata* and 24 *T. americana* vigorous, unsprayed trees on the University of Wisconsin-Madison campus. *T. calcaratus* were not present on the foliage samples. The reason for the lack of *T. calcaratus* in this area is unknown, but soil compaction and lack of leaf litter in urban areas may inhibit their development. The mean trunk diameters of *T. cordata* and *T. americana* were 28 and 48 cm, respectively. Adults of *T. calcaratus* were collected from *T. americana* foliage near Avoca, WI on April 27, 2001. They were provided with an acclimation period, in which they were exposed to both *Tilia* species for 24 h in the same cells in which they were subsequently assayed. One *T. calcaratus* was added to each Munger cell (Munger, 1942) which contained one leaf or bud, depending on phenological stage of sample trees, each from *T. americana* and *T. cordata*. Foliage was surface-sterilized with a 10% bleach/90% water solution and rinsed with distilled water. Foliage was replaced every 12 h. Numbers of *T. calcaratus* present on each *Tilia* species, and mortality, were recorded at 12 h intervals for 36 h following the acclimation period. Assays were conducted in an incubator at 20 °C, with a 16-h light:8-h dark photoperiod. The null hypothesis that adult *T. calcaratus* shows no preference between *T. americana* and *T. cordata* foliage was evaluated using binomial tests (95% confidence interval) for each interval of the bioassay (Analyse-it, 2001).

2.2. Field assay

Fifty seedlings each of *T. americana* and *T. cordata*, were obtained from a nursery in southern Wisconsin. They were planted on April 15, 2001 at a site in northern Wisconsin known to have high *T. calcaratus* populations (N45°13.442, W88°26.789) (Werner et al., 2005). Each *T. cordata* seedling was paired with a *T. americana* seedling; they were planted one meter apart from one another in random locations throughout the understory of this forested site. Seedlings were paired to ensure that individuals of each species were exposed to similar microsite conditions that might influence thrips numbers, such as slope, aspect, light exposure, and soil type. Seedlings were approximately 30 cm tall at the time of planting. *T. calcaratus* were sampled from three buds or leaf clusters from each seedling on May 10, May 24, and July 22. All seedlings were removed from the site at the conclusion of the experiment.

An independent samples *t*-test was used to compare numbers of *T. calcaratus* obtained on each *Tilia* species (Analyse-it, 2001). Separate tests were performed for adults and larvae and for each collection date, as previous analyses indicated that developmental stage and collection date have significant effects on *T. calcaratus* abundance (Werner et al., 2004).

2.3. Phenological synchrony comparison

We sampled *Tilia* phenology, thrips emergence, and thrips abundance on foliage at six *T. americana* sites in the Great Lakes region of North America (Grand Rapids, MN; Rhinelander, Woodruff, and Spooner, WI; Marquette and Roscommon, MI), and four *T. cordata* forest sites in Europe (Maksimir, Croatia; Nesodden, Norway; Uppsala, Sweden; Punkaharju, Finland). Sites ranged 45°–66°N latitude and 93°W–29°E longitude (Table 1). Emergence traps consisted of green plastic containers (diameter of open end = 22.86 cm, closed end = 19.05 cm) with two 3 cm diameter holes drilled on opposite sides. A clear, plastic vial was placed over each hole to collect thrips as they emerged from the soil and traveled towards light. Each container was inverted (closed side up) and placed on the soil under *Tilia* canopies. Each of the 10 sites contained four emergence traps, with one in each corner of a 20 m × 20 m plot.

Traps were monitored approximately every 4 days from bud break until leaves were fully expanded. Bud stages were categorized according to Kolb and Teulon (1991): stage 1 = bud scales swollen from midwinter condition, bud scales not separated; stage 2 = bud scales start separating, green scale interior visible; stage 3 = bud scales loose, leaf margins visible; stage 4 = leaves visible but still folded, less than 2.54 cm long; stage 5 = leaves beginning to unfold and greater than 2.54 cm long. The average date each bud stage was observed in each continent was calculated for each of six sites in North America and four sites in Europe.

A foliage sample was collected using a pole pruner from accessible *Tilia* branches in each plot during each visit beginning at bud break. A sample consisted of the three outermost buds or leaf clusters on a sample branch. Thrips from emergence traps and foliage samples were placed in vials containing 70% ethanol and mailed to the University of Wisconsin for identification. Problematic specimens were sent to the USDA ARS Systematic Entomological Laboratory (Beltsville, MD) for identification. A Chi-squared analysis was used to determine if equal numbers of *T. calcaratus* were obtained during each bud stage in emergence traps and foliage samples for each continent.

