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Local population dynamics of two co-existing birch aphid species : competition or intrinsic cycles of abundance ?

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ABSTRACT. Populations of four aphid species coexisting on their *Betula pendula* host-plant were followed in Brussels for two years. The population dynamics of *Euceraphis betulae* and *Symydobius oblongus* exhibited consistent patterns in 2001 and 2002, but *Callipterinella tuberculata* and *Betulaphis brevipilosa* populations exploded in 2001 and in 2002, respectively. When *C. tuberculata* was abundant, the population of *B. brevipilosa* was low. The reverse was true in 2002 as *C. tuberculata* became abundant only when the *B. brevipilosa* population declined, leading us to suspect competition between the two species. However, instead of avoiding each other, they were positively associated on shoots, probably as a result of aggregation at suitable feeding sites. Colonies of both species were similar or larger in mixed aggregates than in monospecific ones. Moreover, the colony size of each species in mixed aggregates was independent from that of the other species. Since there is no direct evidence of competition between those two species, the alternate changes in abundance could rather result from the intraspecific properties of aphid life cycles that self-induce consecutive years of high and low population growth in relation to fluctuations in the environmental conditions. These two co-existing species thus deserve further close study to elucidate their relationships.

KEY WORDS : aphids, *Betula pendula*, competition, population dynamics.

INTRODUCTION

The dynamics of aphid populations are complex and often unresolved phenomena, involving numerous regulating factors such as natural enemies, weather conditions, host-plant quality and defensive responses, complex polymorphic life cycles, as well as intra- and interspecific competition (DIXON, 1977). Among these factors, interspecific competition has been proved to be a very widespread phenomenon in guilds of herbivorous insects (for a review, see DENNO et al., 1995).

Studies have widely reported the coexistence of several aphid species on the same host-plant, as well as niche differentiation between co-occurring species (DIXON, 1992). However, no clear-cut picture emerges concerning their interactions despite a large and often controversial body of literature that evidenced either no competition (e.g. LAWTON & STRONG, 1981; HAJEK & DAHLSTEN, 1986) or direct (e.g. BERGESON & MESSINA, 1997; GIANOLI, 2000) as well as indirect (e.g. PETERSEN & SANDSTROM, 2001; MESSINA et al., 2002) competition between co-occurring aphid species.

A guild of at least fourteen aphid species relies more or less exclusively on birch trees (ATKINSON, 1992), but little is known about their interactions. HAJEK & DAHLSTEN (1986) described the important association of three aphid species coexisting on *Betula pendula* Roth trees. They hypothesized from the co-occurrence of the three species and from the high number of unoccupied leaves that interspecific competition was unlikely, although their niches largely overlapped.

We report here, in a native association in Belgium, the preliminary study of four aphid species co-occurring on *B. pendula* Roth. During two successive years, we made regular surveys of one tree characterized by high densities of aphids, where we hypothesized that competition phenomena were more likely to be detected. This 2-year study describes, with high resolution, the population dynamics of those aphid species, and tentatively identifies which mechanisms best account for changes in aphid abundance. Quite understandably, such a detailed approach is time-consuming and therefore precludes multiple replications in space and time. Nevertheless, such intensive study (as opposed to the more extensive sampling of classical ecology studies) is increasingly acknowledged as a good way to highlight the dynamics of a local population as well as its underlying mechanisms.

MATERIAL AND METHODS

Aphid populations were investigated in Brussels, Belgium, during 2001 and 2002. We counted aphids on all the shoots of a selected branch of a birch tree, *Betula pendula* Roth, growing as an ornamental on the university campus. Observations began from bud burst (early May in 2001 and early April in 2002) and repeated until almost complete fall of the leaves (late September-early October in both years). We counted the number and species of aphids occurring on each shoot approximately every two weeks.

Four aphid species belonging to the Myzocallidinae sub-family and Calaphidini tribe were recognized on the tree in both years : *Symydobius oblongus* van Heyden (1837), *Euceraphis betulae* Koch (1855), *Betulaphis brevipilosa* Börner (1940) and *Calliperinella tuberculata* van Heyden (1837). They all are autoecious species restricted to birch trees (Atkinson 1992), and are easily distinguished in the field on the basis of size and colour differences. *S. oblongus* feeds primarily on the twigs of the present or preceding year, while the three other species feed mainly on leaves (personal observation). Very careful and gentle observation was required due to the great mobility of *C. tuberculata* and *E. betulae* and to the fact that all adults of the latter species are alates and fly readily when disturbed.

