Cereal aphid populations in non-crop habitats show strong density dependence

RICCARDO BOMMARCO,* SIMON WETTERLIND† and
ROLAND SIGVALD*

Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, SE-750 07 Uppsala, Sweden; and †Department of Life Sciences, University of Skövde, PO Box 408, SE-541 28 Skövde, Sweden

Summary

1. Few studies have addressed how density-dependent and density-independent regulation of population growth and abundance varies among habitats for a species that requires multiple habitat types to complete its life cycle. Understanding such relationships, however, are of direct relevance to the control of crop pest insects that regularly move between crop and non-crop habitats.

2. We used autoregressive models to analyse a series of seasonal catches of the cereal aphid *Rhopalosiphum padi.* The data were collected from regional suction traps and egg counts on the overwintering host, over a period of 14–31 years, at four locations in Sweden. *R. padi* is an obligate host-alternating species in Sweden and seasonal catches reflect habitat use in a year: the primary woody host in winter and spring, the cereal crops in summer, and the perennial grasslands in the autumn.

3. Strong direct density dependence acting within the year was found, but the strength varied between seasons depending on habitat use by the aphids during the year. Only a weak indication or no indication at all of density dependence was found during the period of residency on the primary host in the winter and spring periods.

4. Density dependence occurred when *R. padi* utilized summer cereals (42% of the variation was explained), and even stronger density dependence occurred in the perennial grasslands in the autumn (70% variation explained). Stochastic fluctuations in the winter and spring were balanced by a strong density dependence in the cereal and grassland habitats in the summer and autumn periods, which reduced variability in population fluctuations.

5. Weather, measured as seasonal average temperature and accumulated precipitation, did not affect aphid abundance fluctuations much, explaining only 1–9% of the variability.

6. *Synthesis and applications.* Our results suggest that density-dependent regulation of *R. padi* occurs in late summer grasslands and early summer cereals. The mechanisms causing these patterns are not understood, making it difficult to provide specific pest management recommendations at this stage. The results do indicate, however, that pest management needs to involve a landscape-level approach, taking into account mechanistic information about the plant, herbivore and predator interactions in multiple habitats visited by the herbivorous pest.

Key-words: aphids, biological control, crop pest, pest management, population regulation, *Rhopalosiphum padi*

Correspondence: Riccardo Bommarco, Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, SE-750 07 Uppsala, Sweden (fax +46 18 672890; e-mail Riccardo.Bommarco@ekol.slu.se).

Introduction

A central issue in ecology is understanding the relative influence of density-dependent and density-independent processes affecting population growth and abundance of fluctuating populations over time (Royama 1992). This information is crucial for the application of ecology

to pest management (Hassell, Latto & May 1989) as well as for understanding broad-scale community structure (Pianka 1974; Ives 1995). Analysing spatial and temporal variability in population abundance requires long time series collected over large geographical ranges (Lundberg *et al*. 2000) and such data are lacking for most communities and even for many species of immediate economic interest, such as pest organisms.

Abundance time series are most often based on census counts performed once a year. A problem with yearly censuses is that within-year changes in population processes cannot be inferred from such data series. Census data collected seasonally can provide insight regarding when during the year density-dependent or density-independent processes dominate (Williams, Ives & Applegate 2003). This is particularly relevant for organisms that produce several generations in a year (Woiwod & Hanski 1992; Sequeira & Dixon 1997; Azerefegne, Solbreck & Ives 2001).

Furthermore, many organisms shift habitat seasonally, and require access to multiple resources or hosts to complete their life cycle and to reproduce successfully. These resources are often separated spatially and may be found in widely different landscape elements. Examples are organisms that overwinter in one habitat and reproduce in another, species that require life stage-specific resources, and herbivores such as host-alternating aphids that shift seasonally between multiple hosts in response to resource limitation and adverse weather conditions (Moran 1992). The relative strength of density-dependent and density-independent effects may differ widely among habitats. Analysing seasonal abundance data, which are linked to habitat use within a year, allows us to explore how, where and when in a year the population abundance of a habitat-alternating species is most influenced by density-dependent processes. Although ubiquitous in nature, few studies have addressed the habitat-specific density dependence and seasonal dynamics for habitat-alternating species.