3. Results

3.1. Host choice bioassay

T. calcaratus showed no preference for either *Tilia* species in laboratory assays (Table 2). No differences in distribution were observed at 36, 48, or 60 h after initial placement in Munger cells (Table 2). At the final inspection seven (46.7%) adults were on *T. americana*, and eight (53.3%) were on *T. cordata* ($t = 0.25$, $p = 0.8062$). Thrips switched host species 27 times from one interval to the next, with no discernable pattern (Table 2).

3.2. Field assay

No significant differences in *T. calcaratus* numbers on the 50 pairs of *T. americana* and *T. cordata* seedlings were observed, regardless of insect developmental stage or

Table 1
Locations of *Tilia* forest sites used to compare *T. calcaratus* in North America and Europe in 2001

Site name	Abbreviation	Continent	Latitude, longitude	Duration of emergence trapping
Roscommon, MI	ROMI	North America	N44°51'56", W83°3'57"	April 26–June 25
Felch, MI	UPMI	North America	N46°02'00", E87°47'00"	April 24–May 25
Woodruff, WI	WDWI	North America	N45°55'16", W91°50'57"	April 20–May 27
Rhinelander, WI	RHWI	North America	N45°30'58", W89°19'8"	April 6–May 25
Grand Rapids, MN	GRMN	North America	N47°11'5", W93°33'22"	April 19–May 23
Spooner, WI	SPWI	North America	N45°55'55", W91°52'18"	April 13–May 25
Nesodden, Norway	NORW	Europe	N66°24', E10°35'	April 10–May 18
Maksimir, Croatia ^a	CROA	Europe	N45°49'47.3", E16°01'49.8"	April 2–April 25
Punkaharju, Finland	FINL	Europe	N61°41', E29°20'	April 24–June 15
Uppsala, Sweden	SWED	Europe	N61°, E16°	April 15–May 19

^a There was a second Croatian site at Šumski vrt, but no thrips were obtained at that location.

Table 2

Thrips calcaratus adults occurring on *Tilia cordata* and *Tilia americana* foliage during two-way choice laboratory bioassay

Time since initial placement in Munger cell (h)	Degrees of freedom	<i>T. cordata</i>	<i>T. americana</i>	Two-tailed <i>p</i> -value	Not on foliage	Dead	No. switched since previous period
36	19	8	12	0.5034	1	1	11
48	17	7	11	0.4807	0	3	10
60	14	8	7	1.0000	1	2	6

Twenty-four adults were placed on each *Tilia* species. Readings began every 12 h after 24 h acclimation period. Binomial test (proportion of *T. calcaratus* on *T. americana* or *T. cordata* \neq 0.5) only applied to live thrips observed on foliage for each period.

Table 3

Distribution of *Thrips calcaratus* on *Tilia cordata* and *T. americana* seedlings (50 each) planted in a forested site in northeastern Wisconsin, 2001

Life stage	Date	Total <i>T. calcaratus</i> /tree species		Mean \pm S.E. <i>T. calcaratus</i> /seedling		<i>t</i> -Value	<i>p</i>
		<i>T. cordata</i>	<i>T. americana</i>	<i>T. cordata</i>	<i>T. americana</i>		
Adults	May 10	3	4	0.06 (0.06)	0.08 (0.04)	0.28	0.7801
	May 24	24	17	0.48 (0.13)	0.34 (0.08)	−0.93	0.3554
	July 22	1	0	0.08 (0.04)	0.00 (0.00)	−1.00	0.3198
Larvae	May 10	1	0	0.02 (0.02)	0.00 (0.00)	−1.00	0.3198
	May 24	38	41	0.76 (0.24)	0.82 (0.28)	0.16	0.8698
	July 22	0	0	0.02 (0.02)	0.00 (0.00)	na	na

The effect of *Tilia* species on *T. calcaratus* abundance was compared using independent samples *t*-test (d.f. = 49); na (not applicable) indicates that independent samples *t*-test could not be performed.

collection date (Table 3). Most *T. calcaratus* were obtained on May 24, which is similar to previous reports on the seasonal occurrence of this species (Werner et al., 2004). Nearly equivalent numbers of adult *T. calcaratus* were obtained on May 10, with three on *T. cordata* and four on *T. americana* ($t = 0.28$, $p = 0.7801$). Twenty-four adult *T. calcaratus* were obtained on *T. cordata* and 17 on *T. americana* on May 24 ($t = -0.93$, $p = 0.3554$). *T. calcaratus* larvae likewise occurred equally between seedling species on this date, with 38 obtained on *T. cordata* and 41 on *T. americana* ($t = 0.16$, $p = 0.8698$) (Table 3).

