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AN OVERVIEW OF THE FUNCTIONING OF *SITOBION AVENAE* POPULATIONS AT THREE SPATIAL SCALES IN FRANCE

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Dedryver C.A., Fiévet V., Plantegenest M., Vialatte A. – An overview of the functioning of *Sitobion avenae* populations at three spatial scales in France.

In this paper we give 3 snapshots of our recent work on *S. avenae* at field, landscape and country scales.

From April to June wheat fields are continuously colonized by winged *S. avenae* and previously established colonies experience high extinction rates. This leads to changes in spatial distribution of aggregates of aphids and to a progressive spatial homogenisation of the populations in fields, and highlights the role of spring immigrants in the field dynamics of *S. avenae*.

In the surrounding landscape, the *S. avenae* populations on cultivated cereals (wheat, maize, barley) do not differ genetically. Conversely, aphids from weed margins and pastures (mostly on Poaceae) clearly differ from those on cereals, indicating a low level of gene flow between the 'uncultivated' (mostly perennial) and cultivated system (annual). Consequently weeds and pasture grasses are probably poor sources of *S. avenae* for further infestation of cereal fields.

The role of surrounding crops and weeds as a source of aphids infesting wheat was assessed by stable isotopic ratios and population genetic tools. In autumn, up to the beginning of October, most *S. avenae* landing on wheat originated from maize and after this from cereal volunteers. In spring the influx from surrounding cereal volunteers varied between years, but uncultivated Poaceae played a minor role.

At country scale on cereals, clonal reproduction and parthenogenetic overwintering prevails everywhere in France, but there is a trend toward increasing sexuality northward. The weak genetic differentiation of the regional populations on cereals and the presence of many identical genotypes in most of the regions sampled confirm the high dispersal ability of *S. avenae*. The high occurrence of widespread genotypes in multiple copies, belonging to the same genetic pool, which persist over several years in France and other countries in Europe, indicates a homogenising effect of selection by millions of hectares of cereals

KEY WORDS: grain aphid, field scale, landscape scale, country scale, forecasting models.

INTRODUCTION

Sitobion avenae, the grain aphid, is one of the most potentially damaging pests on cereals in Europe; directly by feeding on plants and indirectly by transmitting viruses (PLUMB, 1995). However, its build-up on wheat during spring varies from year to year and high levels of infestation may have become less frequent since the seventies, at least in the west of France (Figure I). Consequently, cereals should now only be sprayed with aphicides when indicated by decision tools based on a sound knowledge of cereal aphid population dynamics. *S. avenae* population dynamics at both the field scale (DEDRYVER 1978; CARTER *et al.*, 1982; ENTWISTLE & DIXON 1986; DE BARRO *et al.*, 1994; PLANTEGENEST *et al.*, 1996) and regional scale (HARRINGTON *et al.*, 2004) was intensively studied in the past, leading to forecasting tools (CARTER *et al.*, 1982; PIERRE & DEDRYVER 1984; PLANTEGENEST *et al.*, 2001). Moreover, several studies of *S. avenae* population genetics gave a better assessment of its dominant modes of reproduction in different climatic areas of Europe and its migratory capacity (LOXDALE *et al.*, 1985; DE BARRO *et al.*, 1995; SIMON *et al.*, 1999, PAPURA *et al.*, 2003; LEWELLYN *et al.*, 2003; LEWELLYN *et al.*, 2004).

However, there remained several serious gaps in our knowledge of *S. avenae* population dynamics at field and

country scales, and the role of the landscape surrounding crops in the cereal growing areas in France.

At the field scale, (i) most emphasis in the past was given to the study of population growth in time, neglecting spatial processes, and (ii) aphid immigration into fields was most often thought to occur only over a short period and initiate a temperature-dependant increase in the numbers of wingless morphs. There was a need to take

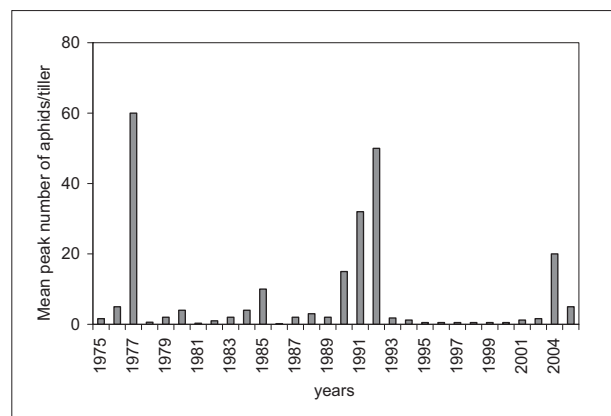


Figure I – Maximum number of *S. avenae* per wheat tiller in the Rennes area, from 1975 to 2005 (mean of 2-15 fields, depending on the year).

into account the role of the whole period of crop infestation by winged aphids in the spatial and temporal dynamics of *S. avenae* in cereal fields.

