Do Host-Plant Interactions and Susceptibility to Soil Cultivation Determine the Abundance of Graminivorous Sawflies on British Farmland?¹

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ABSTRACT Larvae of the sawfly genera *Dolerus* and *Pachynematus* feed on cereals and grasses in farmland habitats and can cause crop damage. In Britain they are not economic pests, but they have a role in the wider ecology of agricultural ecosystems as important sources of food for birds. They have a patchy distribution across the landscape and are particularly associated with areas of cereals undersown with grass. In a survey of British farmland, larvae of these two genera were significantly more abundant in fields of sown perennial rye-grass, *Lolium perenne* L., than in crops of winter wheat, *Triticum aestivum* L., and spring barley, *Hordeum vulgare* L. Host-plant relationships and the effect of soil cultivation on overwintering survival were considered as factors underlying this distribution. In oviposition trials, perennial rye-grass was the preferred host of most species tested, and winter wheat was avoided. Growth rates and survival of larvae in performance trials were significantly higher on rye-grass than on cereals. Soil cultivation during the overwintering period caused up to 50% additional winter mortality of pupae in some years. However, in other years there was no additional mortality, indicating that another factor must be involved following the soil disturbance, such as winter frosts. The observed differences in host-suitability could strongly influence larval distribution on farms, depressing abundance in cereal habitats. Post-cultivation mortality may reinforce this effect. Varying cultivation regimes and availability of undisturbed grassland could be used to manipulate the abundance of these sawflies on farms.

KEY WORDS *Dolerus*, *Pachynematus*, sawflies, cereals, grasses, perennial rye-grass, host-plant interactions, cultivation, Hymenoptera, Tenthredinidae

There are two genera of externally-feeding graminivorous sawflies that regularly feed in cereal crops, *Dolerus* and *Pachynematus* (Hymenoptera: Tenthredinidae). Both genera have been reported from crops of winter wheat, *Triticum aestivum* L., and spring barley, *Hordeum vulgare* L., (Freier & Wetzel 1984, Miczulski & Lipinska 1988, Miczulski & Lipinska 1988, Xu & Chen 1991) and from a range of grasses such as

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Lolium spp., Poa pratensis L. and Dactylis glomerata L. (Mühle & Wetzel 1965). Dolerus and Pachynematus species are of minor economic importance in Britain, but have caused sporadic crop damage in continental Europe (Faber 1970, Wetzel & Freier 1980, Miczulski & Lipinska 1988), Asia (Okutani, 1956, Xu & Chen 1991) and North America (Riley & Marlatt 1891, Kamm 1975). In contrast, research in Britain has found that graminivorous sawflies have a positive role in the agricultural ecosystem as food for many bird species for which farmland is the primary habitat, such as the gray partridge, Perdix perdix L. (Green 1984, Potts 1986). These sawflies are declining in abundance in British cereal fields (Aebischer 1991) and in this context research has been conducted to enhance their abundance on farms in Britain (Barker et al. 1999, Barker & Reynolds 1999). A more detailed understanding of their ecology is of value for those seeking to control or conserve these insects.

An extensive survey of 62 km² of farmland in Sussex, in southern England, has been conducted by The Game Conservancy Trust for over 30 years, with detailed invertebrate data being available for all cereal fields in a 34 km² core area. Potts & Vickerman (1974) noticed that graminivorous sawflies exhibited a patchy distribution within this area, being most abundant around fields of perennial rye-grass, Lolium perenne L., that had been undersown into spring cereal crops in the previous cropping year and allowed to grow on after harvest; this distribution was confirmed in more recent work with this dataset (Aebischer 1990, Aebischer & Ward 1997). The practice of grass undersowing is in decline in Britain, as part of a general move from spring-cropping and mixed arable/livestock farming to autumn sown cereals, principally winter wheat (O’Connor & Shrubb 1986). Aebischer (1990) identified a strong correlation between the decline of grass undersowing and the decrease in sawfly numbers in the area studied.

