

Influence of the surrounding landscape on the colonization rate of cereal aphids and phytovirus transmission in autumn

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Abstract Ecological control has often focused on factors enhancing control of pests by their natural enemies, while factors reducing the colonization rate of crops by pests have been comparatively neglected. We present an approach to assess landscape influence on the intensity of wheat colonization by a major crop pest, the aphid *Rhopalosiphum padi*. We used trays containing wheat seedlings to monitor field colonization by *R. padi* and barley yellow dwarf viruses' transmission in two areas in France in autumn. We assessed the influence of landscape components likely affecting aphid colonization, i.e. maize and grasslands as source of migrants on the number of

aphids landing per tray, as well as the host plant of origin and the viruliferous potential of migrants. During the survey, maize was the main source of migrants. Virus transmission was detected in a few cases (4 % positive assays). Colonization was increased by the presence of maize, but reduced by the presence of grasslands at the landscape scale considered here (i.e. at a radius of 1000 m). Our study contributes to a better understanding of disease dynamics in agricultural landscapes. By identifying features of the landscape that surrounds fields and affects these dynamics, growers can develop more efficient crop protection strategies relying on habitat manipulation and rational use of pesticides.

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Key message

- The rate of crop colonization by vectors determines pathogen-induced damage to crops. Little is known on the influence of landscape composition on aphid colonization and virus transmission rate.
- Both local and landscape variables significantly affect *Rhopalosiphum padi* colonization rate of wheat seedlings. Maize was the main source of migrants, and few aphids were viruliferous. Colonization rate increased with crop areas and decreased with grasslands.
- Similar studies conducted at a multispecies scale could contribute to a better understanding of pathogen colonization.

Introduction

Agricultural intensification in Europe has led to both an increase in the use of chemicals and a reduction in the surface covered by natural or semi-natural habitats (mainly permanent pastures) (Bianchi et al. 2006) and has resulted in a dramatic loss of farmland biodiversity (Krebs et al. 1999; Donald et al. 2001; Stoate et al. 2001; Geiger et al. 2010). In response, European countries promoted agricultural changes reducing environmental impact, focusing on reducing the use of pesticides (Bonnieux et al. 1998; Birch et al. 2011). Agroecology that relies on landscape or ecosystem management and alternative agricultural practices aim at reducing the risk of pest outbreaks, either by enhancing control of pests by their natural enemies or by diminishing the rate of crop colonization by pests. Hence, to design efficient strategies of landscape manipulation, a clear understanding of landscape properties influencing pest risk is required (Ricci et al. 2009).

In vector-transmitted pathogens, the rate of crop colonization by vectors is a major determinant of pathogen-induced damage to crops (Fabre et al. 2003). Knowledge of the main source of migrants aids the comprehension of vector-transmitted plant disease dynamics (Carrière et al. 2014) as host plants vary in their importance as pathogen reservoirs and the proportion of viruliferous migrants will differ according to the host plant of origin. The effect of landscape structure on natural enemies and dynamics of pests has been intensively studied, highlighting the role of semi-natural elements on pest regulation (reviewed in Bianchi et al. 2006; Veres et al. 2013; see also Tscharrntke et al. 2008; Chaplin-Kramer et al. 2011). Landscape factors influencing the particular step of crop colonization by pests have received, by contrast, less attention (Wissinger 1997; Irwin et al. 2007; Parry 2013). Understanding the influence of landscape composition on crop colonization rate is therefore critical to improve pest management strategies (Wissinger 1997; Bianchi et al. 2006; Carrière et al. 2014). This influence is often species or taxa specific and habitat's functionality should be considered when selecting landscape variables and spatial scales to test to reduce the number of parameters and collinearity in the models and to help interpreting those (Veres et al. 2013). In aphids, the abundance of source habitats in the landscape could possibly influence colonization rate at scales up to hundreds of km due to their long-range flight capacity (Irwin et al. 2007). However, it is now recognized that there is a continuum from local flight (i.e. trivial flight, Favret and Voegtlin 2001) to migration *sensu stricto* (i.e. innate behavioural migration) and that winged aphids mainly disperse over short distances (Parry 2013). While aphid flight is mainly passive, termination of aerial transport is

usually directed by aphids (Irwin et al. 2007; Parry 2013). For most pest species, the amount of ground cover present is inversely proportional to aphids landing rates (Irwin et al. 2007). It has been shown that a greater number of aphids landed in agricultural plots rather than in semi-natural habitats (Favret and Voegtlin 2001).

