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Post hibernation dispersal of three leaf-eating beetles (Coleoptera: Chrysomelidae) colonising cultivated willows and poplars

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Abstract

1 We studied the spring dispersal of three common chrysomelids, from overwintering habitats into cultivated willow and poplar coppices at four sites in southern England over 2 years.

2 Adult *Galerucella lineola*, *Phratora vulgatissima* and *P. vitellinae* overwintered under the bark of mature trees or in other niches that simulated this habitat, within a few hundred metres of the coppice plantation. Relatively few beetles remained in the coppice fields during the winter.

3 *Phratora vitellinae* at the poplar sites emerged several weeks later than *G. lineola* and *P. vulgatissima* at the willow sites, reflecting the later leafing of poplar compared to willow. For all species, dispersal was by flight, with most activity during warm periods. Dispersal continued for several weeks for the willow-feeding species but was shorter for *P. vitellinae.*

4 All three species initially colonized the edge of the coppice field. Typically, 80% or more of the beetles colonising a plantation were within 8 m of the edge. Both *Phratora* spp. accumulated in the plantation edge zone for several weeks before leaving this area and colonising the crop interior.

5 The patterns of dispersal and colonization identified by this study may facilitate chrysomelid management practices in infested short rotation coppice that avoid the need for insecticide applications over the entire plantation.

Keywords *Chrysomelidae*, *Galerucella lineola*, *Phratora vitellinae*, *Phratora vulgatissima*, poplar, short rotation coppice, willow, winter dispersal.

Introduction

An ability to predict temporal and spatial patterns of movements of insect pests in agricultural ecosystems increases the opportunities for controlling them. For example, in North America, an understanding of the dispersal capabilities of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) into and through potato fields has led to crop management practices designed to avoid or control re-invasions. Colorado beetles emerge from overwintering habitats in the soil and fly to potato fields nearby (Lefevere & Kort, 1989; Voss & Ferro, 1990). Immigration distances, however, are limited (Follet *et al*., 1996; Weisz *et al*., 1996) and dispersal through a crop is usually gradual (Williams, 1988; Weber *et al*., 1995). This means that field rotations can be planned to limit beetle densities from year to year by avoiding re-invasions (Follet *et al*., 1996), and buffer crops or other obstacles employed to intercept and control them (Ferro *et al*., 1991; Hoy *et al*., 1996).

In the U.K., new short rotation coppice (SRC) biomass crops have been developed which are vulnerable to attack by several Chrysomelidae (Sage, 1994). SRC consists of fast growing willow, *Salix* spp., or poplar, *Populus* spp., clones grown in rows at close spacings and coppiced every 2 to 4 years. The crop is usually chipped and has several uses, but may become widely planted as a renewable energy fuel source (MAFF, 1994; Bates, 1995). Of around 50 plantations of up to 100 ha in the U.K., in 1994 and 1995, *Phratora vulgatissima* (Coleoptera: Chrysomelidae) was recorded from most willow and *Phratora vitellinae* from most poplar sites. *Galerucella lineola* was recorded from most sites that also contained *P. vulgatissima* (Sage & Tucker, 1998). Although willow SRC is more extensively grown in Sweden, chrysomelids are less common there (Forsberg *et al*., 1991).

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Table 1 Sites in southern England used for this study including date established and longitude North and latitude West.

Site code	Tree species	Area (ha)	Date established	County	Lat. N.	Long. W.
W1	Willow	1.8	1986	Avon	51° 25′	2° 41′
W2	Willow	5.0	1990	Oxon	51° 42′	1° 35′
P1	Poplar	0.6	1990	Surrey	51° 11′	1° 51′
P2	Poplar	5.0	1990	Avon	51° 23′	2° 30′

Native willow and poplar trees are thought to be the initial colonization sources for these chrysomelids (Sage & Tucker, 1998). They overwinter in or near the coppice fields as adults and then re-colonize the crop canopy in the spring where they feed and oviposit. The larvae continue to feed on the coppice leaf before pupating in the soil. The emerging adults feed, disperse or produce a second generation before seeking sites to overwinter (Kendall *et al*., 1996; Griffiths, 1997). Over successive years, populations are capable of large increases in numbers and at several sites in the U.K., chrysomelid herbivory has caused substantial leaf area losses (Sage & Tucker, 1997) which may affect coppice growth and hence biomass yields (Larsson, 1983; Bach, 1994).

In this study, in order to identify any patterns of chrysomelid infestation in SRC plantations, we investigate the spring movements of adult beetles into and through the coppice canopy at several SRC sites. An understanding of these movements may help to develop methods to manage or control these potential pests.

Methods

Study sites and overwintering surveys

Three SRC sites in southern England, two willow plantations (sites W1 and W2) and one poplar plantation (P1) were selected for this study in 1994 (Table 1). The willow sites contained *P. vulgatissima* and *G. lineola* and the poplar site contained *P. vitellinae*. In late 1995, the coppices at site W1 and P1 were removed and in 1996 further work was conducted at site W2 and another site, P2.

Searches for overwintering chrysomelids were conducted between December and February 1994–95 and 1995–96 at each site. Within the crop, crevices on coppice stems and stools, dead herbage and the soil surface were searched. Trees, hedgerows, fence posts, wood piles, buildings, etc. up to 400 m from the coppice were also examined. The aim of these searches was to provide guidance for subsequent trapping of emerging adults in the spring.