An intensive four-year survey of sawflies on farms in southern England during the peak larval season (Barker et al. 1999) found that larvae were not equally abundant in all graminaceous crops. Larvae were most abundant in fields of undisturbed perennial rye-grass grown as a seed-crop; average numbers in fields of spring barley and winter wheat were six times lower. Larvae were caught in 95% of the rye-grass fields in comparison with 40% of the cereal fields.

Three factors have been identified that appear to have key roles in determining these patterns of sawfly abundance: insecticide use, differences in host-suitability of different cereals and grasses, and the vulnerability of overwintering sawflies to soil cultivation. Dolerus and Pachynematus larvae are very susceptible to broad-spectrum insecticide use (Trenchev, 1984, Sotherton 1990, Moreby et al. 2001) and populations may take as long as 7 years to recover from a single direct application of insecticide (Aebischer 1990). Studies of trends within The Game Conservancy Trust’s long-term Sussex invertebrate study have shown that applications of fungicide and autumn aphicide may also reduce sawfly numbers in subsequent years (Ewald & Aebischer 1999). However, the pattern of decline recorded by the study is too complex and has been too long-term for insecticide use to be the sole explanation, as it began long before insecticide use became commonplace in British farm practice.

In their four-year intensive survey of graminaceous crops, Barker et al. (1999) did not consider the differences between cereal and grass crops to be due to pesticide use because none of the fields had been sprayed with summer insecticide before sampling, all had been sprayed with fungicide, and all were part of the
same rotation so that any long-term residual effects of pesticide applications would have affected insects in all crops. They reanalyzed their data and showed that the significant differences between crops remained after modeling the effect of the previous crop on sawfly abundance to account for residual effects between years. Instead they highlighted the potential impacts of other changes in farming practice which have greatly increased the proportion of winter wheat sown and reduced the planting of spring barley and of rye-grass. From studies of host-plant relationships, they argued that winter wheat seems to be a comparatively poor host for sawfly larvae, so that increasing its prevalence in the farming landscape has reduced the availability of sawfly habitat (Barker & Maczka 1996, Barker et al. 1999). In addition, planting of winter cereals increases the autumn cultivation of farmland. As both sawfly genera overwinter in the soil, Pachynematus spp. in cocoons and Dolerus spp. as free prepupae/pupae in a simple earth cell, they are potentially affected by soil disturbance. Many soil invertebrates are negatively affected by cultivation (Edwards & Lofty 1975) and there is indirect and direct evidence that soil cultivation reduces the overwintering survival of graminivorous sawflies (Potts & Vickerman 1974, Vickerman 1978, Barker et al. 1999).

This paper will discuss some of the evidence that these two factors, host-plant relationships and soil cultivation, affect the abundance of sawflies, concentrating on studies of the oviposition preferences and larval performance of one Dolerus species, and on two experiments on the impact of cultivation on overwintering survival.

**Materials and Methods**

**Sawfly host-plant relationships: Oviposition preferences and larval performance.** In a series of experiments, we have tested the oviposition preferences and larval performance of a range of Dolerus and Pachynematus species on winter wheat and spring barley cultivars commonly grown on surrounding farms and on locally cultivated perennial rye-grass and red fescue (Festuca rubra L.) varieties (Barker & Maczka 1996, Barker et al. 1999). We present here a typical example, comparing previously unpublished data from an oviposition trial for Dolerus haematodes Schrank with the matching larval performance data (previously presented in Barker et al. 1999).