Rhopalosiphum padi (Linnaeus, 1758) is one of the most damaging cereal pests in Europe, colonizing many Poaceae species (Leather et al. 1989) and *Prunus padus* trees as its primary host. Its high dispersal abilities (Loxdale and Brookes 1988; Nottingham et al. 1991; Delmotte et al. 2002) make *R. padi* one of the main virus vectors responsible for the barley yellow dwarf (BYD) disease's transmission to small-grain cereals in autumn (Leclercq-Le Quillec et al. 1995). Aphid and virus reservoirs in European landscapes include small-grain cereals and maize as well as perennial grasses from pastures and meadows (Dedryver and Harrington 2004). Habitat structure (landscape openness and heterogeneity) may influence the rate of virus transmission, aphids preferentially landing on crops rather than in semi-natural habitats (Favret and Voegtlin 2001). On another hand, Fabre et al. (2005) showed that the higher the proportion of small-grain cereals relative to maize, the higher the proportion of viruliferous aphids in spring and summer. Studies conducted during autumn on *R. padi* and another grain aphid *Sitobion avenae* (F.) suggested that maize could be an important source of aphids that colonize winter cereal fields in the early autumn in northern France, acting as a bridge crop when wheat is not available (Vialatte et al. 2006; Gilabert et al. 2014). On the other hand, it has been previously shown that pasture and meadows are summer refuges for *R. padi* and BYD viruses (Barro and Wallwork 1992). Taken together, these results suggest that maize is likely an important source of vectors in BYD epidemics, but a poor virus reservoir, while grasslands could be source of vectors and of viruses.

In this study, we investigated the influence of landscape composition on winter wheat colonization by the aphid *R. padi* and BYD epidemics in autumn. With regard to BYD epidemiology, autumn appears to be the most critical period in western France (Leclercq-Le Quillec et al. 2000). Indeed, autumn corresponds to the main period of *R. padi* flight activity (Hulle et al. 1994) and so determines the intensity of primary infections. In addition, infected host plants often show a lower winter survival rate (Paliwal and Andrews 1990; Collin et al. 1997), such that autumnal infections have a greater impact on yield than spring ones. We focused on the influence of (1) the potential source crops in the landscape (maize and grasslands at the period of sampling) and (2) the local habitat to assess *R. padi* landing preferences. We monitored colonization of a

network of trays containing sentinel wheat seedlings over a four-week period in two contrasted areas of western France, one of which was a cereal-growing and the other was a mixed crop- and livestock-farming area. This allowed to cover a large gradient of landscape composition regarding potential source crops. We used stable isotope analyses to track the likely origin of migrants and empirical and correlative analyses of landscape composition around experimental trays. We hypothesized that most *R. padi* migrants would originate from maize and that local colonization intensity would increase with maize proportion in the landscape. In addition, we predicted that the proportion of viruliferous aphids would be higher in areas with a larger proportion of important virus reservoirs such as grasslands and small-grain cereals and in the region with an intensive cropping system with a high ratio of area sown with small-grain cereals vs. the area sown with maize.

Study areas and methods

Study areas

The study was carried out in the autumn 2007 in two western France study sites: “Zone Atelier Armorique” (48°36'N, 1°32'W; <http://osur.univ-rennes1.fr/zoneatelier-armorique/>), hereafter referred as ARM, and “Zone Atelier Plaine et Val de Sèvres” (46°11'N, 0°28'W; <http://www.zaplainevaldesevre.fr/>), hereafter referred as PVS (Fig. 1). In both study sites, land use is assessed annually based on direct field observations and/or aerial photographs and mapped onto a geographical information system (ArcGis 9.2—ESRI Redlands, CA, USA). These two study sites were selected to cover a large gradient of proportion of maize and grasslands. Indeed, the ARM study area is dominated by hedged farmland, woodlands and permanent grasslands (Fig. 1), while the PVS study area is mainly occupied by intensive cropping systems dominated by winter cereals (Fig. 1).