We used seasonal abundance estimates of a cereal aphid, *Rhopalosiphum padi* (L.), based on weekly suction trap catches of migrating aphids and egg counts in the winter. These data have been collected for 14–31 years in four geographically separated locations in Sweden (Fig. 1 and Table 1). In Sweden,
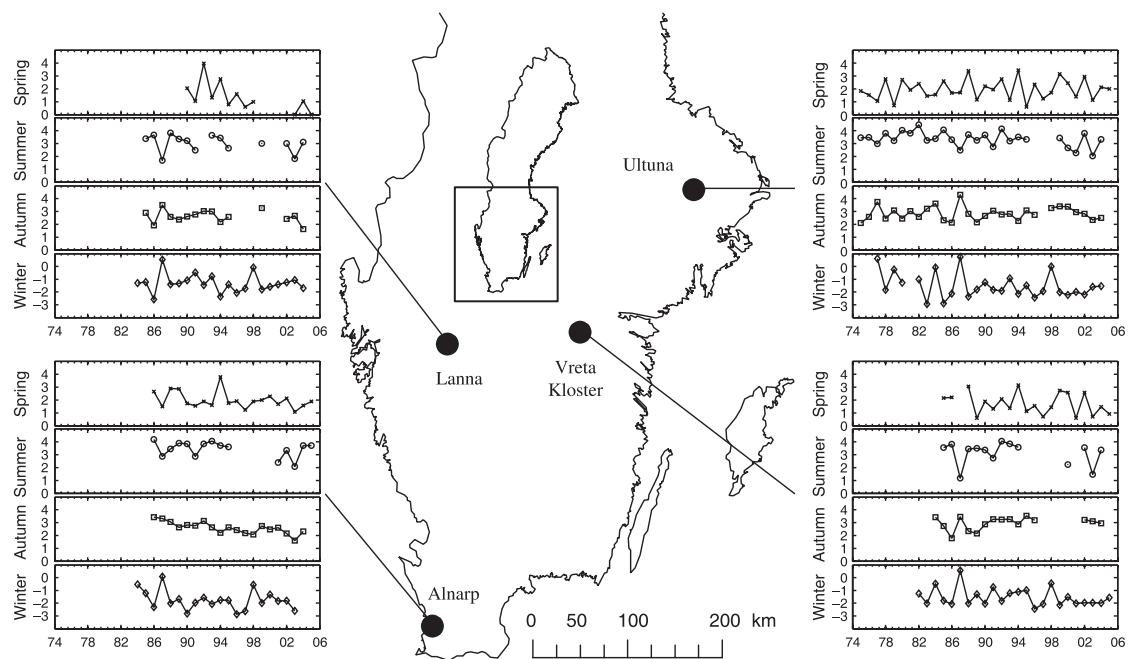
Fig. 1. Log population abundance of *R. padi*, $n(t)$, vs. year, for each location and season. Spring, summer and autumn catches of migrants caught in suction traps; winter abundances estimated from egg counts on the primary host *P. padi*.

Table 1. Average (SE) logarithmic seasonal suction trap catch and winter egg density in each location. n = number of years with non-missing data for each season and location

| Location | Geographic position of suction trap | Suction trap catch | | | | | | Eggs bud^{-1} | |
		Spring	n	Summer	n	Autumn	n	Winter	n
Ultuna	59°82′ 17°66′	1·97 (0·14)	31	3·36 (0·11)	27	2·85 (0·10)	29	−1·51 (0·19)	27
Vreta Kloster	58°48′ 15°53′	1·71 (0·19)	20	3·13 (0·24)	14	2·96 (0·12)	16	−1·52 (0·14)	24
Lanna	58°34′ 13°13′	1·32 (0·18)	21	3·07 (0·18)	15	2·63 (0·13)	15	−1·32 (0·15)	21
Alnarp	55°66′ 13°07′	2·00 (0·14)	20	3·44 (0·16)	15	2·59 (0·10)	19	−1·76 (0·17)	20

R. padi is a host-alternating species that feeds on a variety of grass species in the summer (Blackman & Eastop 2000). In the winter, it is obliged to overwinter as an egg on its primary woody host *Prunus padus* (L.). The eggs hatch from mid-March to mid-April in southern Sweden, and from beginning to late April in central Sweden. Two to three parthenogenic generations are then produced on the trees (Dixon 1971; Wiktelius 1984). The final aphid generation on *P. padus* consists of winged individuals that, from mid-May to mid-June, migrate to various grass species, among them cereals on which *R. padi* can become a pest (Leather, Walters & Dixon 1989). During the summer, wingless and winged aphids are produced parthenogenetically. The proportion of winged aphids gradually increases as a combined result of the cereals maturing and high aphid densities in the crop (Wiktelius 1992). As the crop matures and is harvested, the aphids are confined to perennial grasslands in late summer and autumn (Wiktelius 1987). In mid-August, shorter day length triggers the development of winged morphs that, during August–October, migrate back to the woody winter host, *P. padus*, where sexual morphs mate and lay eggs near the buds of young shoots (Leather 1980).