**Oviposition preference of D. haematodes.** Oviposition trials followed the methods given in Barker & Maczka (1996) and were designed to offer individual female sawflies a choice of potential host plants at growth stages corresponding to those in the field. With D. haematodes, we collected five adult females in 1996 and four in 1997. They were caged individually in 0.5 × 0.5m wooden boxes with netting lids, each containing one pot of each of four host-plants: red fescue, perennial rye-grass, spring barley (‘Chariot’), and winter wheat (‘Hunter’ in 1996 or ‘Consort’ in 1997). These had been collected from the field and potted several weeks earlier so they were all healthy and growing well. Females were left for ten days; during this time they were provided with sugar solution as a food source and the plants were watered as necessary through the netting lids. The boxes were then opened and the number of eggs laid was recorded for each plant. Multivariate compositional analysis (Aebischer et al. 1993) was carried out on the log-ratio of the numbers of eggs laid for each pair of plant species (e.g. log (No. eggs on
Usage of log ratios overcomes the problem of non-independence of proportional data (Aitchison 1986). A year factor was included to test for difference in relative preferences between years; as this was not significant \( (F = 1.75, \text{df} = 3.5, P > 0.05) \), the general pattern of preferences could be examined across the pooled dataset. To allow calculation of log ratios where no eggs were laid on one or more plants in a replicate, zero values were substituted by a small positive value an order of magnitude less than the smallest recorded nonzero proportion before logarithmic transformation. Results of the analysis are robust to such substitutions (Aebischer et al. 1993). Significance of differences was tested by assessing means and standard errors of the differences against the \( t \) distribution.

Larval performance of \textit{D. haematodes}. Larval performance tests were conducted by confining neonate larvae with leaves of one of the host plants being tested (red fescue, perennial rye-grass, spring barley (‘Chariot’), and winter wheat (‘Hunter’ in 1995 or ‘Consort’ in 1997) and measuring growth rates and survival. In 1995 and 1997 neonate \textit{D. haematodes} were collected every day as they hatched from eggs laid by females caged on rye-grass and from plants used in oviposition trials, and allocated at random to a diet of one of the four host plants. They were placed individually in Petri-dishes on moist filter paper and supplied with several cut leaves of their allocated host. Larvae were weighed to the nearest 0.1mg and given fresh leaves to eat every 2 days. Survival to the prepupal stage was recorded and the effect of plant host on survival was analyzed using a log-likelihood \( (G) \) test. Instantaneous growth rates were calculated from the slope of the relationship between the logarithmically-transformed larval weights and time in days for all larvae which survived for more than 5 days (those with sufficient data for the calculation). An analysis of variance was used to test for differences in mean growth rates between hosts.

Impact of soil cultivation on graminivorous sawflies. To test whether cultivation influences the overwintering survival of sawflies, we conducted trials collecting sawflies from cultivated and uncultivated experimental areas of fields. Small scale experiments in 1996 and 1997 showed a significant effect of cultivation on the number of \textit{Dolerus} adults emerging in the trapped areas but catches of \textit{Pachynematus} were too low to show any effects (Barker et al. 1999). In 1998 and 1999, we selected two fields known to have had comparatively high sawfly densities in the preceding summer and greatly increased trapping efforts, to increase the likelihood of obtaining statistically-relevant catch sizes.

In winter 1997, plots were laid out in two adjacent fields in a farm in West Sussex in southern England. One field was cropped as a grass ley (perennial rye grass and clover) following an undersown spring barley, and the other was uncultivated stubble following a winter wheat. Three treatments were compared: winter plowing (in November 1997) followed by power harrowing in late February 1998, early spring plowing and harrowing (both in late February 1998), and the uncultivated control. Cultivation was timed to follow normal agricultural practice on the farm. A randomized block design was used, with two 15 m × 1.3 m strips of each of the three treatments randomly positioned within two blocks on each field. Ten emergence traps were placed along each strip in mid-March, after cultivation but before the start of emergence. Traps were these same as those used in previous experiments (Barker et al. 1999), consisting of a 1m × 1m × 0.25 m deep wooden box with a 1.5mm mesh black netting lid stapled into position and
with one corner left pinned for access. Each box contained a yellow water trap (210 × 100 × 60mm aluminum trays sprayed with yellow paint filled with a dilute detergent solution) as a collector. Traps were checked twice weekly for sawflies in the water traps and for live sawflies, which were usually found on the netting lids; all sawflies were removed each time. Trapping was continued for the duration of the adult flight period, and continued for two weeks after the last individual had been caught (May 22, 1998). This ensured the results were not biased by any differences in emergence times from different treatments. All insects caught were identified and recorded. Vegetation growing within the traps was periodically trimmed with shears through the box opening after checking the traps for sawflies.