Sampling design

We monitored the colonization of sentinel wheat plants by aphids using plastic trays divided into 130 cells, each containing a single wheat seedling (cv Orvantis) sown in compost (FERTISS®, Fertil S. A., France) (Fig. 2). A total of 39 trays (19 and 20 in PVS and ARM, respectively; Fig. 1) were placed on bare soil at the edge of fields of maize (respectively, 5 and 2 trays in ARM and PVS), grasslands (8 in each site) or small-grain regrowths (respectively, 7 and 9 trays in ARM and PVS), hereafter referred as the “crop type”. The survey was carried out during 4 weeks between the 30th of September and the

29th of October 2007, as autumn usually corresponds to the main *R. padi* flight activity in western France (Hulle et al. 1994). At the end of each week, the number of colonized seedlings (infested with winged aphids or nymphs) was counted for each tray and all of the 130 seedlings were removed and replaced with new ones. Since we never observed more than one winged aphid per seedling, we assumed that all nymphs found on a seedling were the offspring of a single-winged female that colonized the wheat sentinels before giving birth and thus that the number of colonized seedlings is a reliable proxy for the number of migrants. All colonized seedlings were kept individually in a greenhouse for a further week to allow viruliferous aphids to transmit BYD viruses (BYDV; Fig. 2). Winged aphids were then stored at −20 °C until isotopic analyses were performed. After a further week in a glasshouse allowing virus multiplication, seedlings were stored at −20 °C until their use in virus detection assays.

Origin of migrants

The abundance ratio in natural carbon isotopes ($\delta^{13}\text{C}$ ratios) differs according to the photosynthetic pathways (C_3 or C_4 type) used by plants (Mole et al. 1994). These differences are transmitted to the next trophic levels (Boecklen et al. 2011), allowing the researcher to distinguish, for example, between insects feeding on C_3 and C_4 plants. As the C_3 or C_4 signature persists for at least 14 days in cereal aphids, the analysis of their stable isotopic ratios of carbon allows the determination of the photosynthetic pathway of the host plant on which they developed (Vialatte et al. 2006). C_4 photosynthetic grasses are mostly restricted to tropical and subtropical grasslands or to temperate North and South American and African grasslands and are absent or in a small fraction outside these areas (Still et al. 2003; Edwards et al. 2010; Osborne et al. 2014). In France, only two crop species have a C_4 photosynthetic pathway: maize and sorghum, respectively, comprising 97 and 3 % of the C_4 surface area (source: DISAR 3.11; available at <https://stats.agriculture.gouv.fr/disar/>). C_4 weeds, such as *Sorghum halepense*, are rare and restricted to the Mediterranean south. During the period of the survey, annual crops with a C_3 isotopic signature, such as wheat or barley, were not available, as they had been harvested in the previous July, but a small part of their land was covered by cereal volunteers, and C_3 plants were mostly represented by grasslands. We therefore could distinguish aphids that developed on maize from those that developed on grasslands.

Eighty-eight winged aphids (59 from ARM and 29 from PVS) were analysed for their isotopic ratios. Winged aphids were freeze-dried for 24 h and then placed individually in tin capsules. Abundance ratios of natural