The seasonal migration events, when the host-alternating aphids move between habitats, can be distinguished as three distinct peaks in the suction trap catches each year (Wiktelius 1982; Dixon 1998). Suction trap catches have been shown to be positively correlated with aphid population size on the ground (Carter *et al.* 1980; Howard & Dixon 1990). Seasonal catches of migrants therefore reflect aphid population size in each main habitat type visited by the aphids in a year; the woody host in the spring, the cereals and grasslands in the summer and the perennial grasslands in the autumn (Wiktelius 1987; Dixon 1998). These suction trap data, merged with regional counts of eggs in the winter on the primary host, allow us to use time-series analysis to explore the relative importance of density-dependent and density-independent processes affecting the *R. padi* aphid populations in each habitat. Catches from geographically separated locations enable us to assess the level of synchrony in population fluctuations among local aphid populations. Finally, by using climate data we can examine the extent to which the density-independent variation can be explained by weather factors. Although several studies have examined aphid abundance time series (Dixon 1990; Woiwod & Hanski 1992; Alyokhin, Drummond & Sewell 2005), few have considered the effects of seasonality, and then only for non host-alternating tree-dwelling aphids (Sequeira & Dixon 1997; Jarošík & Dixon 1999). To our knowledge no studies have analysed long-term time series and concurrently considered the effects of season, habitat use and weather in multiple geographically separated locations for a host-alternating aphid species (but see Maudsley *et al.* 1996).

Materials and methods

THE DATA SET

Rhopalosiphum padi migrants were collected weekly from 12-m high suction traps (Macaulay, Tatchell & Taylor 1988) at four locations ranging from Alnarp in the very south to Ultuna in eastern Sweden (Fig. 1). There was one trap in each location and all traps were situated on an open grass field. In all locations the surrounding landscape was dominated by agricultural land. The catches were summed into three seasonal parts each year: spring, summer and autumn catches. The spring period started in week 14 (beginning of April), when the eggs start hatching (Wiktelius 1984; R. Bommarco, unpublished data), and ended in the week when a temperature sum of 482 day degrees (DD) above 5 °C had been accumulated, usually after mid-June. This temperature sum threshold was obtained from 6 years of suction trap catches where the phenology of emigrants from *P. padus* was carefully observed by morph determination (Wiktelius 1982). The threshold was calculated as the average accumulated temperature sum on the day when the last migrant was caught each year (mean 482, SE 37·6, $n = 6$). The summer period then lasted until week 32 (mid-August), when day length triggers the production of migrants to the primary host (Wiktelius 1982). The autumn season lasted to week 44 (end of October), when egg production ceases. The winter season was defined as the period from week 45 to week 13 the following year. The cumulative catch was calculated for each season, year and location. For the Ultuna location we also used the seasonal suction trap data published by Wiktelius (1987) for the period 1975–85.

The winter population abundance, expressed as number of eggs bud^{-1} on the primary woody host, was estimated from yearly egg counts in the region surrounding the suction trap location within a 70-km radius. A minimum of 200 buds on randomly chosen fresh yearly shoots was examined by eye for eggs. On average, 16 trees (minimum two, maximum 58 trees) were examined at each location in each year. On sunny days the shiny eggs could be counted in the field; on cloudy days several shoots were cut from the tree and 200 buds were examined with a lens in the laboratory. The counts were performed either in November or in February–March prior to hatching. In several instances ($n = 194$ distributed over 11 years) counts were performed on the same tree both in November and February–March to estimate winter mortality. The data showed a strong correlation between autumn and spring log egg density ($r = 0·86$, $P < 0·0001$, $n = 137$; zero observations were removed prior to analysis). The average egg mortality from November to February was 25·6%. Based on the correlation, autumn counts were recalculated to spring egg abundances by reducing the egg population by 25·6%. This was done only in cases where an autumn count, but not a spring count, was

available. The average spring egg abundance was calculated for each year and location, and was analysed together with the suction trap catch data.

Aphid abundance data were $\log_{10}$ transformed prior to analysis. Zero counts provide a problem in analyses of population time series. Zero observations were found for egg counts but not for suction trap catches. We therefore performed all tests adding the minimum observed abundance, which was 0·001, to all egg count observations prior to transformation, i.e. $n_t = \log_{10}(N_t + 0.001)$. This decision was based on the assumption that *R. padi* was present at each location, season and year, but that it sometimes occurred at levels too low to be detected by the sampling methods. Suction trap catches were transformed as follows: $n_t = \log_{10}(N_t)$.