At the country scale, there was little knowledge of how the aphid over-wintered, i.e. of between region differences in reproductive modes, and consequently of the role of local overwintering versus immigration from afar on the population dynamics in spring.

Finally, little attention was given to the environment surrounding the fields, the 'landscape,' as a shelter and short distance source of the migrants colonizing neighbouring fields.

This paper presents short overviews of the results recently obtained at these three different spatial scales and the new research questions arising from them.

1. THE ROLE OF THE CONTINUOUS INPUT OF ALATES DURING THE SEASON AND THE NUMEROUS FAILURES IN COLONY ESTABLISHMENT IN SHAPING THE SPATIAL PATTERN AND TEMPORAL CHANGES IN THE DISTRIBUTION OF *S. AVENAE* IN FIELDS

The daily input of winged *S. avenae* into a wheat field was assessed from April to July in 2003 and 2004, using a vacuum sampler (VIALATTE *et al.*, 2007). Three important results were obtained. First, aphids continuously colonized the field for a period of at least two months, from mid-April to mid-June (after which it became impossible to separate immigrants from winged aphids produced in the field). Second, the between-year input of alates differed markedly. The average was 0.25 aphids/m²/day and the maximum 5 aphids/m²/day in 2003, and 1.25 aphids/m²/day and 15 aphid/m², respectively, in 2004. Finally, daily suction trap catches and daily input of *S. avenae* were highly correlated in 2003, but not in 2004, which suggests that a part of the input of aphids in 2004 was not recorded by the suction trap catches, i.e. it probably originated from the surrounding environment.

In 2004, the spatial distribution pattern of cereal aphids in a winter wheat field and its temporal changes during the growing season were investigated (FIÉVET *et al.*, 2007).

Local extinction and colonisation rates remained high during wheat field colonisation suggesting a high population turn-over. During this period, between 20 and 60% of the colonies disappeared after one week but were continuously replaced by others founded by new immigrants. This accords with previous genetic studies, which show a rapid within-field replacement of aphid genotypes in crop fields (FENTON *et al.*, 1998; HAACK *et al.*, 2000), and the few previous works on the spatial dynamics of *S. avenae* in wheat (WINDERS *et al.*, 1999). Consequently, at the field scale, aphid distribution was temporally and spatially heterogeneous, with the main aggregates 'moving' in space and time and a progressive decline at the end of the sampling period.

2. THE CONTRIBUTION OF THE SURROUNDING LANDSCAPE TO FIELD INFESTATION DEPENDS ON THE CROPPING SYSTEM AND THE POSSIBILITIES FOR *S. AVENAE* TO OVER-WINTER THERE.

We used stable isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios to infer the natal host plant of individuals of *S. avenae* colonising wheat fields in autumn (VIALATTE *et al.*, 2006). The $\delta^{13}\text{C}$ ratios depend on the photosynthetic pathways (C₃ or C₄ type)

used by plants and these differences are passed on to herbivores. In agro ecosystems, the use of fertilizers or land-use practices resulting in ammonification induces differences in the nitrogen ratios ($\delta^{15}\text{N}$) of plants, which can also affect $\delta^{15}\text{N}$ in herbivores. We showed that among the numerous plant sources of *S. avenae*, maize, which is the only C₄ plant intensively grown in Western France, provided most of the *S. avenae* caught by suction traps or landing on wheat in fields early in autumn (October), whereas in November, after the maize harvest, colonizers originated exclusively from C₃ plants (cereal volunteers and/or pasture and wild grasses).

We have developed an unvalidated bayesian model for identifying aphids from different C₃ plants, which identifies aphids from the Poae tribe with an estimated error of 14%. Applied to field samples this model indicates that in western France the Poae (e.g. rye-grass and many other pasture grasses) account for very few of the *S. avenae* colonizing wheat compared to Triticeae (cereal volunteers), particularly in spring.

Population genetic studies revealed two genetic clusters corresponding respectively to populations from cereals (early autumn sown Triticeae and volunteers) and field margins and pastures (Poae and wild Avenae) in local over-wintering populations of *S. avenae*, collected in 2003 and 2004. A similar analysis of winged aphids colonising wheat from April to June revealed that in 2003 most of the aphids belonged to a third genetic cluster not present in the aphid populations over-wintering in the surrounding landscape, indicating that in that year the colonising aphids came predominantly from non-local sources. In contrast, in 2004 most of the colonising aphids came from local cultivated sources (Triticeae) with a few from local field margins and non local sources (VIALATTE *et al.*, 2007). This is associated with differences in the winter climate in the two years, harsh in 2003, with few parthenogenetic morphs of *S. avenae* over-wintering locally, and mild in 2004, with the possibility that many *S. avenae* over-wintered locally.

3. LOW GENETIC DIFFERENTIATION OF *S. AVENAE* POPULATIONS FROM CEREALS ACROSS LARGE TEMPORAL AND SPATIAL SCALE COULD RESULT FROM A HIGH LEVEL OF MIGRATION AND SELECTION BY MILLIONS OF HECTARES OF CEREALS.