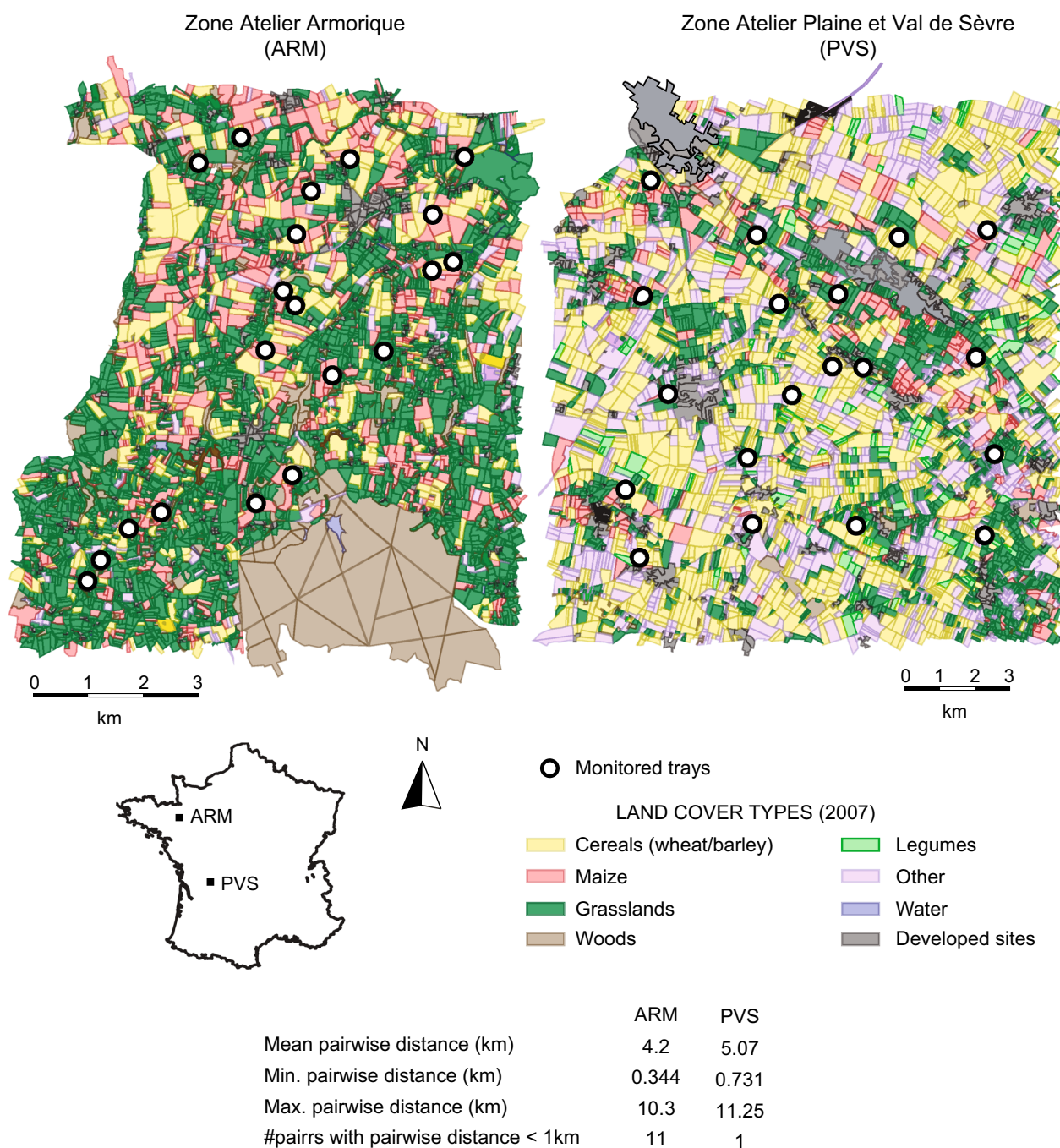


Fig. 1 Maps of the two studied areas indicating land use in spring 2007. The mean, minimum and maximum distances between trays within each site are given

stable isotopes of carbon ($\delta^{13}\text{C}$) were measured by continuous-flow isotope-ratio mass spectrometry (CF-IRMS) using a Europa Scientific ANCA-NT 20-20 Stable Isotope Analyser with ANCA-NT Solid/Liquid Preparation Module (Europa Scientific LTD, Crewe, UK). Isotopic ratios were expressed in thousandths, as the difference, δX , between the isotopic ratio in a sample and that of an

arbitrary standard (Pee Dee Belemnite for carbon). The analytical precision achieved for leucine standards analysed along with the samples was 0.2 ‰. Following Vialatte et al. (2006), we considered the host plant of origin of an aphid with a $\delta^{13}\text{C}$ ratio lower than -22 was a C3 plant, whereas an aphid with a $\delta^{13}\text{C}$ ratio higher than -20 was considered to have developed on a C4 plant.