Daily weather recordings were obtained from weather stations managed by the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping, Sweden), located 3–35 km from each suction trap. We used records of daily average temperatures, accumulated precipitation and temperature sums above a 5 °C threshold. The weather data were divided into seasonal periods using the same yearly breakpoints as described above for the aphid abundance data. Average temperature and accumulated precipitation were calculated for each year, season and location.

STATISTICAL ANALYSES

If the growth of a population is affected by density-dependent processes, there exists, by definition, an influence of population density on population growth rate. If there is no such relationship then the population growth is density independent (Royama 1992). Hence, to quantify the relative importance of density dependence or independence on population fluctuations from a time series, a relationship between density and population growth rate must be examined. To do this we assumed the dynamics of a *R. padi* population to be that of a first-order log linear autoregressive function, AR(1). The AR(1) model assumes that population densities measured at one time can be predicted from the density estimated in the previous time step alone (Box, Jenkins & Reinsel 1994). Although very simple, the AR(1) model has been applied successfully to model dynamics from population abundance time series for several species and communities (Dennis & Taper 1994; Ives *et al.* 2003; Williams, Ives & Applegate 2003; Viljugrein *et al.* 2005).

It is straightforward to apply the AR(1) model on a seasonal time scale (Williams, Ives & Applegate 2003), which is of particular interest for studying habitat-alternating species such as *R. padi*. That *R. padi* has more than one complete generation turnover each season (Leather, Walters & Dixon 1989) is a further argument for using the AR(1) model. Applying AR(1) on a seasonal time scale has also been shown to be highly relevant for aphids (Sequeira & Dixon 1997). We therefore fitted the following seasonal model to *R. padi* time-series data:

$$n_t = a_s + (1 + b_s)n_{t-1} + \varepsilon_s \qquad \text{eqn 1}$$

The variables a_s and b_s are autoregression coefficients, with subscript s denoting season. The remaining variable ε_s is the residual error that incorporates density-independent population fluctuations not explained by the AR(1) model. The residual variability can be caused by both biotic and abiotic factors as well as actual errors, such as measurement errors (Shenk, White & Burnham 1998). The population rate of change between two seasons is $R_t = N_t/N_{t-1}$ or, expressed as log densities, $r_t = n_t - n_{t-1}$. The relationship between population growth rate in one season and population density in the same season is then:

$$r_t = a_s + b_s n_t + \varepsilon_s \qquad \text{eqn 2}$$

The strength of density dependence is captured by the coefficient b_s. When b_s is zero no density dependence exists. A negative b_s indicates density dependence, and a b_s greater than zero indicates a destabilizing positive density dependence. The two coefficients a_s and b_s are obtained from linear regression of r_t on n_t, and $\varepsilon(t)$ comes out as the regression residual. The seasonal model was fitted separately to the time-series data from each location. A series of diagnostics was performed on the residuals, $\varepsilon(t)$, to assess whether the assumptions of the AR(1) model were met and that the linear model correctly captured the structure in the data. Analysis of covariance was performed to detect whether strength or direction of seasonal density dependence differed among locations for each season.

Although not explained by the AR(1) model, the residual variation, $\varepsilon(t)$, is caused by something. One possibility is that at least part of this variability is caused by a source that is common for all locations. If this is the case, spatial synchrony in residual variation should be detectable among locations. We examined this by performing pairwise correlation between locations of residual time series. We then bootstrapped the pairwise correlations and calculated 95% confidence intervals for synchrony in residuals among locations. A significantly positive correlation would indicate that factors influencing population change act, at least partly, in synchrony among locations.

The density-independent time series, $\varepsilon(t)$, contain population abundance changes induced by abiotic factors such as broad-scale climatic factors. It is possible to test for the possible influence of weather when corresponding time series exist. We tested the effect of weather by regressing $\varepsilon(t)$ on average daily temperature and accumulated precipitation for each season and location. Procedure REG was used for the autoregressive modelling and procedure GLM for the analysis of covariance in SAS 9·1 for Linux (SAS 2005). Bootstrapping was performed in R 2·2·1 for Linux (Ihaka & Gentleman 1996).