3.3. Phenological synchrony comparison

Six species of Thysanoptera, comprising 244 individuals, were obtained in emergence traps and foliage samples

Table 4

Adult Thysanoptera collected in North America and Europe

Species	North America	Europe
(a) Emergence traps		
<i>Thrips calcaratus</i>	77	33
<i>Thrips minutissimus</i>	0	9
<i>Dendrothrips ornatus</i>	0	3
<i>Taeniothrips inconsequens</i>	2	0
<i>Oxythrips</i> sp.	0	1
(b) Foliage samples		
<i>Thrips calcaratus</i>	94	10
<i>Thrips minutissimus</i>	0	14
<i>Aeolothrips</i> spp.	0	1

(Table 4). *T. calcaratus* accounted for 88% of total trap catch. Three species, *T. minutissimus*, *D. ornatus*, and an *Oxythrips* species, were obtained only in Europe (Table 4).

Minimum April temperatures ranged from 0.3 °C near Roscommon, MI to 5.3 °C in Croatia (Fig. 1). Maximum April temperatures ranged from 9.2 °C in Finland to 16.2 °C in Croatia. April precipitation, ranged from 2.8 cm in Sweden to 23.4 cm in Grand Rapids, MN. May precipitation ranged from 2.1 cm in Finland to 14.2 cm in Roscommon, MI (Fig. 1). In spite of climatological differences among sites, *Tilia* bud break and leaf opening occurred at similar dates in Europe and North America (Fig. 2). The slight lag in bud break phenology of the pooled European sites is likely due to the inclusion of mainly northern locations for the inter-continental comparison (Fig. 2).

T. calcaratus emerged at least as early in Europe as in the United States (Fig. 3). This pattern held whether data were pooled across sites in each continent or sites were compared individually (Werner, 2004). Highest numbers of *T. calcaratus* were obtained in emergence traps during bud stage two in both Europe and North America. Similarities between Europe and North America were also observed when comparing foliage samples, with highest numbers of *T. calcaratus* obtained during bud stage five in both continents (Fig. 3). However, sample sizes from foliage in Europe were relatively low, with only 10 individuals obtained. Chi-squared analysis confirmed that numbers of *T. calcaratus* obtained were significantly different among bud stages for emergence trap and foliage sample data (Fig. 3).

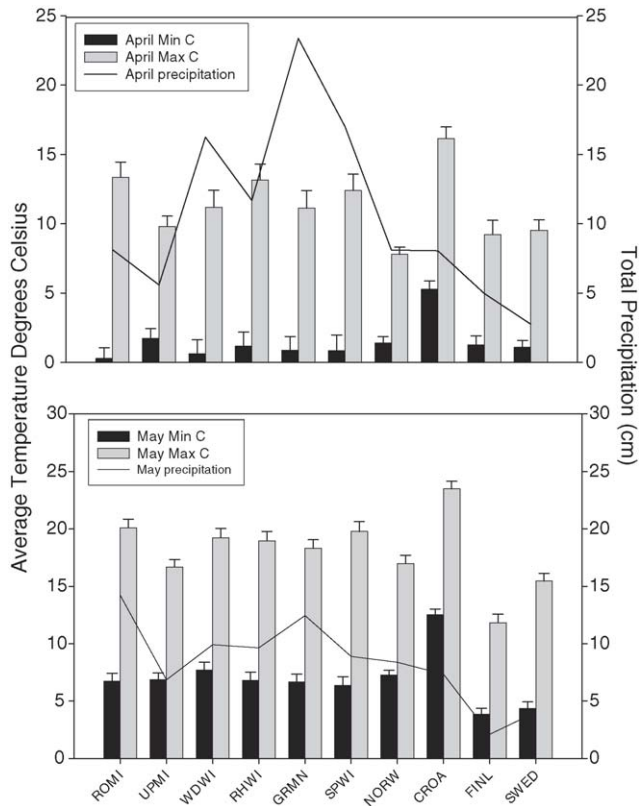


Fig. 1. Weather data used in *Tilia* bud break and *Thrips calcaratus* emergence synchrony experiment. NOAA Weather Station locations for 2001 temperature/precipitation data were: ROMI = Gaylord/Gladwin; UPMI = Escanaba/Iron Mountain; WDWI = Minocqua/Park Falls; RHWI = Rhinelander/Merrill; GRMN = Grand Rapids/Hinckley; SPWI = Hayward/Spooner Ranger Station; NORW = Oslo/Oslo; CROA = Maksimir/Maksimir; FINL = Savonlinna/Punkaharju; SWED = Uppsala/Uppsala.