Colonization of sentinel wheat seedlings

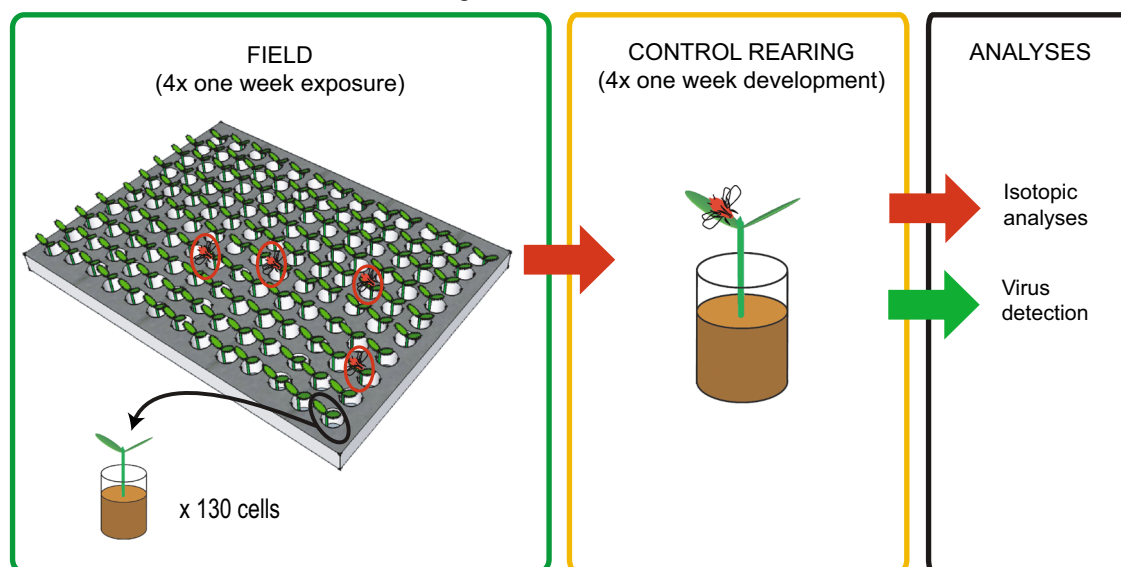


Fig. 2 Study design

Virus detection

Leaf samples of each seedling were tested for the presence of *Barley yellow dwarf virus*—PAV (the most frequent BYD virus in crops in Western Europe) using a triple antibody sandwich (TAS) ELISA (enzyme-linked immunosorbent assay) protocol. Samples were extracted by grinding one leaf with 200 μ l of general extraction buffer. We then followed the ADGEN TAS-ELISA protocol (Adgen, Neogen Europe LTD, Ayr, Scotland) for virus detection. Briefly, polyclonal antibodies bound to the surface of a microtitre plate captured the antigen of interest, and a rat monoclonal antibody was used to detect the antigen. An anti-species antibody-enzyme conjugate was then used to detect the monoclonal antibody. The colorimetric reaction was incubated for 2 h at room temperature before the absorbance was read using a spectrophotometer (Titertek Multiskan, MCC). Typically, a sample is considered positive when the absorbance value is greater than three times that of a negative control. However, in our case, absorbance values of negative controls were often close to 0. Therefore, a sample was considered positive when its absorbance value was greater than 0.1.

Landscape influence on aphid colonization

Landscape variable selection

In order to specifically test the influence of maize and grasslands, we calculated their proportion in circular buffer

zones of 1000 m of radius centred on the monitored trays. The distance was set to 1000 m to avoid artificially large correlation due to overlapping buffers (see Fig. 1). Pairwise Pearson correlation between the proportion of maize and grasslands at 1000 m was low ($r = 0.36$; $p < 0.01$), allowing us to include both variables in a single model without having collinearity issues (Dormann et al. 2013).

Statistical model

We explored how aphid colonization was influenced by local and landscape variables using Bayesian mixed models assuming a Poisson distribution for count data as implemented in the R package MCMCglmm (Hadfield 2010; Hadfield and Nakagawa 2010). Two random intercepts were included in the model: the field identity to account for the sampling design ($N = 39$ levels) and an observation-level random effect to account for overdispersion. Response variable was the number of seedlings colonized. The week of observation ($N = 4$ levels) was included as a fixed factor. To investigate local influence on aphid colonization rate, the crop type of the field where trays were set was included in the model ("crop type", three levels: grassland, maize and small-grain volunteers). Scaled proportion of maize and of grasslands at 1000 m (Ma_{1000m} and Gr_{1000m}) was finally included in the model. We ran 100,000 iterations with a burn-in period of 10 000 and a thinning interval of 100 and using uninformative priors.

Results

Aphid colonization

In total, during the 4 weeks of collection, aphids were observed on 494 seedlings [2.4 % of the total number of seedlings; 289 (2.8 %) in ARM and 205 (2.1 %) in PVS]. *R. padi* was the most abundant aphid species that settled on our sentinel wheat: of the 494 seedlings found with aphids, 466 (94.3 %) were colonized by *R. padi* and 28 (5.7 %) by other species (mainly *S. avenae* and *Metopolophium dirhodum*). Considering *R. padi* only, we found 148 seedlings with winged aphids and 318 with only nymphs. Over the 4 weeks, we collected at least one aphid from each of the monitored trays, with the exceptions of one in ARM and one in PVS.