RESULTS

Population Dynamics

In both 2001 and 2002 the four aphid species co-occurred on the birch branch but the population dynamics of the guild differed greatly between the two years, as shown in Fig. 1a-b. *S. oblongus* was the least common species in both years though tended by *Lasius niger* L. ants throughout the season. Its demography was similar in 2001 and 2002, but it disappeared sooner in 2002. Most probably, the heavy rains of the beginning of July 2002 washed off this exposed large-sized aphid from the twigs. *E. betulae* also showed consistency in its demography in both years with a maximum abundance in May and extinction in mid-July.

On the other hand, the population dynamics of *C. tuberculata* and *B. brevipilosa* dramatically changed over successive years. *C. tuberculata* was very abundant in 2001 (Fig. 1a), with a drastic decline at the beginning of July followed by a smaller second peak of abundance in late August. *B. brevipilosa* was uncommon in 2001, almost rare, reaching its maximum population when *C. tuberculata* began its summer decline, and disappearing from the tree in the first days of August. In the following year the situation was reversed (Fig. 1b) : *B. brevipilosa* numerically dominated the aphid population from the end of May till the end of June 2002, and *C. tuberculata* was scarce until *B. brevipilosa* population began to collapse in mid-June.

Thus the population dynamics of both species in this local aphid community greatly differed from one year to the next. As population dynamics of aphids are quite complex phenomena (Dixon, 1977, 1992), we refined our study of *C. tuberculata* and *B. brevipilosa* populations in search of evidence that could allow a better understanding of the relationship between the two species. The following analyses took into account only mid-June data because the two species were simultaneously present in sufficient numbers at this time. Moreover, *C. tuberculata* was ant-tended in July and August which could dramatically alter its interactions with *B. brevipilosa* (this latter species being neither preyed on nor tended by *L. niger*, personal observation).

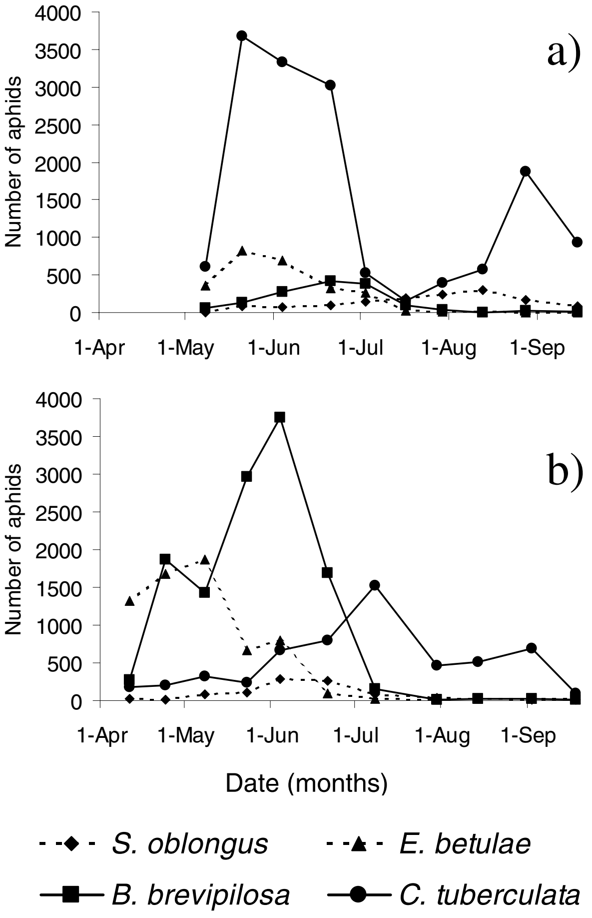

Fig. 1. – Population dynamics of four aphid species coexisting on *Betula pendula*, for a) the year 2001, and b) the year 2002.

Co-occurrence on shoots

We never noted avoidance or agonistic behaviour between the two species in either year. The number of birch shoots occupied by monospecific colonies of *C. tuberculata*, monospecific colonies of *B. brevipilosa*, or mixed colonies in both years are presented in Table 1. In 2001 and 2002 we found that the two species exhibited a positive association on shoots : they were significantly

TABLE 1

Occurrence of *C. tuberculata* and *B. brevipilosa* on birch shoots. For each year, the number of shoots occupied on the 21st June by monospecific colonies, mixed colonies or none, were compared using Fisher exact test.