Trapping emerging chrysomelids

In March 1995, three window traps and three gutter traps were placed around the perimeter of each of the sites W1, W2 and P1. A window or flight interception trap (Owen, 1993) consisted of a wooden frame (1 × 2 m) with strong clear plastic sheeting stretched over each face. The frame was orientated vertically and supported with the bottom edge 0.5 m above the ground. A 1-m length of plastic guttering with sealed end-pieces was attached to the bottom edge of the screen on each side and filled with a water and 50% preservative (car antifreeze) solution to collect beetles. In preliminary trials, we found that most chrysomelids projected towards the screen bounced beyond the guttering and were not collected. However, by smearing the plastic sheeting with clear petroleum jelly to dampen impacts, we improved the catch rate to nearly 100%. The window traps were located mid-way between the coppice and previously identified beetle overwintering sites and orientated parallel to the coppice edge. The two faces indicated the direction of movement of beetles when caught (towards or away from the coppice). Each window trap had a gutter trap placed nearby, similarly orientated. A gutter trap consisted of similar lengths of guttering, laid in a trench side by side, again to indicate direction. A plastic cup half filled with the solution used in the window traps, was placed in a hole at one end to collect invertebrates.

Eight emergence traps were placed within the coppice at each site. Emergence traps were located randomly within the plots and placed over areas of bare soil, cut stools or dead vegetation. The traps consisted of four plywood ‘walls’ attached to corner posts to make an open-ended box 1 m long × 0.5 m wide × 0.5 m tall. The corner posts were pushed into the ground so that the walls formed a gap-free fit with the soil surface. A pitfall trap and yellow dish trap, both filled with the preservative solution used above, were placed inside the box before sealing the top with a fine plastic mesh.

All traps were set up in mid-March with preliminary catches collected for the week to 27 March (week 0). Each trap was visited on the same day each week, but each site was visited on different days. For site P1 then, week 1 refers to the seven days to 4 April, site W2 to 5 April and site W1 to 6 April. When, occasionally, a sample was not collected on the appropriate day, a correction was made to adjust the sample to provide a 7-day equivalent. Samples were collected and returned to the laboratory for sorting until 18 May (week 7 at site W1).

Chrysomelids in the coppice canopy (1995)

Insect sampling from the crop canopy began on 12 April (week 2) at site W2 (the largest site). Insects were collected from within the coppice canopy by shaking the coppice stems, and allowing the insects to fall onto a cotton sheet laid out on the ground between the coppice stools. The sheet was arranged to cover 2 m^2 in area and its shape depended upon crop spacing and weediness. Adjacent stems were then shaken to dislodge invertebrates in the crop canopy in an even manner. Chrysomelids were counted immediately on the sheet to avoid collection and storage. The two superficially similar *Phratora* spp. can often be separated in the hand by colour and body shape, although this method is not considered reliable due to some overlap (Kendall *et al.*, 1996). However, collection sampling to estimate population size (reported elsewhere) confirmed species at all four sites. Furthermore, in extensive sampling at over 30 U.K. SRC sites, *P. vitellinae* was not found on most modern willow clones (despite its common name, brassy willow beetle), and *P. vulgatissima* (blue willow beetle), was not found on the commonly planted poplar clones (Sage & Tucker, 1997).

The beating and counting method enabled rapid assessments to be made and Southwood (1978) suggests that a sufficiently high proportion of chrysomelids are collected by beating shrubs to provide an absolute measure. Numbers collected were converted and are subsequently referred to as the density of beetles per m^2 plan of coppice. The location of beat samples changed during the spring as the distribution of the colonising beetles in the coppice became apparent. Initially, two samples were collected near to the coppice edge but, by May, six beat samples were collected on the same day each week at this site, at 5-m intervals along a transect perpendicular to the crop edge in the *Salix viminalis* clone SQ683 (see below). This sampling indicated a distinct pattern of colonization by both *P. vulgatissima* and *G. lineola* which was investigated in more detail in 1996 at site W2 and for *P. vitellinae* at site P2.

Chrysomelids in the coppice canopy (1996)

In 1996, invertebrate beat samples were collected from the coppice canopy throughout the spring at sites W2 and P2. Samples from both sites were collected on the same day each week starting with week 1, covering the 7 days from 28 March to 4 April (and hence equivalent to week 1 in 1995 at site P1) and finishing on week 10, to 6 June. Both sites were sufficiently large to collect several independent samples up to 30 m into the coppice and at least 30 m from other edges. At site W2, four edge transects were sampled in four different clones or age classes, with beats taken at six points along each: at the edge, edge + 2 m, + 4 m, + 8 m, + 15 m, and + 30 m. Each transect ran from the crop edge facing a belt of mature trees and scrub 10 m away. The first was in a block of 3-year-old SQ683 *S. viminalis* on 4-year-old stools approximately 4 m tall. The second and third transects were in blocks of 3-year-old Q83 *S. triandra* × *S. viminalis* and Dasyclados *S. caprea* × *S. cinerea* × *S. viminalis*. The fourth was in a 3-m tall block of 1-year-old Bowles Hybrid *S. viminalis* on 2-year-old stools.