In winter 1998/ spring 1999 we concentrated on the effects of winter cultivation and used coverings of agricultural fleece to manipulate winter soil temperatures, in an attempt to test the possibility that the effects of cultivation could be mediated through subsequent exposure to extreme winter weather. Four blocks, two on an undersown grass ley field and two on winter wheat stubble, were each marked out into eight strips randomly allocated to one of four cultivation/ frost covering treatments. Half the strips were ploughed and power harrowed in late November, with the rest left uncultivated. Immediately afterward, half of both the ploughed and the unplowed strips were covered with agricultural fleece to reduce their exposure to frost. The following March the fleece was removed and nine emergence traps were placed on each strip. The traps were sprayed with glyphosate in early April to keep them clear of vegetation.

**Analysis of cultivation treatments.** In both years, the total catch of sawflies was calculated for each strip of traps within each block. The density of sawflies was only about two per m² of the trapped area, so analysis was carried out assuming an overdispersed Poisson distribution using log-linear modeling in GENSTAT 5 (Payne et al. 1987). Factors were included for block and for cultivation treatment, and, in 1999, for covering treatments. Significance was assessed from the deviance ratio, which approximates to an F-statistic (Payne et al. 1987).

**Soil temperatures.** To demonstrate that the agricultural fleece was effective in moderating the impact of cold temperatures on the soil, we placed a maximum/ minimum thermometer within a pot in the soil on each plot type in both fields in the 1998/1999 winter. However, we could only take readings every two weeks and this did not provide sufficient resolution and accuracy to detect differences. Therefore in winter 1999/2000 we repeated the plowing and covering treatments in plots on one winter wheat cereal stubble field, and placed one Hobo H8 Temperature/Relative Humidity data logger (Onset Computer Corporation) in one of each plot type at soil height (set within a flower pot dug into the ground and wrapped in rubber to exclude moisture). Where fleece was used, this covered the monitors; monitors were protected from rain by a plywood sheet raised above the ground to allow free air circulation. The monitors were set to record the temperature every half hour from November until late February. Here we present the data from the covered and the uncovered ploughed strips to test the effect of the fleece covering. We analyzed the data for the 14 occasions on which temperature fell below freezing during this period, using paired t-tests to see if there were between-treatment differences in the average minimum temperatures reached and the duration in hours of each period spent below 0°C (data were log (n+1)-transformed to normalize before analysis).
Results

Oviposition preference of *D. haematodes*. *D. haematodes* females laid the highest proportion (over 40% on average) of their eggs on perennial rye-grass, with almost all the rest split equally between spring barley and red fescue (Fig. 1). Only one of a total of 269 eggs was laid on winter wheat, and there was a significant difference between usage of wheat and that of spring barley, perennial rye-grass and red fescue (*F* = 2.55, df = 3.5, *P* < 0.001), although there were no significant differences in usage among these three hosts.

Larval performance of *D. haematodes*. Larval survival varied significantly between hosts (Table 1), and was highest on perennial rye-grass but also good on spring barley. Comparison of these two species showed that there was no difference in relative survival between them in either year, although the comparison was close to significance in 1995 (G-tests with 1 df, 1995: *G* = 3.10, *P* = 0.08, 1997: *G* = 0.35, *P* = 0.55). Less than half the larvae reared on red fescue survived, and survival was very poor on winter wheat—in 1995 all larvae on this host died. In 1995 growth rates on perennial rye-grass were 30% higher than on all other hosts. In 1997 low replicate numbers for larvae on red fescue and winter wheat made the overall growth rates difficult to compare, but larvae grew equally well on both perennial rye-grass and spring barley.

Cultivation experiments. In spring in both 1998 and 1999, sawflies started to emerge in late March and peak emergence was in early May, with catches

![Fig. 1. Mean proportion of the total number of eggs laid per female on each host plant, with standard errors (error bars). The usage of winter wheat was significantly lower than that of the other three hosts (*P* < 0.001 in tests of pairwise differences)](image)
continuing until the end of May. Total catches in 1998 were 487 sawflies, of which 458 were *Dolerus* spp. and 25 were *Pachynematus*. In 1999 we caught 497 *Dolerus* adults and 203 *Pachynematus* adults, with a few individuals of other species making a total of 694 individuals. The most common *Dolerus* species were *D. puncticollis* Thomson, *D. gonager* F. and *D. haematodes*, and two *Pachynematus* species were caught, *P. xanthocarpus* Hartig and *P. extensicornis* Norton.