Results

The time-series data exhibited strong seasonal fluctuations but no long-term trends were evident at any location when regressing the complete series of *R. padi* abundance against time ($P = 0.13$). Missing values in the time series were either caused by a temporarily failing suction trap or because samples were determined to species level for a limited time period in a season. In cases where one or more weeks were missing for a certain season and location, the whole season was discarded and regarded as a missing value. Because the AR(1) model employed was based on seasonal time-series components, gaps in the time series were not critical to the performance of the model but would reduce the degrees of freedom. Fairly large catches of *R. padi* were made throughout the sampling period (Fig. 1 and Table 1), which reduced problems with sampling errors for low sample sizes.

PATTERNS OF DENSITY DEPENDENCE

Pervasive patterns of density-dependent regulation were found but the strength of density dependence varied sharply among seasons. In the spring period, when the aphids are still on their primary host, density dependence was detected in two out of four locations, explaining, on average, 25% of the variation (Table 2 and Fig. 2). During subsequent seasons, density dependence was highly significant in all locations, explaining, on average, 42% of the variation in the summer cereals. Density dependence culminated in the perennial grasslands in the autumn period, with the lowest values of the slope *b*, which indicated a strong density dependence (equation 2), and with 70% of the variation explained. No density dependence was detected in any location among the overwintering eggs in the winter period. The model was not significant and explained only 5% of the variation during this period (Table 2 and Fig. 2).

The seasonal patterns of density dependence were consistent among locations. An analysis of covariance showed no difference in strength or direction of seasonal density dependence among locations for each season (ANCOVA, spring $F_{3,79} = 1.5$, $P = 0.42$; summer $F_{3,62} = 0.2$, $P = 0.89$; autumn $F_{3,61} = 2.2$, $P = 0.10$; winter $F_{3,67} = 1.0$, $P = 0.42$).

To assess whether the AR(1) model chosen was appropriate, we performed a series of diagnostics on the residuals. We plotted standardized residuals from each location against predicted values. Residuals were evenly scattered along the predicted value *x*-axis, as would be expected if model assumptions were correct. We also tested the residuals for normality, for each location as well as for each location and season separately. All tests confirmed a normal distribution (Shapiro–Wilk's test, $P > 0.05$).

SOURCES OF ENVIRONMENTAL VARIABILITY

In the AR(1) model, environmental variation is included in the error term. A hypothesis is that the residuals vary synchronously among locations and may thereby be caused by a common source of variability (Buonaccorsi *et al.* 2001). We investigated this by testing whether the residual time series were correlated among locations. There was significant synchrony in the residual variation among locations in all seasons. The synchrony was particularly strong in the summer period (Table 3).

To explore whether climate factors could explain part of the density-independent variation we related the residual error with seasonal mean daily temperature or seasonal accumulated precipitation in regression

Table 2. Results of autoregressive analysis for density dependence of population growth rate to the following season $n(t + 1)$ and population size $n(t)$ presented in Fig. 2

Location	Time period considered	Intercept a_s (eqn 2)	Slope b_s (eqn 2)	F^*	n	r^2	P
Ultuna	Spring	2·82	−0·46	14·3	27	0·36	0·0009
	Summer	2·63	−0·64	27·8	27	0·52	< 0·0001
	Autumn	3·97	−1·34	58·2	27	0·70	< 0·0001
	Winter	−4·71	0·12	0·14	26	0·01	0·71
Vreta Kloster	Spring	2·61	−0·39	3·3	20	0·15	0·09
	Summer	2·71	−0·71	8·0	13	0·42	0·02
	Autumn	3·58	−1·22	63·1	13	0·85	< 0·0001
	Winter	−3·50	−0·31	0·7	16	0·05	0·42
Lanna	Spring	2·19	−0·34	2·41	21	0·11	0·14
	Summer	2·36	−0·50	7·2	15	0·36	0·019
	Autumn	3·35	−1·24	42·3	15	0·77	< 0·0001
	Winter	−3·86	−0·02	0·0	15	0·00	0·95
Alnarp	Spring	2·57	−0·69	11·3	19	0·40	0·004
	Summer	2·59	−0·58	7·5	15	0·37	0·017
	Autumn	1·57	−0·68	11·3	14	0·49	0·006
	Winter	−2·77	−0·65	2·75	18	0·15	0·12