At site P2, a similar number of beat samples were collected from each of two transects. The first was in a 3-m tall plot of 2-year-old Beaupre *P. trichocarpa* × *P. deltoides* on 3-year-old stools which faced an area of mature mixed ash *Fraxinus excelsior* and oak *Quercus* spp. woodland approximately 50 m away. The second was in a plot of 4-year-old Boelare *P. trichocarpa* × *P. deltoides* stems on 5-year-old stools which in places exceeded 6 m in height. The sampling ran from the base of a single mature oak tree 6 m from the crop edge.

Analyses

The numbers of beetles caught in the three window traps and the three gutter traps in 1995 were compared using repeated measures analysis of variance (ANOVA) over the 7-week sampling period. The total catch for each trap was calculated and these data were log-transformed ($\ln(x + 1)$) to normalize distributions. Trap location was included as a factor in the analysis to account for the pairing of traps. The three site/beetle combinations, *P. vulgatissima* at site W1, *G. lineola* at W2 and *P. vulgatissima* at W2, were considered separately. The analysis includes a ‘between subjects’ test, which considers the significance of any difference between the two types of trap over the whole sampling period, and a ‘within subjects’ test, which investigated trends in differences over time. Almost all dispersal activity by *P. vitellinae* at site P1 occurred during week 6, so the comparison in this case was made using a paired *t*-test for that one week.

A comparison was then made of beetle numbers caught by the two window trap faces, also using repeated measures ANOVA over time. The ‘in’ and ‘out’ faces (towards and away from the plantation, respectively) were paired in the analysis by including trap location in the model. The data were log-transformed and each site/beetle combination considered separately as before. A *t*-test was again used for *P. vitellinae* at site P1. Data from the eight emergence traps at each of the three sites in 1995 were used to calculate the mean number of beetles emerging per m^2 of ground. This enabled a numerical comparison with densities recorded from the crop canopy.

Beetle abundance data from the 1996 within-crop beat samples for the four transects at site W2 and the two transects at P2 were analysed in a similar way to the 1995 window and gutter trap data. The six sampling points along each transect line were considered as separate treatments within the transect. Repeated measures ANOVA over time was used on the log-transformed data. Transect was included as a factor so that beetle numbers were compared between sampling points and over time on a per transect basis. Each site/beetle combination was considered separately. The method again enabled significant trends in beetle abundance with distance from the crop edge over the whole sampling period or over time to be identified. All statistical analyses were carried out using SYSTAT (Wilkinson, 1990).

Results

Overwintering

At site W2, aggregations of up to 200 adult *P. vulgatissima* and 20 *G. lineola* were found under the loose bark of mature willows *S. fragalis* and *S. alba* and of elder *Sambucus nigra*, within 20 m of the coppice. Smaller numbers were recorded under the bark of fallen branches and willow logs. *Galerucella lineola* in particular were also found in the hollow stems of dead standing herbage, particularly umbellifers *Umbelliferae* spp. and willow-herb *Epilobium* spp. At site P1, adult *P. vitellinae* were found under the bark of conifer trees 40 m from the coppice and in cracks in nearby wooden fence posts. At site P2, *P. vitellinae* filled every crevice in the trunk of mature oaks (*Quercus* spp.)

5–10 m from the coppice. Trees with loose bark in mature woodland up to 250 m from the coppice contained aggregations of up to 500 beetles. At site W1, *P. vulgatissima* were common under the bark of hedgerow trees and in a row of disintegrating concrete fence posts up to 200 m from the coppice. Individuals and small aggregations were also found within the coppice at this site, amongst dead herbage and in coppice shoot lesions caused by rust cankers (see Kendall *et al*., 1996).

Beetle trapping

Beetles were recorded in traps throughout the 7-week sampling period at sites W1 and W2 in 1995 (Fig. 1). Over the whole study period, significantly greater numbers were caught in the window traps than the gutter traps (Table 2). Comparing samples over time (on a weekly basis), this difference was still significant at both sites. The interaction 'time × trap-type' was also significant in these analyses, indicating a change in the difference between trap catches over the period as the window trap catches tended to zero (Fig. 1).

At site P1, almost all *P. vitellinae* activity was confined to week 6 (Fig. 1). Many more beetles were caught in window traps than the gutter traps in that week (Table 2). Relatively few beetles were caught in the ground emergence traps at all three sites. (Fig. 1, site W2, 0.6 beetles per m^2 per week; site W1, 1.8; site P1, 0.5). There were no differences in numbers from emergence traps covering cut stools or dead herbage compared with those over bare earth or leaf litter.

More *P. vulgatissima* were captured by the outward-facing sides of the window traps (away from the coppice) than the inward sides at site W1 over the whole period (Table 3). At site P1, more *P. vitellinae* were caught on the 'out' faces than the 'in' faces in week 6. At site W2, Fig. 1 indicates a similar trend to W1 for *P. vulgatissma* for most of the sampling period but the overall difference for both *P. vulgatissima* and *G. lineola* was not significant (Table 3). However, the within-subjects analysis indicates that the trend over time for the window trap samples at site W2 was significant. The significance of the interaction 'time × trap-face' for *P. vulgatissima* identifies a change in the difference between window trap faces over the period. Figure 1 indicates that the trend is towards more beetles on the trap inward faces at the end of the sampling period. This change was also evident for *G. lineola* at W2 but was not significant.