In 1998 there were no differences between any of the plowing treatments for either graminivorous genus (\(F_{2,18} = 1.16, P = 0.34\), Fig. 2). In 1999 the mean catches of sawflies per square meter were very similar in all treatments (Fig. 3); neither plowing nor covering nor the combination of the two affected the catch of either sawfly genus (\(Dolerus\): Cultivation effect \(F = 1.65, P = 0.22\), Covering effect \(F = 0.41, P = 0.66\), Interaction \(F = 0.19\), *Pachynematus*: Cultivation effect \(F = 0.10, P = 0.76\), Covering effect \(F = 0.18, P = 0.68\), Interaction \(F = 2.53, P = 0.12\). All df were 1, 25 and all \(P\) values were > 0.05).

**Soil temperatures.** Temperature monitoring in 1999/2000 showed that on the 14 separate occasions in which freezing temperatures were recorded in winter 1999/2000 the agricultural fleece did influence the soil temperature. There was a difference in minimum temperature of 1°C between covered and uncovered ploughed plots (mean minimum temperature = −0.4°C on covered areas, SE = 0.35, mean minimum temperature = −1.44 on uncovered areas, SE = 0.41, \(t = 3.97, df = 13, P < 0.01\)). Longer periods were also spent below freezing temperatures on the uncovered area during each frost (mean time spent below 0°C =

Table 1. Survival and growth rates of *D. haematodes* larvae on four host plants, with results of log-likelihood analyses (\(G\)) on relative survival and ANOVAs (\(F\)) on growth rates (from Barker et al. 1999).

<table>
<thead>
<tr>
<th>Year</th>
<th>Hosts</th>
<th>Perennial rye-grass</th>
<th>Red fescue</th>
<th>Spring barley</th>
<th>Winter wheat</th>
<th>(G) or (F) (df)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>% survival</td>
<td>91%</td>
<td>42%</td>
<td>71%</td>
<td>0%</td>
<td>64.51 (3)</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>(n)</td>
<td>(22)</td>
<td>(26)</td>
<td>(24)</td>
<td>(31)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean growth</td>
<td>0.092 a</td>
<td>0.064 b</td>
<td>0.069 b</td>
<td>0.064 b</td>
<td>27.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>rate (SE, n)</td>
<td>(0.002, 26)</td>
<td>(0.002, 20)</td>
<td>(0.002, 25)</td>
<td>(0.005, 13)</td>
<td>(3, 80)</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>1997</td>
<td>% survival</td>
<td>75%</td>
<td>27%</td>
<td>64%</td>
<td>8%</td>
<td>17.48 (3)</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>(n)</td>
<td>(12)</td>
<td>(15)</td>
<td>(14)</td>
<td>(13)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean growth</td>
<td>0.064 a</td>
<td>0.064 b</td>
<td>0.087</td>
<td>0.088 d</td>
<td>0.338</td>
<td></td>
</tr>
<tr>
<td></td>
<td>rate (SE, n)</td>
<td>(0.010, 12)</td>
<td>(0.020, 4)</td>
<td>(0.005, 10)</td>
<td>(0.010, 3)</td>
<td>(1, 20)</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

\(a\)Letters after growth rates indicate significant difference between pairs of treatments using Tukey’s HSD. Larvae for which growth rates were obtained did not all survive to pupation, and some larvae that died accidental deaths were excluded from survival calculations, so sample sizes for survival and growth rate calculations may differ.

\(b\)\(df\) = degrees of freedom.

\(c\)\(P\) = probability.