*Model *F*-value.
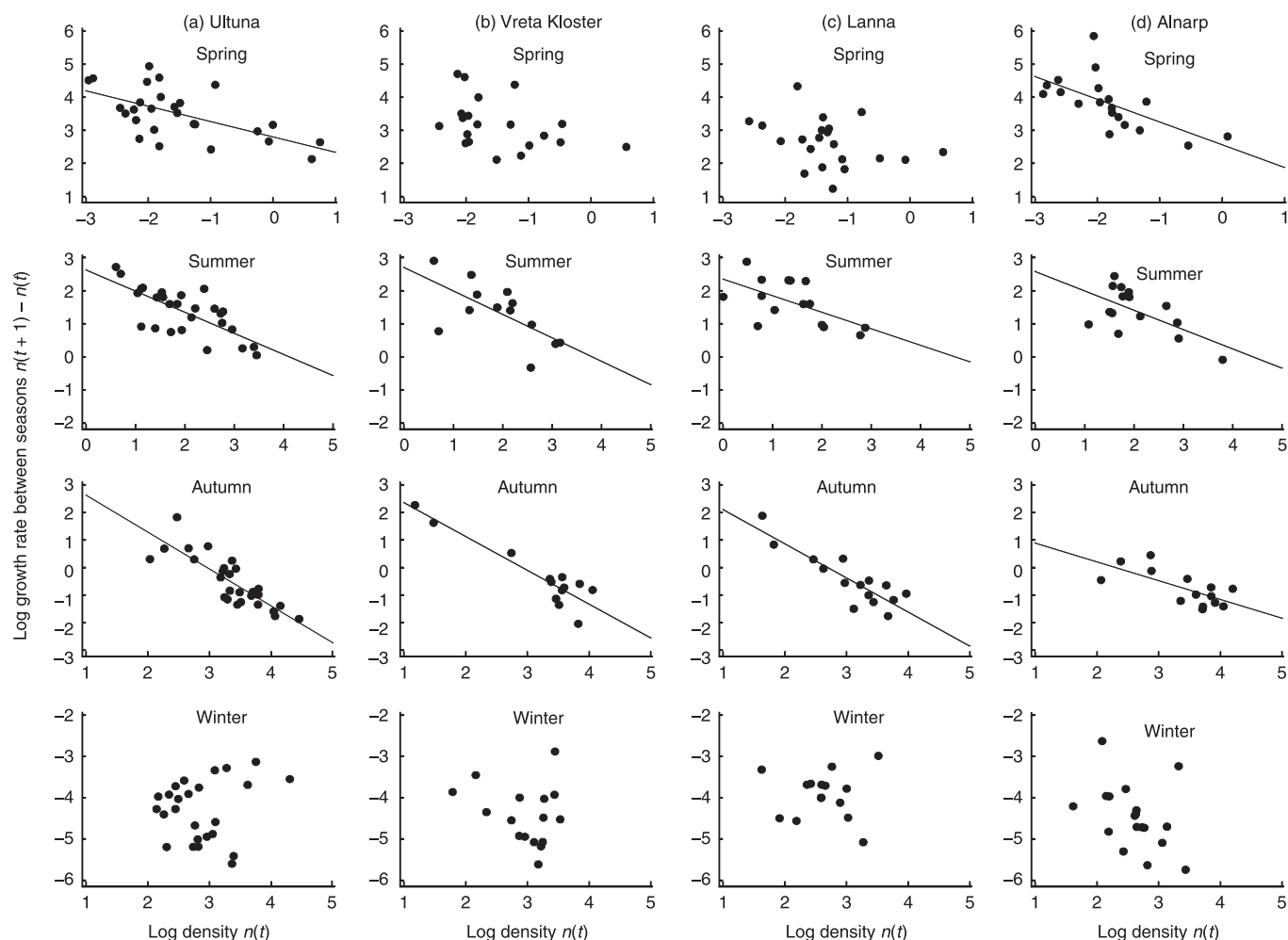
Fig. 2. The fitted seasonal AR(1) models indicating degree of density dependence. Only models with significant slope are fitted to data in the diagrams. The seasonal catches reflects *R. padi* habitat use in a year: the primary woody host in the winter and spring periods, the cereals in the summer and the perennial grasslands in the autumn period.

models. These climate factors explained 1–9% of the variation and were in no case significant (Table 4).

Discussion

We have demonstrated convincing patterns of direct density dependence for *R. padi* that explained a large part of the variability in population fluctuations across a large geographical range. The results largely corroborate previous findings where a high incidence of density-dependent regulation has been detected from time-series analysis of several aphid species (Dixon

Table 3. Correlation among all locations and for each season of residuals from the autoregressive models presented in Table 2

Time period considered	Average correlation	Bootstrapped 95% confidence interval*
Spring	0·59	0·50, 0·69
Summer	0·82	0·76, 0·86
Autumn	0·40	0·14, 0·56
Winter	0·44	0·33, 0·57

*Bootstrapped confidence intervals are based on 1000 samples.