In 1995, *P. vulgatissima* were first recorded in window trap samples at willow sites W2 and W1 in week 1 (to 5 and 6 April, respectively). From week 2, ending 12 and 13 April, significant beetle flight activity (in proportion to the whole sampling period) was recorded each week until mid-May (week 6, Fig. 1). *Galerucella lineola* were active a week earlier at site W2, with a few records in the preliminary samples during week 0 (to 28 March) and proportionally large numbers in samples for week 1 until week 6 (10 May). As already indicated, virtually no dispersal activity by *P. vitellinae* at the poplar site P1, was recorded before or after week 6.

Canopy beat sampling (1995)

The chrysomelid samples collected from the crop canopy at site W2 in 1995 recorded colonization by *G. lineola* during week 2 (to 12 April) and *P. vulgatissima* during the following week (to 19 April). Over the following 2 or 3 weeks, this sampling indicated that following initial colonization, most beetles of both species accumulated in the crop canopy at the very edge of the coppice (Fig. 2). Samples collected 10 m or more into the crop contained relatively few beetles. By week 6, however (to 10 May 1995), most beetles had left the crop edge zone and moved further into the coppice. The 1996 sampling programme investigated these trends in more detail.

Canopy beat sampling (1996)

Galerucella lineola and *P. vulgatissima* at site W2, colonized the coppice edge 2 to 3 weeks later in the season than in 1995, with a significant number *of P. vulgatissima* at the edge in three of the four transects (up to 120/m^2 plan of coppice) for the first time during week 5, ending 2 May (Fig. 3a,b, compare Fig. 2). The second transect (clone Q83) was initially colonized by a small number of both species during week 4 (to 25 April), but there were virtually no further records of *P. vulgatissima* in this clone in subsequent samples (Fig. 3a). *Phratora vulgatissima* in Q83 at site W2 was excluded from subsequent analyses. At site P2, significant numbers of *P. vitellinae* (200/m^2 plan of coppice) were first recorded colonising the crop canopy of transect 1 (Boelare) in week 6 and transect 2 (Beaupre) in week 7 (to 16 May), 1 or 2 weeks after the willow feeding species at sites W2 (Fig. 3c, compare 3a and 3b).

The abundance of *P. vulgatissima* at W2 and *P. vitellinae* at P2 decreased with distance from the crop edge along all transects (except transect 2 at W2, see above) for several weeks following initial colonization (Fig. 3a,c). The repeated measures ANOVA indicated that this trend was significant for the whole sampling period for both beetles (Table 4), despite the apparent change towards fewer beetles at the edge at the end of the sampling period. The within-subjects analysis indicated that this trend was significant over time, but that the difference between samples with distance along the transects eventually declined (Table 4, 'time' × 'distance' interaction).

For *G. lineola* at site W2, no trend in beetle abundance with distance was apparent for the whole sampling period (Table 4). The trend over time shown in Fig. 3b was, however, significant and again the relationship with distance from edge changed over time (Table 4, 'time' × 'distance' interaction). Although these trends are less apparent than for the *Phratora* spp., *G. lineola* still initially colonized the edge (week 4), but for a shorter period.

Leafing times

At site W2, initial leaf emergence on the willows occurred on 3 April 1995, and on 11 April 1996. The poplar leaf first emerged on 26 April 1995 at site P1 and 2 May 1996 at site P2.