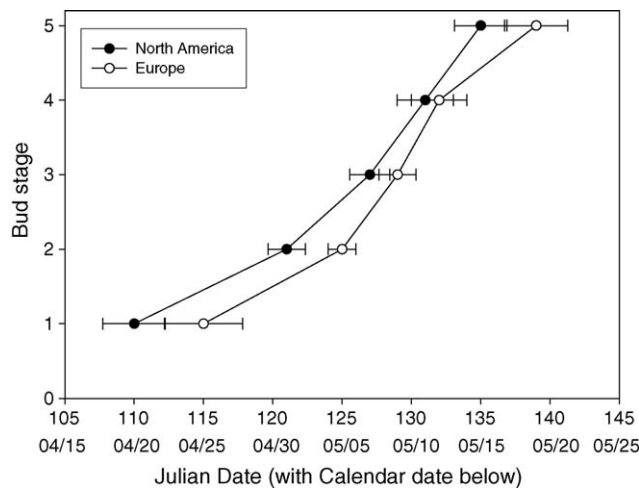


Fig. 2. Bud stage of *Tilia* from sites in North America and Europe used in *T. calcaratus* phenological comparisons. Bud stage refers to condition of *Tilia* buds, as defined by Kolb and Teulon (1991), and described in detail in Section 2 of this paper. Date indicates the average date each bud stage was observed at each of six sites in North America and four sites in Europe. All dates in which a given bud stage was observed were included in the average (date = sum of dates in bud stage X divided by total number of observations in bud stage), even if a bud stage was observed for more than one time period at the same site.

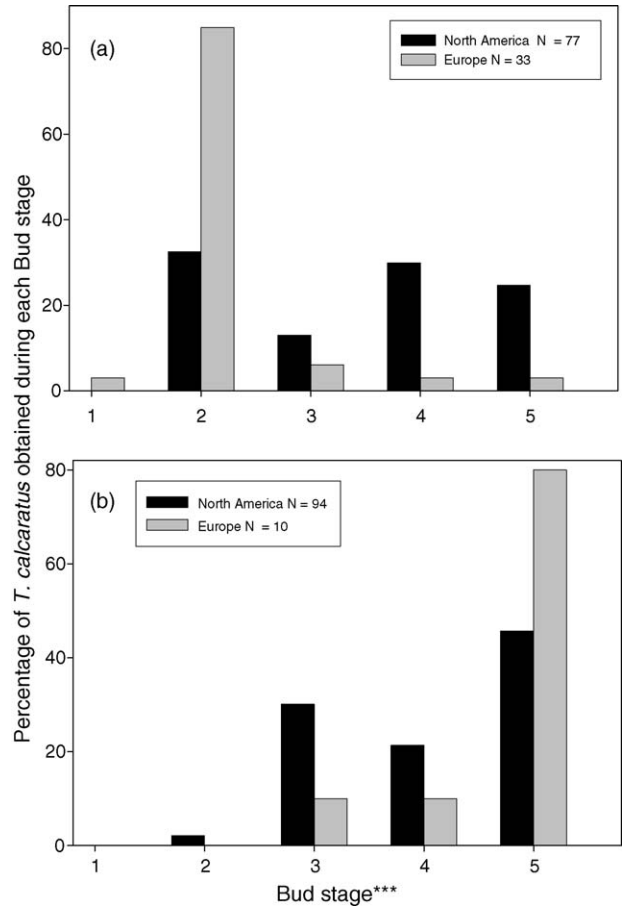


Fig. 3. Percentage of *T. calcaratus* obtained from six North American and four European sites during each *Tilia* bud stage in May 2001. *Abundance varied by bud stage in North America: Chi-squared = 27.86, $p < 0.0001$, d.f. = 4, and in Europe: Chi-squared = 84.32, $p < 0.0001$, d.f. = 4, and the distribution of thrips across bud stages varied between continents: Chi-squared = 30.08, $p < 0.0001$, d.f. = 4. **Abundance varied by bud stage in North America: Chi-squared = 70.57, $p < 0.0001$, d.f. = 4, and in Europe: Chi-squared = 23.00, $p < 0.0001$, d.f. = 4. Chi-squared analyses could not be performed between continents for foliage data due to low sample sizes. ***Bud stage refers to condition of *Tilia* buds, as defined by Kolb and Teulon (1991) and described in detail in Section 2 of this paper: (a) emergence traps* and (b) foliage samples**.