1990; Woiwod & Hanski 1992; Maudsley *et al*. 1996; Sequeira & Dixon 1997; Jarošík & Dixon 1999; Alyokhin, Drummond & Sewell 2005). Setting the temporal resolution of the analysis at the scale of seasons proved fruitful. Clear patterns emerged where the degree of density dependence differed sharply among seasons. As the seasonality in the case of *R. padi* can be translated to yearly habitat use by the aphids, the results clearly show that the relative importance of density-dependent and -independent processes acting on the aphid populations differ among habitats. Starting on the primary host in the spring period, density dependence was significant in two out of four locations. Density dependence then becomes more pronounced in the summer period, when a large proportion of migrant aphids come from cereals. During this period the perennial grasses may also be colonized, but the population size and production of migrants in this habitat are much lower in summer (Wiktelius 1987). The main contribution of migrants to the suction traps during this period therefore comes from cereals, something that is corroborated by strong correlations between cereal field counts and suction trap catches (R. Sigvald, unpublished data). Density dependence was

Table 4. Proportion of residual from the autoregressive models presented in Table 2 that is explained by the seasonal weather variables average temperature and accumulated precipitation. Results are averaged among location (i.e. $n = 4$ in all cases), with SE in parentheses. The proportion of the model explained by each variable was calculated by dividing $MS_{variable}$ with MS_{error}

Time period considered	Accumulated precipitation % explanation by model	Model *P*-value range	Average temperature % explanation by model	Model *P*-value range
Spring	3·9 (2·8)	0·08–0·90	9·3 (3·2)	0·05–0·50
Summer	6·7 (2·6)	0·21–0·50	7·4 (6·0)	0·07–0·77
Autumn	0·8 (0·6)	0·57–0·89	4·9 (1·4)	0·32–0·55
Winter	2·6 (1·4)	0·34–0·97	2·0 (1·5)	0·20–0·97

particularly strong, with a large part of the variation explained and steep negative slopes, *b* (equation 2), in the autumn period, when the aphids are confined to the perennial grasslands. Finally, no indication of density dependence was found in the overwintering egg stage or the primary host in the winter period. From this we conclude that the populations are most sensitive to stochastic variability on the primary host during the winter and spring periods. These stochastically induced fluctuations are, however, balanced by a strong density-dependent regulation in the cereal and grassland habitats in the summer and autumn periods, which reduces variability in population fluctuations.

Analysis of the model residuals demonstrated a high level of synchrony among locations. Also, the seasonal patterns of density dependence were remarkably similar among locations, although separated by, at most, 580 km. This suggests that a great part of both density-dependent and -independent processes operates at large scales. The persistent patterns of density dependence are somewhat surprising considering that both the suction trap catches and regional egg counts do not represent local population samples. This should make it more difficult to detect possible density dependence. If density-dependent regulation occurs at a local scale that is smaller than that of the dispersal, which is highly likely for aphids, then mixing of the populations can obscure signs of density dependence (Hassell 1987). None the less, the patterns of density dependence are remarkably consistent among locations, with a clear signal coming through the multitude of local interactions.

The climate variables failed to explain the residual variation. Again this corroborates previous findings for aphids. Where considered, weather has not had a great importance for determining long-term aphid dynamics (Jarošík & Dixon 1999; Alyokhin, Drummond & Sewell 2005). There is a general contention that host-alternating aphids that are pests on agricultural crops would be sensitive to weather. For instance, one proposed mechanism is that summer rainfall boosts plant production, which would enhance aphid population growth in the grassland habitat (A'Brook 1981; Wiktelius 1987; Maudsley *et al.* 1996). Several studies also show close links between plant productivity and quality to herbivores such as aphids (Waring & Cobb 1992). In the current study, we could not find any evidence

that rainfall (or temperature) influences population growth in the autumn period, or in any other period of the year. We may have failed to detect an influence of weather because we had chosen the wrong population model or the wrong weather variables. Weather might act in a non-linear fashion and thus remain undetected because of the assumption of linearity, and weather can have a time-lagged effect on population response (Benton, Plaistow & Coulson 2006). Furthermore, seasonal averages may not adequately describe important climatic drivers, because catastrophic events such as cold spells or heavy rainfall or winds may greatly affect population abundance. That would, however, fail to explain the large-scale synchrony found in the current study. It is also important to remember that species' interactions can give rise to stochastic abundance fluctuations (Ives 1995), which demonstrates the importance of monitoring the interacting species and not only the pest aphid and the weather in isolation.