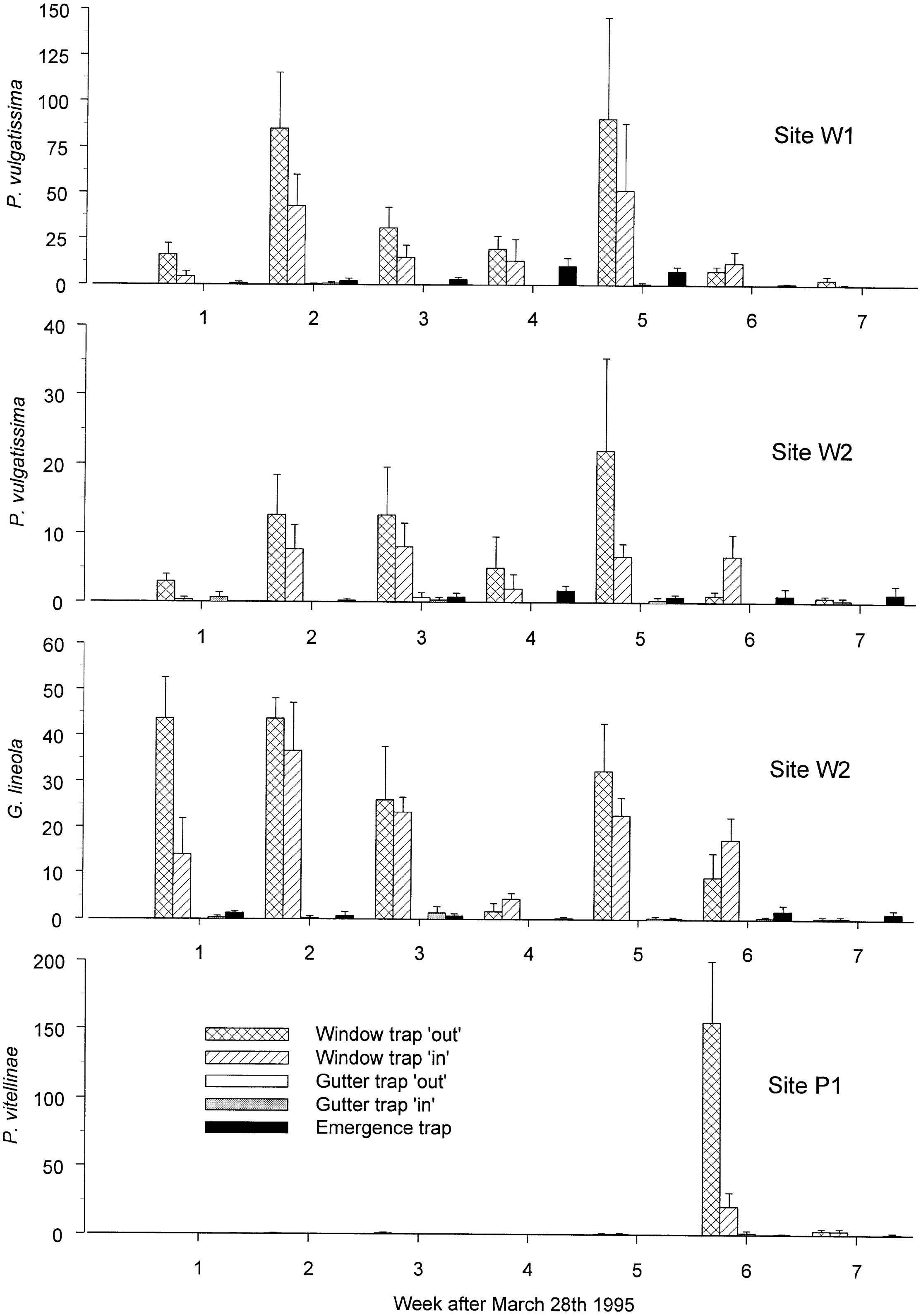

Figure 1 Comparing chrysomelid numbers caught per week in the window and gutter dispersal traps at the three study sites in 1995. At site W1, week 1 is to 4 April, site W2 to 5 April and P1 to 6 April. Data from the ground emergence traps are also included. Mean and standard errors ($P < 0.05$) are shown for the three window traps, three gutter traps and eight emergence traps in each case.

Table 2 Results of repeated measures ANOVA (*t*-test for site P1) comparing beetle numbers in window and gutter traps for the whole study period (between subjects) and over time (within subjects, including interaction).

Site – beetle	Between subjects	Within subjects	Interaction: Time × trap-type
W1 – *P. vulgatissima*	$F_{1,2} = 42.14^{*}$	$F_{6,12} = 24.07^{***}$	$F_{6,12} = 13.39^{***}$
W2 – *P. vulgatissima*	$F_{1,2} = 29.10^{*}$	$F_{6,12} = 5.47^{**}$	$F_{6,12} = 3.70^{*}$
W2 – *G. lineola*	$F_{1,2} = 422.8^{**}$	$F_{6,12} = 32.9^{***}$	$F_{6,12} = 23.96^{***}$
P1 – *P. vitellinae*	$t_2 = 130.4^{***}$		

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NS = $P > 0.05$.

Table 3 Results of repeated measures ANOVA (*t*-test for site P1) comparing inward and outward faces of window traps for the whole study period (between subjects) and over time (within subjects, including interaction).

Site – beetle	Between subjects	Within subjects	Interaction: Time × trap-face
W1 – *P. vulgatissima*	$F_{1,2} = 36.95^{*}$	$F_{6,12} = 33.73^{***}$	$F_{6,12} = 0.89$ NS
W2 – *P. vulgatissima*	$F_{1,2} = 11.60$ NS	$F_{6,12} = 23.55^{***}$	$F_{6,12} = 4.94^{**}$
W2 – *G. lineola*	$F_{1,2} = 0.041$ NS	$F_{6,12} = 14.36^{***}$	$F_{6,12} = 1.87$ NS
P1 – *P. vitellinae*	$t_2 = 4.85^{*}$		

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NS = $P > 0.05$.

Table 4 Results of repeated measures ANOVA investigating trends in the abundance of beetles along transects into the coppice for the whole study period (between subjects) and over time (within subjects, including interaction).

Site – beetle	Between subjects	Within subjects	Interaction: Time × distance
W2 – *P. vulgatissima*	$F_{5,10} = 36.54^{***}$	$F_{6,60} = 65.00^{***}$	$F_{30,60} = 7.27^{***}$
W2 – *G. lineola*	$F_{5,15} = 0.54$ NS	$F_{6,90} = 142.0^{***}$	$F_{30,90} = 5.42^{***}$
P2 – *P. vitellinae*	$F_{5,5} = 113.6^{***}$	$F_{5,25} = 39.7^{***}$	$F_{25,25} = 7.54^{***}$

$^{***}P < 0.001$; NS = $P > 0.05$.