Origin of migrants

Among the 88 analysed *R. padi*, only one exhibited an ambiguous isotopic signature and could not be assigned as having originated from a C3 or C4 plant. The majority of migrants originated from C4 plants in both ARM and PVS (ARM: $N_{C3} = 6$ and $N_{C4} = 52$; $\chi^2 = 40.68$, $df = 1$, $p < 0.001$; PVS: $N_{C3} = 7$ and $N_{C4} = 22$; $\chi^2 = 23.8$, $df = 1$, $p < 0.001$). In addition, proportions of aphids with a C3 or a C4 signature did not differ significantly either between ARM and PVS (GLM assuming a binomial distribution; $\chi^2 = 2.74$, $df = 1$, $p = 0.1$) or between the crop type (GLM; $\chi^2 = 3.77$, $df = 2$, $p = 0.15$).

Proportion of viruliferous migrants

A total of 437 seedlings (256 in ARM and 181 in PVS) were tested for BYDV-PAV (57 colonized seedlings were too small to be analysed). The proportion of positive assays was significantly higher in PVS ($N = 17/181$) than in ARM ($N = 6/256$; GLM assuming a binomial distribution; $\chi^2 = 10.63$, $df = 1$, $p = 0.001$). In PVS, 12 trays contained one to three seedlings with BYDV-PAV; in ARM, 5 trays contained one or two seedlings with BYDV-PAV. All positive seedlings had been colonized by the aphid species *R. padi*.

Of the 88 seedlings colonized by a winged aphid analysed for host plant origin, BYD tests were positive for eight seedlings. This proportion was similar to the proportion found in the entire population of aphids. Of these eight seedlings, seven were colonized by an aphid with an isotopic signature of a C4 native host plant and one with an aphid originating from a C3 plant.

Maize and grasslands influence at the landscape scale

Bayesian mixed models indicated a significant and strong effect of the sampling week (Fig. 3) with a colonization rate decreasing with time and a significant local effect, with less migrants in trays located at the edge of grasslands compared to the other two field types, maize and cereal volunteers. There was a global positive effect of the proportion of maize and a negative effect of grasslands on the rate of colonization by *R. padi* (Table 1; Fig. 4).

Discussion

In this study, we examined the dynamics of colonization of sentinel wheat seedlings by an aphid species vector of plant viruses. We used an approach that allows investigation of the surrounding landscape's influence on the colonization rate of plants by aphids, as well as determination of their host plants of origin and viruliferous potentials. We found landscape composition had significant effects, both at local and larger scales, on the number of aphids that settled on wheat seedlings. As some were BYDV carriers, landscape composition may also influence disease dynamics (Carrière et al. 2014). Temporal replication would, however, be required to confirm our results and validate hypotheses, as landscape influence may vary with time (Menalled et al. 2003; Veres et al. 2013; Plečaš et al. 2014), and because only a low infection rate was detected in our sampling.

Rhopalosiphum padi was the primary aphid species settling on seedlings and was associated with BYDV transmission, which is consistent with previous observations in Western Europe (Plumb 1990; Leclercq-Le Quillec et al. 1995, 2000; Fabre et al. 2005). We observed a decrease in colonization rate over the 4 weeks. This could be explained by two factors: (1) temperatures dropped during the last 2 weeks, resulting in decreased aphid flight activity, and (2) local aphid reservoirs were depleted as a result of density-dependent *R. padi* population regulation (Maudsley et al. 1996; Bommarco et al. 2007) or of ploughing of cereal volunteers or maize harvesting. This latter factor was likely most important as most migrants originated from maize.

The importance of local sources relative to distant ones, which will determine, for example, the genetic background and viruliferous potential of migrants, is of interest in pest control (Vialatte et al. 2007). Although *R. padi* has long-range dispersal capabilities and shows a high level of gene flow, little is known on its effective dispersal at the landscape scale. Short-distance movements are now viewed as the main part of aphid flight activity, long-distance

Fig. 3 Boxplot showing the number of seedlings colonized per week of experiment and for each local habitat type. The first week of sampling corresponded to the week between September 30 and October 6