\(d\)The growth rates for red fescue and winter wheat were not included in the analysis in 1997 due to the low numbers of replicates.
6.4 h on covered areas, SE. = 8.9, mean time spent below 0°C = 8.9 h on uncovered areas, SE. = 2.8, \( t = 2.92, \text{df} = 13, P < 0.05 \).

**Discussion**

**Host-plant relationships: oviposition preference and larval performance.** In our experiments female *D. haematodes* avoided ovipositing on winter wheat when given a choice and larval survival was poor on this cereal. Growth rates were greatest on perennial rye-grass, significantly so in the 1995 trial. Perennial rye-grass and spring barley were good hosts for this sawfly. In general we have found winter wheat to be a poor host for most *Dolerus* and *Pachynematus* species tested in our research. In choice tests almost all species laid the majority of their eggs on perennial rye-grass and avoided winter wheat (Barker & Maczka 1996, Brown 1996, C.J.M.R., unpublished data). Growth rates and survival of larvae were higher on rye-grass than the other three hosts, with survival often particularly poor on winter wheat (Barker & Maczka 1996, Barker et al. 1999). The only exception was *P. xanthocarpus* Hartig, which preferred to oviposit in winter wheat and had larvae that performed well on this host (C.J.M.R., unpublished data, Eastwood 1999). The suitability of the other cereal tested, spring barley, varied between sawfly species, with some species thriving on it, but others, such as *D. puncticollis*, not surviving well (Barker et al. 1999).
Overall, the differences in sawfly preference and performance on different hosts were clearly of sufficient magnitude to affect field populations, supporting the hypothesis that host-plant requirements might influence field distribution between crops. In particular, they could explain the very low density of larvae in winter wheat and comparatively high densities in perennial rye-grass observed in our survey of British farms (Barker et al. 1999); the only two winter wheat fields with high larval densities in this study were two with high densities of grass weeds. Vickerman (1974) found a significant reduction in sawfly numbers when grass weeds were sprayed out in a winter cereal crop, and Haris (1995) found that various grass species were the primary hosts of *Dolerus* species rather than neighboring wheat fields. However, there are some discrepancies; in particular, spring barley appeared to be a good host for some species in laboratory trials, but catches were low in this cereal. Also, surveys in other countries have reported much higher sawfly densities in both winter wheat and spring barley (e.g. Freier & Wetzel 1984, Miczulski & Lipinska 1988, Xu & Chen 1991). One explanation may lie in differences between cereal cultivars, which affect their suitability for sawflies (Heyer & Wetzel 1988) or may involve colonization in local hot-spots from neighboring high density populations in grasses, as observed by Haris (1995). The presence of an understory of grass weeds or a previous grass crop in the field may

![Fig. 3. Mean catch per square meter of emerging graminivorous sawflies from areas of soil with two treatments applied. Soil strips were either covered with agricultural fleece to reduce frosts or left uncovered; half the strips of each type were plowed in winter whereas the remainder were un-plowed. Error bars are standard errors of the mean. There were no significant differences between treatments.](image-url)
also bolster sawfly numbers, as observed in two of our survey fields. Variations in crop phenology may change females’ readiness or ability to accept cereals as hosts, even though it may not change their suitability (Haris 1995, Eastwood 1999); this may explain the lack of colonization of spring barley, as in modern British crop rotations, this cereal is only available as a growing crop at the tail end of the adult flight period.

Cultivation. In 1998, neither spring nor winter cultivation had any effect on the emergence of sawflies from the soil. This result was surprising in the light of previous results demonstrating quite marked effects, with twice as many sawflies emerging from unplowed as from plowed areas, albeit on a small scale (Barker et al. 1999). The 1996 and 1997 winters and springs were markedly colder than those of 1998, with more frosts. Long-term modeling has found that dolerine sawfly population sizes fall after cold winters (Aebischer 1990). We therefore considered that the apparent effect of plowing in 1996 and 1997 in reducing adult emergence might not have been due to direct mechanical damage to pupae during soil disturbance, but to have acted indirectly by bringing them closer to the soil surface and so increasing their exposure to frosts. Dolerine sawflies pupate down to about 20 cm below the soil surface, where they can be brought up by the action of the plough; pupae have been observed on the soil surface immediately after plowing (A.M.B., unpublished data). The experiment conducted in 1998/1999 was designed to test the idea that freezing is the cause of mortality of sawflies in plowed soil, by manipulating the surface temperature using agricultural fleece. Temperature recording (in 1999/2000) showed that the fleece did reduce the severity of the effects of frost on the soil surface, so our experiment had the potential to discriminate between the effects of cultivation and of exposure to cold temperatures. However, the winter was a mild one with only brief periods of freezing temperatures, so that there was little difference in temperature exposure between covered and uncovered treatments, and showed little impact of plowing. Our experiment showed little impact of plowing on overwintering mortality but under these conditions we could not test the impact of low temperatures on pupae so the results remain inconclusive.