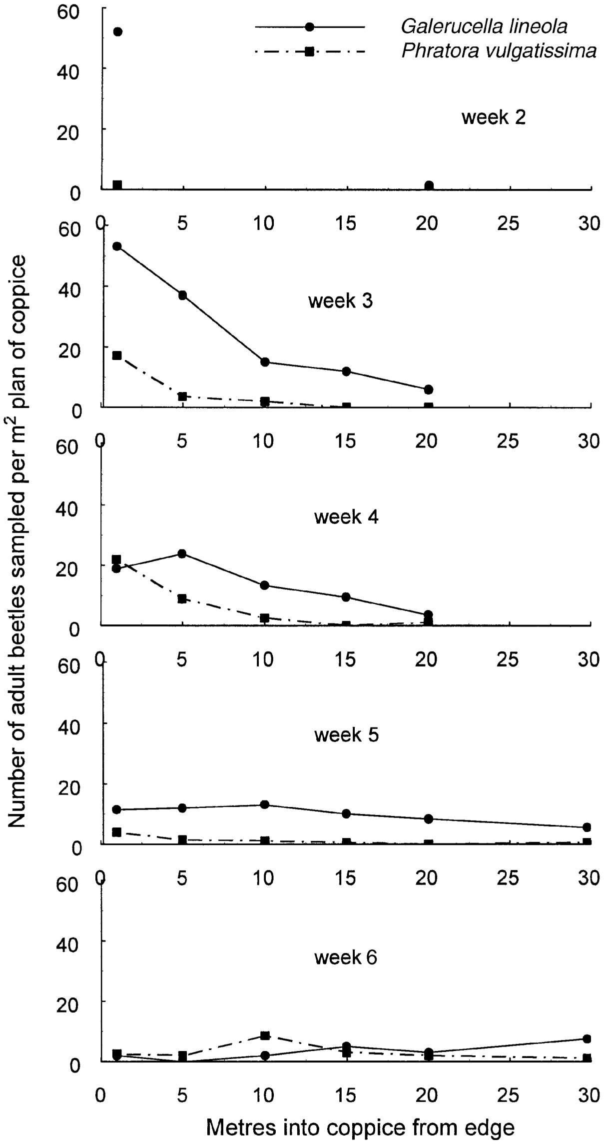

Figure 2 The abundance of chrysomelids collected from the coppice canopy each week from week ending 12 April 1995 at site W2. Sample points were along two transects leading from the field edge into the coppice canopy.

Discussion

Overwintering

Few chrysomelids were found within the coppice plantations during overwintering searches at three of the four study sites, and the numbers captured by the emergence traps at all four did not account for the numbers and distribution of beetles subsequently recorded in the coppice canopy. It is also likely that numbers collected from the emergence traps were an over-estimate as it was apparent that some had entered the traps from outside by crawling under the netting during weeks 4 and 5, particularly at site W2 (Fig. 1). While many chrysomelid species such as the Colorado beetle overwinter in soil (Lashomb *et al.*, 1984), there is no evidence that these arboreal feeding species do (Hutchinson & Kearns, 1930a,b; Sage, 1994). On old willows and poplar trees, they have the opportunity to overwinter on their food plants but in frequently cut SRC, appropriate crevices are limited. Most chrysomelids feeding on SRC crops are therefore obliged to find alternatives outside the coppice itself, under the bark of nearby mature trees or in crevices that effectively simulate this habitat.

Emergence and dispersal

Compared to the window traps, few beetles were caught in the gutter traps at any site during the trapping period. Furthermore, the window traps would have missed beetles flying above 2.5 m or below 0.5 m, and hence underestimated the proportion of