4. Discussion

These results suggest that altered host plant relationships are not likely responsible for increased impacts of *T. calcaratus* on *T. americana* in North America. Because *T. calcaratus* showed no preference for *T. americana* over *T. cordata* in either the laboratory choice or field planting assays, it seems unlikely that higher chemical defenses in *T. cordata* could explain why *T. calcaratus* undergoes outbreaks in North America but not Europe. Likewise our hypothesis that differences in the timing of *T. calcaratus* emergence relative to the phenological stages of *T. americana* versus *T. cordata* was not supported. *T. calcaratus* was clearly associated with *Tilia* bud break in both Europe and North America. Sample sizes in Europe were low, supporting the view that *T. calcaratus* naturally exists at extremely low levels in its native range. Since this study was based on behavioral preferences, we cannot exclude potential

differences in development rates or fecundity between *T. calcaratus* feeding on European and North American *Tilia* species as a component of differential impacts between continents.

Release from competition likewise seems to be an unlikely explanation of why *T. calcaratus* undergoes outbreaks in North America but not Europe, as reports of abundant populations of other herbivores on *T. cordata* are lacking, both in the literature and in our European sites (Table 4). It seems more likely that a lack of natural enemies in North America may allow *T. calcaratus* to escape population regulation. *T. calcaratus* emerges earlier in the season than does the predator *L. mali*, (Werner et al., 2005). By the time *L. mali* is active, *T. calcaratus* has already had a chance to asexually reproduce, thus escaping heavy predation (Werner et al., 2005). In contrast, *L. mali* is highly synchronized with the native herbivore, *N. tiliae*. Both species appear later in spring and persist throughout the summer (Werner et al., 2005). In addition to *L. mali*, other potential enemies of *T. calcaratus* include parasitic wasps, entomopathogenic nematodes and fungi, predaceous Hemiptera, Neuroptera, Coleoptera, and other predaceous Thysanoptera (Lewis, 1973; Mills, 1991; Brownbridge et al., 1999). However, the impact of these other natural enemies has not been studied in the native or introduced ranges of *T. calcaratus*. The absence of host plant-related differences in the laboratory (Table 2), field (Table 3) and intercontinental comparison (Figs. 2 and 3) also supports the view that enemy-free space could be responsible for the largely unchecked population growth of *T. calcaratus* in North America. Given our results, more extensive sampling should be conducted to characterize the natural enemy complex in Europe. If a lack of natural enemies is validated as the main reason for increased impacts of *T. calcaratus* in North America, specialized pathogenic or insect biocontrol agents, especially those that are able to reduce populations in early spring, may offer the best strategy for controlling this species in the Great Lakes region.

Although *T. calcaratus* alone is not likely to threaten the long term sustainability of *T. americana* throughout its North American range, forest managers should be aware of its potential to cause dieback and contribute to mortality, especially if weather, soil chemistry, pathogens, or other factors are also affecting basswood health at a given site (Werner et al., 2005). Early spring foliage sampling should be conducted to determine the extent of *T. calcaratus* populations at a given site (Werner et al., 2004). If populations are high, managers may be able to use similar techniques as those to control pear thrips, such as treating the soil with pathogens (Parker et al., 1997), chemically treating seedlings (Stanosz, 1994), or using prescribed burns on the site (Brose and McCormick, 1992). However, there are no known effective means of controlling *T. calcaratus* outbreaks at present.

Because species often become injurious only after they have been introduced into a new region, it is difficult to predict the ecological and economic risks associated with their importation. Basic information on the life histories and population dynamics of non-pest forest species is often lacking, intensifying this uncertainty. Thus, our results lend a cautionary

note to the implicit assumption in many trade agreements that the invasive potential and impact of various endemic insects and pathogens can be predicted. The low population densities and complete absence of symptoms associated with *T. calcaratus* in Europe make it highly doubtful that its current role as the major threat to forest health of North American basswood stands (Raffa et al., 1992; Rieseke and Raffa, 1996; Werner et al., 2005) would have been predicted. This uncertainty, coupled with the devastating consequences of many introduced species make prevention of new introductions of paramount importance.

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