		C. tuberculata		**Fisher exact test**
		Absent	**Present**	
B. brevipilosa	***2001***			
	Absent	25	22	p = 0.0002
	Present	5	33	
	2002			
	Absent	27	9	
	Present	30	32	p = 0.0115

more often found in mixed colonies than expected from random distribution (Fisher exact test : p=0.0002 and p=0.0115 in 2001 and 2002, respectively). A constrained crowding of both species due to lack of space was unlikely, since 29.4% and 27.5% of the shoots (still growing in June) remained unoccupied in 2001 and 2002, respectively.

Size of colonies in monospecific and mixed aggregates

For the two species of aphids in both 2001 and 2002, we compared the average number of individuals of a given species belonging either to a monospecific colony or an aggregate of both species. *C. tuberculata* in 2001 (Fig. 2a), as well as *B. brevipilosa* in 2002 (Fig. 2b) were more numerous in mixed aggregates than in monospecific ones (Welch corrected t-test : $t_{52=}$3.169, $p < 0.005$ for *C. tuberculata*; Mann-Whitney U test : U=379.5, $p < 0.0005$ for *B. brevipilosa*). However, we found no significant differences between population size in mixed and pure aggregates in 2002 for *C. tuberculata* and in 2001 for *B. brevipilosa*, when they were respectively less abundant (Welch corrected t-test : $t_{8=}$1.330, NS for *C. tuberculata*; Mann-Whitney U test : U=47.5, NS for *B. brevipilosa*).

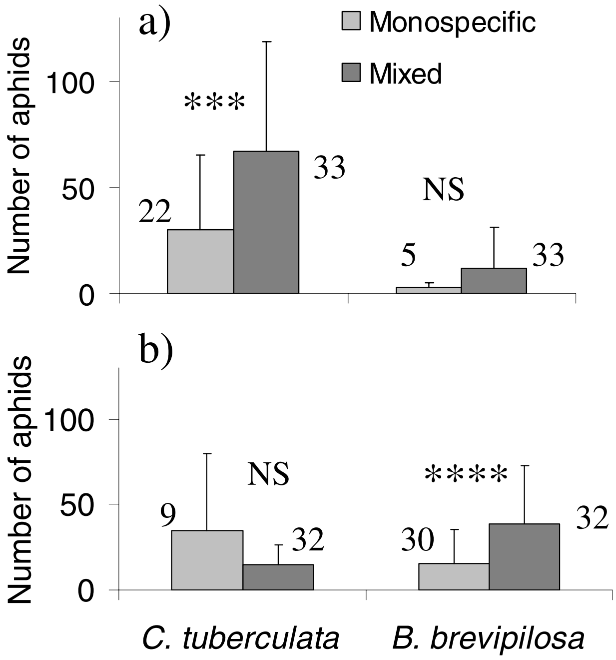

Fig. 2. – Number of individuals (mean ± SD) of *Callipterinella tuberculata* and *Betulaphis brevipilosa* found either in monospecific (light grey) or mixed (dark grey) aggregates on birch shoots in a) the year 2001, and b) the year 2002. Numbers indicate sample size. Statistical comparisons were made using Mann-Whitney test or Welch corrected t-test (*** : p < 0.005; **** : p < 0.0001).

In mixed aggregates, we failed to detect any correlation between the number of individuals belonging to one species and the number of individuals of the other species ($R^2=0.0054$, n=33, NS and $R^2=0.0008$, n=32, NS in 2001 and 2002 respectively, Fig. 3).