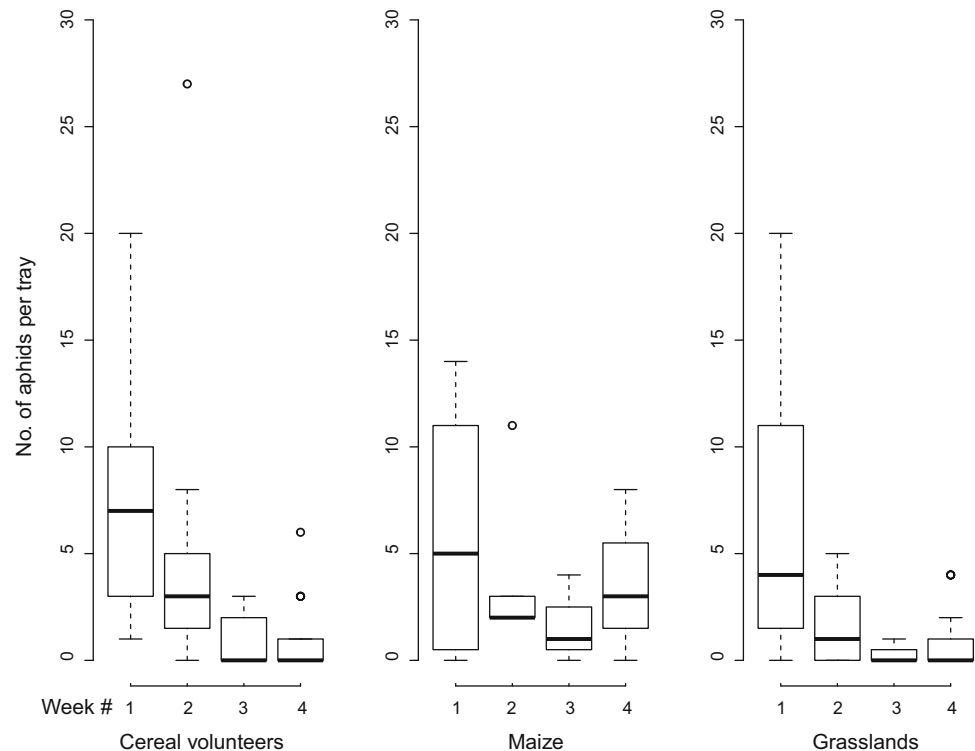


Table 1 Summary of fixed effects from the Bayesian mixed model explaining weekly aphids colonization rates

	Estimate	l-CI	u-CI	P MCMC
<i>Explanatory variable</i>				
Intercept	1.18	0.74	1.68	<0.001
Week 2	−0.97	−1.5	−0.37	<0.001
Week 3	−2.44	−3.14	−1.84	<0.001
Week 4	−1.95	−2.6	−1.37	<0.001
<i>Local variables</i>				
Crop (maize)	0.72	0.12	1.3	0.013
Crop (cereal volunteers)	0.58	0.11	1.07	0.018
<i>Landscape variables</i>				
Maize 1000 m	0.31	0.07	0.55	0.0067
Grasslands 1000 m	−0.27	−0.52	−0.04	0.036

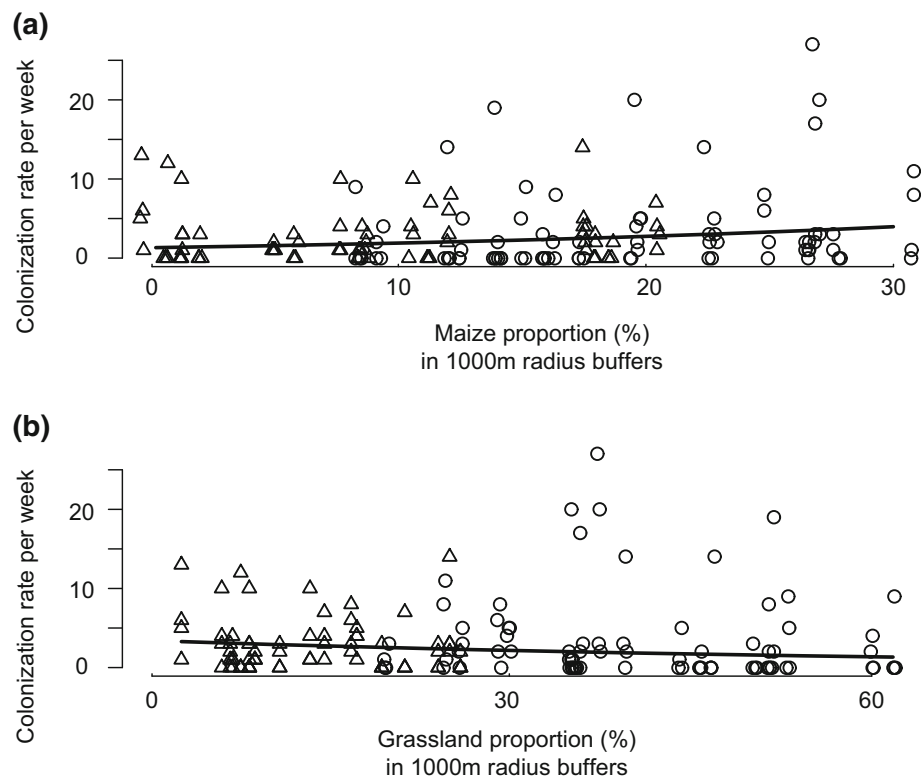
Estimate is the posterior mean; l-CI and u-CI are the lower and upper 95 % credibility intervals