Although we have demonstrated convincing patterns for direct density-dependent regulation from census data, the underlying mechanisms operating on population growth remain unexplained. Density-dependent regulation of a herbivore population is generally caused by the trophic levels above or below the herbivores: from below by the quality and availability of the host-plants, from above by one or several predators and/or pathogens (Lawton & McNeill 1979), or as a combination of these forces (Denno *et al.* 2002). The population density of non-host-alternating tree-dwelling aphids has been demonstrated to depend mainly on resource competition and host-plant quality (Dixon 1977; Sequeira & Dixon 1997). These species are strongly linked to their respective woody hosts and cannot be immediately compared with a host-alternating aphid species that annually switches among hosts and habitats, with no tight relationship to a specific host species, and that utilizes a huge resource provided by agricultural crops and grasslands. Still, there is a possibility that a large abundance of the primary aphid host *P. padus*, and subsequent access to grasslands and 1×10^6 ha of high-quality cereals in south-central Sweden (Statistics Sweden 2004), allows for a great population build up of *R. padi* (Leather, Walters & Dixon 1989). This large aphid population may subsequently not be supported by a conservatively estimated area of $0·7 \times 10^6$ ha of

grasslands available to the aphids in the late summer (Statistics Sweden 2004). The late summer grasslands are probably of lower quality to the aphids compared with the cereals and may act as a sink. However, if this scenario is correct, late summer rainfall would be expected to boost grass productivity and aphid population growth. Exploring mechanisms for aphid population regulation, the possibility that the aphid population may consist of separate clones specialized on different plant hosts, needs to be taken into account (Vialatte *et al.* 2005).

Alternatively, predators exert top-down regulation of the aphid populations. Several predator species have been demonstrated to suppress aphid growth (Schmidt *et al.* 2003; Snyder & Ives 2003; R. Bommarco, unpublished data). In Sweden, predators have been demonstrated to suppress *R. padi* populations both on the primary host in the spring (R. Bommarco, unpublished data) and on cereals (Holland & Thomas 1997; Östman, Ekbom & Bengtsson 2001). These studies, however, do not provide evidence of density-dependent regulation of the aphids. Natural enemies of aphids, such as some parasitoids, must be able to respond numerically in order to regulate an aphid population (Rauwald & Ives 2001) and possibly also track the aphids as they move among habitats in the landscape, such as ladybird beetles do (Hodek 1973). Generalist predators, such as carabids and spiders, may, however, also be important control agents, especially perhaps when acting in combination with more specialized natural enemies (Dwyer, Dushoff & Yee 2004). Abundance time series of natural enemies combined with experiments in each habitat visited by the aphids would be needed to explore large-scale effects of aphid predators.

Deterministic density dependence in census data is not in itself evidence of regulation in nature. However, statistically detected density dependence in long-term time-series data is consistent with the outcome of biological regulatory processes (Royama 1992). Experimental manipulations are needed to provide ultimate evidence. There is a paucity of studies examining regulation of crop pests in multiple habitats taking a comprehensive approach across the year and at a landscape scale (Bianchi, Booij & Tscharntke 2006). Pest management research traditionally focuses on pest suppression in the crop, although it is well known that many pests utilize multiple habitats. The current study provides an example where regulation of the pest is likely to take place outside as well as inside the crop habitat. An important next step will be to explore the combined influence of plant resource abundance and quality, and predators in the non-crop habitats utilized by the pest. The analysis of the census data indicates that, for *R. padi*, such experiments should be performed in perennial grasslands.

CONCLUSIONS

The results presented here reveal that density-dependent regulation of aphid populations is taking place. Density dependence is direct, acting within the year, but varies seasonally, depending on the aphid habitat use during the year. Density dependence was particularly strong outside the crop habitat in the late summer grasslands and was also consistently found in the early summer cereals. The mechanisms causing these patterns are not well understood, making it difficult to provide specific recommendations on pest management strategies. The current study does, however, indicate that pest management needs to involve a landscape-level approach, taking into account mechanistic information about the plant, herbivore and predator interactions in multiple habitats visited by the herbivorous pest. In situations where plant quality is the main driver for aphid population growth, management should focus on factors such as landscape-level nitrogen input (Waring & Cobb 1992) or grassland management and species composition. Landscape composition has also been shown to enhance predator abundance and activity (Bianchi, Booij & Tscharntke 2006). However, the actual effect on the pest population of naturally occurring predators is poorly investigated (Bianchi, Booij & Tscharntke 2006) and more information on the mechanistic links between predators and prey are needed to devise efficient strategies for enhancing biological control by predators (Prasad & Snyder 2006).

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