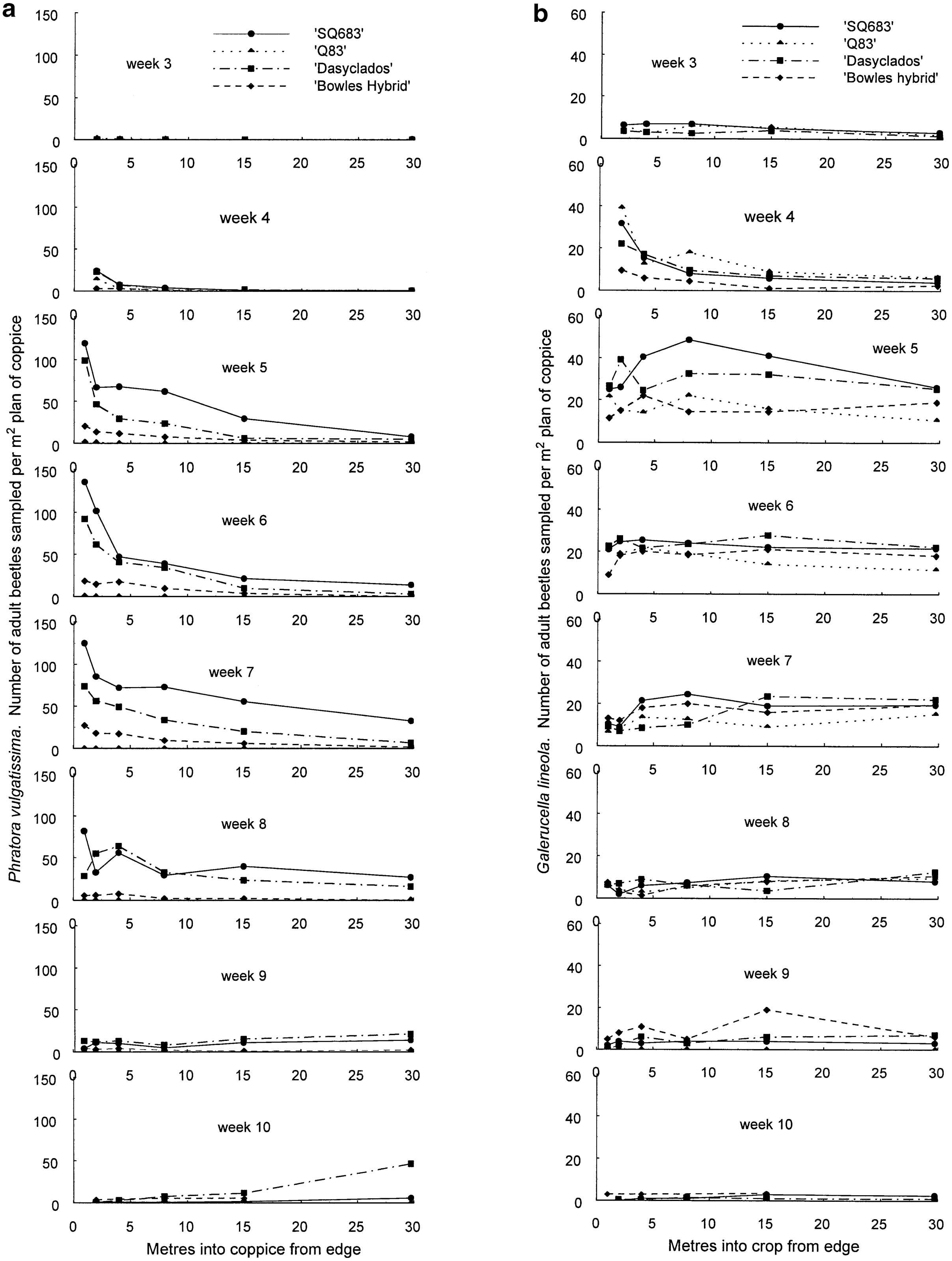

Figure 3 (a) and (b). See p. 68 for caption.

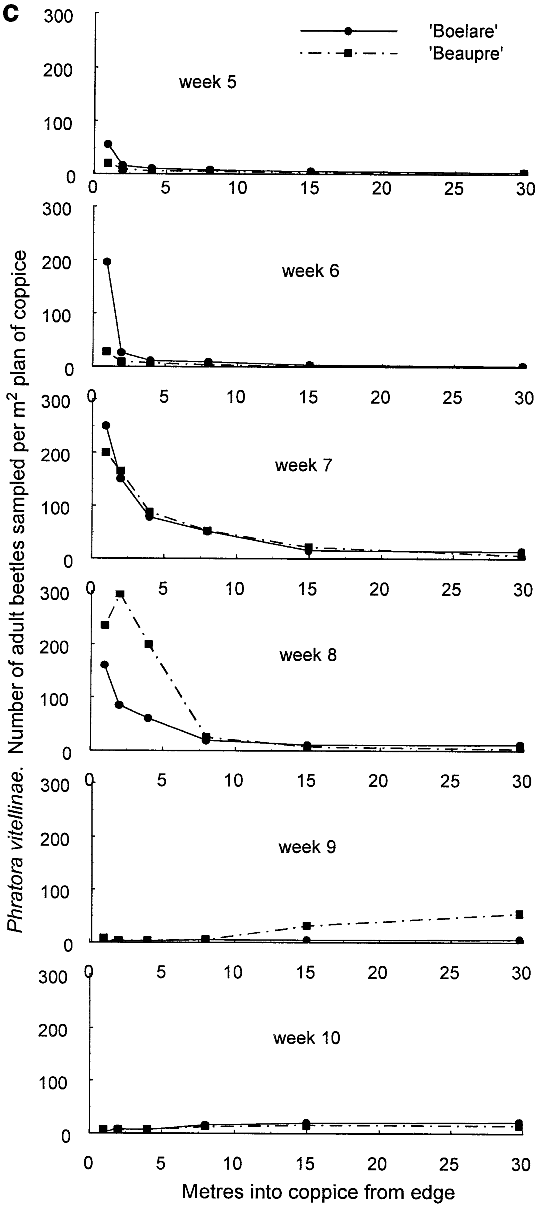

Figure 3 The abundance of three chrysomelids collected from the coppice canopy each week from week ending 4 April 1996 at site W2 and P2. Sample points are along four transects leading from the field edge into the coppice at site W2 (a) and (b), and along two transects at site P2 (c).

beetles flying compared to walking. Like the Colorado beetle, flight is the primary mode of dispersal for all three species in this study (Ferro *et al.*, 1991).

The differences in catches from the two window trap faces, consistent between species and sites, indicates that these traps were not simply recording random flight activity in and around the coppice plantations. Instead, they recorded a net movement of beetles from the overwintering habitats towards the coppice. While this movement was confined to a period of less than 1 week for *P. vitellinae* in 1995, *G. lineola* and *P. vulgatissima* continued to emerge and fly into the coppice over a 4- to 5-week period. The change to more beetles caught on the inward trap faces in week 6 (to 10 May at site W2) marked the end of the dispersal period for these two species. The short dispersal period for *P. vitellinae* observed in this study may be a function of the late leafing of poplars. In the past, many of the clones cultivated in willow beds were palatable to *P. vitellinae* and Hutchinson & Kearns (1930a) found that dispersal by this beetle into these willows lasted from April to late May.