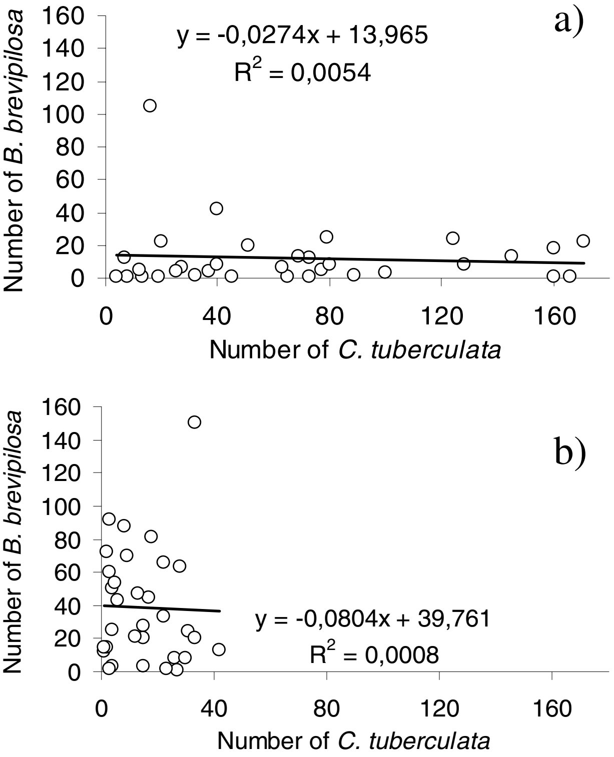

Fig. 3. – Relationship between the number of *Callipterinella tuberculata* and the number of *Betulaphis brevipilosa* in mixed aggregates in a) the year 2001 (n=33), and b) the year 2002 (n=32).

DISCUSSION

Here we showed that among four aphid species co-occurring on *B. pendula*, the local population dynamics of *B. brevipilosa* and *C. tuberculata* could vary greatly over successive years. But what do these variations of abundance actually reflect? The apparent inverse relation in the abundance of those two aphid species at this site might suggest the existence of interspecific competition.

At the level of the aphid colonies, we found *B. brevipilosa* and *C. tuberculata* positively associated on birch shoots. This observation is in agreement with the work of Hajek & Dahlsten (1986), in which the niche of *B. brevipilosa* overlapped widely with that of another *Callipterinella* species (*C. calliptera* Hartig), although a large number of leaves remained unoccupied by aphids. However, this might simply reflect the higher quality of the locations of mixed aggregates compared with those of monospecific ones. Indeed, colonies of both species were similar or larger in mixed aggregates than in monospecific ones. The two species should preferentially meet and settle on a limited number of sites that are suitable for the aphids to feed on and grow.

If spatial displacement between species is an indicator of aphid competition (Dixon, 1992), the reverse statement is not necessarily true : the existence of still unoccupied shoots is not a sufficient criterion to rule out the possibility of interspecific competition, which could still occur at the occupied feeding sites. In this respect, the negative effect of the presence and/or development of one species on the fitness of another one is a more relevant indicator of competitive interactions between coexisting species (e.g. MAY, 1973). At our study site, we failed to detect such effect as *B. brevipilosa* and *C. tuberculata* colony sizes were independent from each other in mixed aggregates. Additionally, in a given year, the presence on the same shoot of the numerically dominant species did not significantly alter the average colony size of the less abundant one.

This lack of correlation – and lack of evidence of direct competition – should however deserve further testing for a wider range of colony sizes of both species. All the combined observations of this study did not provide direct evidence of competition between *B. brevipilosa* and *C. tuberculata* though it is widely reported to occur among aphids (DENNO et al., 1995; DIXON, 1992). Studying additional sites and making surveys for more years would be needed to draw firm conclusions on the relationships between those two aphid species.

On the other hand, a number of factors unrelated to interspecific competition could account for the alternate outbreaks observed. The weight of predation in the shaping of aphid populations often remains unclear, but weather conditions and overall temperature are known to be major forces determining outbreak events in several well-studied species (DIXON, 1977, 1992). Differences in winter temperature in 2000 and 2001 may have favoured *C. tuberculata* in 2001 and *B. brevipilosa* in 2002. Indeed, the more precocious bud burst of the birch in 2002 (see Fig. 1) may have differentially influenced the population growth of the two species if they differ in their hatching dates, which could have dramatically influenced the outcome of their competitive interactions.

Additionally, the intrinsic properties of aphid life cycles could be a self-regulating mechanism causing the variation in abundance exhibited by aphid populations from year to year, in relation with fluctuations in the environmental conditions (DIXON, 1977, 1992). In short, the exhaustion of the host-plant and the crowding of aphids during high abundance seasons can lead to intense production of alates and massive emigration. The remaining aphids would be of smaller size, lower growth rate and fertility. Ultimately, this leads to a population crash for the rest of the season and for the following year due to the poor quality of autumn sexuals, until the aphids and the host plant recover (DIXON, 1975, 1977, 1992). A closer analysis of life history traits of *C. tuberculata* and *B. brevipilosa* with a concurrent survey of environmental factors, as well as experimental testing of the competitive interactions possibly occurring between the two species is now required to ascertain the driving forces leading to changes in abundance of local aphid populations.

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