In our earlier work we calculated that cultivation could account for up to 30% of the difference in sawfly abundance observed between surveyed crops (Barker et al. 1999), but the level of mortality observed in that study might have been atypically high. Deep plowing has been used as a cultural control method for Dolerus species in China (Anon. 1992) but its mode of action has not been not explored. The experiments reported in this paper suggest that mechanical damage alone has little effect. Cold temperatures would seem likely to have an impact on pupae brought to the surface; cultivation to bring sawflies to the soil surface to expose them to very low temperatures and desiccation is successful as a way of controlling the wheat stem sawfly Cephus cinctus Norton in North America (Morrill et al. 1993) where surface temperatures fall 30°C below those of the upper soil layer. Another possible factor is dessication of exposed prepupae due to hot, dry weather after plowing (many farms in Britain now plow immediately after harvest); it is known that hot summer weather reduces sawfly abundance in the following year (Aebischer 1990) but the reasons for this remain unexplored. Increased bird predation on exposed pupae may also reduce survival. These factors need further experimental study to pinpoint the conditions under which cultivation has a serious impact on sawfly populations.
Which factors determine the abundance of graminivorous sawflies on British farmland? Both factors investigated in this study, host-plant use and cultivation, potentially have an impact on the abundance of externally-feeding *Dolerus* and *Pachynematus* species in crops in British farmland. Even with no insecticide use, populations are likely to be seriously depressed in areas of widespread winter wheat production, where only poor quality hosts will be available and the soil will be disturbed every autumn. Obviously, where insecticides are in common use, these will suppress sawfly populations even further. But even in the absence of summer spray use, it seems likely that a varied landscape with grasses and perhaps also spring barley present will have more abundant sawflies than a winter cereal monoculture. Interestingly, Ross (1931) commented on the lack of dolerine sawflies in the ‘vast extent of farm lands’ in Illinois in the 1930s, long before the advent of chemical insecticides.

Of course, host-plant relationships and cultivation regimes will not be the only factors determining sawfly abundance. Their ability to colonize available habitats may be limited by their dispersal capacity, as they are not strong flyers. They are known to be affected by climate, prospering from moderately wet summers and mild winters (Aebischer 1990). Sawflies are also hosts for various parasitoid species, which may be the cause of observed density-dependent changes in population size (Potts 1986, Aebischer 1990), and are prey for vertebrate and invertebrate natural enemies. However, host-plant availability and cultivation represent important factors that can be successfully manipulated by those seeking to control or to conserve these insects. For example, areas of semipermanent undisturbed grassland have the potential to act as sources of these insects for colonization of neighboring cereals, as reported by Haris (1995) from fields of planted grass. They provide suitable host-plants in a habitat with no overwintering disturbance. Where pest control is required, planning cropping so that cereals and grass fields are minimally intermixed, and controlling grass weeds, should reduce this problem, and deep plowing may also help. Conversely, for areas of Britain where conservation of these insects as chick food within farmland is a priority, planting of semipermanent grass field margins in a network across the farm has been recommended. A survey of larval numbers in this habitat (Barker & Reynolds 1999) found that sawfly larvae were widespread in such strips, and were found at higher densities than in cereal fields. This demonstrates how the conclusions from our ecological studies can be successfully used to manage the abundance of these insects in the farmland landscape.

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