At site W2, leaf emergence on 3 April was followed immediately by large numbers of *G. lineola* in the window traps during week 1 (to 5 April). *Phratora vulgatissima* emerged a week later. After this, catches of both beetles declined before increasing again in week 5 (Fig. 1). Low daytime temperatures during this period may have reduced catches – on warm days beetles were noticeably more active (personal observation). At site P1, poplar leaf and *P. vitellinae* emergence occurred around 3 weeks later. In 1996, both leaf and subsequent beetle emergence occurred later than in 1995. A combination of increasing daytime temperatures and day length are known to break diapause in some chrysomelids (Lefevere & Kort, 1989; Fujiyama *et al.*, 1996).

Colonising the crop edge

In both years, the majority of *P. vulgatissima* and *G. lineola* initially colonized the crop canopy within a few metres of the coppice edge at site W2. At site P2 in 1996, a similar pattern of colonization was even more apparent for *P. vitellinae*. This extreme edge distribution suggests first, that most overwintered beetles do not fly any further than necessary (Follett *et al.*, 1996; Kreslavsky *et al.*, 1996), and second, a tendency to aggregate where beetles already occur (Bach & Carr, 1990). The exception to this pattern of edge colonization was *P. vulgatissima* in Q83 at site W2 (Fig. 3a). The beetle initially colonized the clone in week 4, before rejecting it. Q83 is known to be resistant to this beetle, due to the presence of certain phenoglycoside compounds in the leaves of *S. triandra* (Tahvanainen *et al.*, 1985).

By 9 May 1996 (week 6), more than 80% of all *P. vulgatissima* in the field at site W2 were within 10 m of the standing coppice edge. This proportion was even greater for *P. vitellinae* at site P2 by 23 May (week 8). For *P. vulgatissima* and *P. vitellinae*, these edge distributions remained for at least 3 weeks in 1996. At the poplar site, if dispersal by *P. vitellinae* was confined to a short period (as in 1995), the individuals recorded in the edge zone in week 8 at site P2 would have been the same as those recorded in weeks 5 and 6. The consistently low numbers further into the crop at this site indicate that this was the case. For *P. vulgatissima*, numbers within the crop interior increased steadily over the period, suggesting a turnover of beetles as dispersal progressed or an avoidance of the edge by later-emerging beetles. During these periods, beetles of all three species were observed to feed on the young coppice leaf, rapidly defoliating the coppice canopy within the edge zone, and mating.

Dispersing to the crop interior

In 1996, *G. lineola* at site W2 had moved into the crop interior within a week or two of colonising the crop edge, and by week 6 (to 9 May) had spread evenly through the coppice. Both *Phratora* spp. delayed this secondary dispersal for several weeks following colonization of the edge. For *P. vitellinae* at P2, virtually all beetles settled within the first 10 m of crop in both edge lines in week 6, left this area during week 9 (to 30 May) and spread through the main body of the field (Fig. 3c). For *P. vulgatissima* at W2, a similar secondary dispersal was observed, also at the end of May. This secondary movement occurred earlier in 1995 for *P. vulgatissima*, and was also apparent for *G. lineola*. In both years, dispersal from the edge zone coincided with warm weather at the end of May in 1996 and at the beginning of May in 1995.

A consequence of this staged movement is that most females would not have laid their eggs in the crop edge zone, which by mid-May in 1996 had become severely defoliated. In an ongoing study at site W2, Griffiths (1997) found that egg laying in both species commenced as adult numbers in the edges began to decline. This clearly is of benefit to the relatively immobile larvae when the availability of food may affect survival. Most adult beetles then left the study area (or died), by early June for *G. lineola* and late June for *P. vulgatissima*, reducing competition for food between larval and adult stages.

Context

Phratora vulgatissima, *P. vitellinae* and *G. lineola* have been the principal defoliating invertebrate pests of SRC crops in Britain and Ireland each year since 1993 (Sage & Tucker, 1997, 1998). Leaf area losses in excess of 20% have been recorded at several sites every year and Larsson (1983) and Bach (1994) found growth and biomass losses in willow associated with chrysomelid herbivory at these levels. Weed competition in these crops can also develop in the absence of full canopy shade (Stott *et al*., 1990). *Phratora vulgatissima* accumulated rapidly at site W2 during the course of this study (comparing Fig. 2 and Fig. 3a) and in 1997 it became the third U.K. site in which areas of willow coppice suffered die-back as a direct consequence of repeated defoliation episodes over several years (Kendall *et al*., 1996).

The potential exists for biomass plantations to suffer economic losses following infestations. The use of overall insecticide applications in standing coppice has, however, severe practical and economic limitations. Such applications may also affect many non-target species (Sage & Robertson, 1996). Willows and poplars are known to provide habitat for an abundant insect fauna (Kennedy & Southwood, 1984) and recent SRC plantations have already been found to contain many invertebrate species (Sage & Tucker, 1997). An ability to predict patterns of dispersal by these three chrysomelid species into and through coppices and in particular the temporary accumulations of beetles along edges, may provide an opportunity to control damaging populations using relatively small quantities of an insecticide applied from the plantation headland. The method may provide a practical control measure as part of an integrated pest management strategy for biomass crops (Price & Martinsen, 1994; Sage & Tucker, 1995).

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