Changes in the genetic structure and genotypic variation of *S. avenae* collected from cereal crops in Northern France were examined by analysing variation at five microsatellite loci across several years and seasons (DEDRYVER *et al.*, 2008). The very low F_{ST} between populations indicated little regional and temporal differentiation. Repeated genotypes, significant heterozygote deficits, positive F_{IS} values and frequent linkage disequilibria were found in nearly all samples, suggesting an increasing incidence of sexual reproduction in *S. avenae* populations from south to north (Table 1). However, asexual reproduction occurs in all regions. Theoretical models predict that regional differences in climate will result in the same pattern in the incidence of sexual and asexual reproduction in *S. avenae*. In contrast with the little change in allelic frequencies, genotypic composition varied substantially in time and, to a lesser extent, in space. An important part of the changes in genotypic arrays was due to the variation in frequency distribution of common widespread genotypes (Figure II), belonging to the same genetic pool, which persist for

Table 1 – Variations in the reproductive mode of *S. avenae* in France.

	Nord-Pas de Calais	Champagne	Normandie	Bretagne	Midi-Pyrénées	Provence
% Holocyclic clones ⁽¹⁾	24	8	20	17	0	0
% males in field populations ⁽²⁾	17	26	7.5	2.5	<1	–
% mating females in field populations ⁽²⁾	2	2.5	0	0	0	–
Range of F_{is} in field populations ⁽³⁾	0.11-0.33	–	0.17-0.25	-0.3-0.17	0.05-0.16	–

⁽¹⁾ Percentage of holocyclic clones in regional populations based on inducing field collected aphids to produce sexuals in the laboratory (1993-1995).

⁽²⁾ Percentage of clones producing sexual morphs after natural induction (1993-1995).

⁽³⁾ Range of variation in F_{is} in regional *S. avenae* populations (1993-2003). High F_{is} implies heterozygote deficits and importance of sexual reproduction (because of endogamy in *S. avenae*).

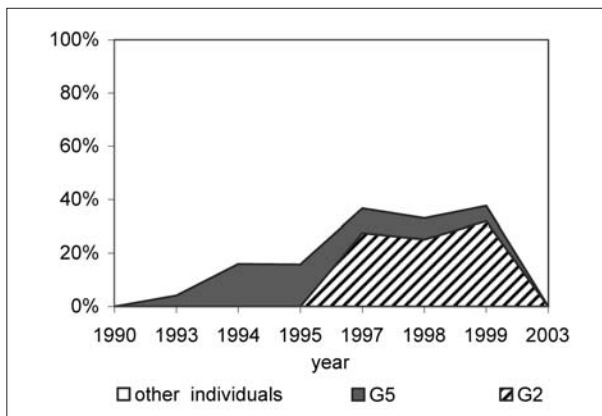


Figure II – The percentage incidence from 1990 to 2003 of two abundant *S. avenae* clones in local populations on cereals and maize near Rennes.

several years and have been detected in other countries (LLEWELLYN *et al.*, 2004). Genotypic composition also varies with climate, as genotypic diversity in spring is significantly correlated with the severity of the previous winter and autumn. We propose that this overall genetic homogeneity of *S. avenae* populations across large temporal and spatial scales is the result of two forces: i) this aphid's great migratory ability and ii) selection pressure of millions of hectares of cereals (mostly wheat) bred from a narrow genetic base.

CONCLUSION

At a field scale winged immigrant input occurred throughout the season and influenced the maintenance of *S. avenae* populations in wheat fields. If this is confirmed then the classical concept of the initial field infestation as the most important factor involved in population growth needs to be modified (CARTER *et al.*, 1982; PIERRE & DEDRYVER, 1984; PLANTEGENEST *et al.*, 1996). In this case, future predictive models of population dynamics will have to consider the possibility of continual immigration by winged individuals, for example by assessing their abundance using suction trap samples (HARRINGTON *et al.*, 2004). Another concern is the strong rate of colony disappearance and its consequences for the size of field populations: if it is the rule, it could explain why there are few outbreaks of *S. avenae* and

highlights the need to determine the causes of the decrease in their incidence.

Studies at the 'landscape' scale indicate that changes in time of spatial heterogeneities (e.g. crop rotation, permanent pastures and hedges) have a role in the local dynamics of a pest insect and consequences for management. However, there are no tools for assessing the distance the aphid migrates and quantifying the role of the surrounding field environment in *S. avenae* dynamics.

Population genetic studies at the country level show (i) that *S. avenae* reproduces both asexually and sexually in France with probably more sex in the north, (ii) and that in any case and in most years, parthenogenetic overwintering is numerically the most important and drives the aphid dynamics at this scale, because of the high migratory capacity of the grain aphid. Further research is needed to disentangle the role of migration, selection and drift in *S. avenae* population homogenisation at the scale of the French cereal growing area.

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