movements being thought to occur more unfrequently (Parry 2013). The local scale has thus been demonstrated to be important for the cereal aphid *S. avenae* (Vialatte et al. 2007). Here, we detected significant effects of both local and landscape variables on wheat colonization by *R. padi* in autumn, suggesting that the local scale too, through the field context, is relevant in *R. padi* autumnal colonization of crops. The trays located at the border of crop cereals (maize or cereal regrowths) were more colonized than the

ones placed at the edge of grasslands. This result is consistent with previous studies evidencing aphid preference to landing in agricultural crops rather than in natural or semi-natural habitats (Favret and Voegtlin 2001). Indeed, for most pest species, the amount of ground cover present, which is 100 % in grasslands, is inversely proportional to aphid landing rate, reflecting their attraction to contrasted grounds (Irwin et al. 2007).

Considering the context of the study, maize and grasslands were hypothesized to influence *R. padi* colonization rate as the possible main sources of aphids in autumn (Dedryver and Harrington 2004; Vialatte et al. 2006; Gilabert et al. 2014). Our results, from both the isotopic and the landscape analyses, demonstrated that maize only played this role, supporting the hypothesis that maize was the main source of cereal aphids in early autumn (Vialatte et al. 2006; Gilabert et al. 2014). We observed indeed (1) that the vast majority of migrants came from a C4 plant and (2) a positive effect of the proportion of maize, but not of grasslands in buffers of 1000 m of radius on the colonization rate of wheat seedlings by *R. padi*. It is, however, possible that maize exerts an even stronger influence at larger landscape scales, as we obtained better models when increasing the considered scale for maize, from buffers with radius of 250 m to buffers with radius of 1000 m (results not shown). Influence of larger scales was, however, not tested here because buffers overlapped, reducing statistical independence. The scale at which a landscape

Fig. 4 Number of seedlings colonized per week according to the proportion of maize (a) and grasslands (b) in the 1000-m-radius buffers centred on the trays. Circles indicate trays in ARM study site and triangle trays in PVS study site. The lines indicate predictions of the MCMCglmm



variable influences pest dynamics depends on the underlying processes and the variable functionality for the studied species (O'Rourke et al. 2011; Martin and Fahrig 2012). Landscape variables may influence aphid colonization rates at larger scales because of their long-range dispersal abilities. The positive influence of maize at 1000 m may thus reflect density-dependent regulation of populations (Maudsley et al. 1996; Bommarco et al. 2007) and the fact that aphids are dispersed from maize to settle on more suitable plants at the end of the maize-growing season.

Grasslands are a potentially important habitat in the context of BYD epidemics and *R. padi* colonization in autumn (Dedryver and Harrington 2004). At the time of the survey, grasslands were the main C3 plants that could serve as both aphid and virus reservoirs. Previous authors who observed higher cereal aphid densities in complex landscapes during spring argued that pest populations benefit from higher availability of undisturbed natural habitats during this season (e.g. Roschewitz et al. 2005; Thies et al. 2005; Plečáš et al. 2014; Birkhofer et al. 2016). However, we observed that grassy semi-natural areas may not be important autumnal sources of colonizers for *R. padi* in comparison with maize, as revealed from both the isotopic and landscape analyses. The latter studies were conducted in June and July though, therefore with different land use, which could contribute to the observed difference with our

study. Grasslands may provide temporally suitable habitats for cereal aphids, and their weak contribution to the migrant pool may be a consequence of either the reluctance of aphids to leave a perennial resource or the higher predation and parasitism pressures exerted in grasslands, resulting in lower aphid densities. It has been shown indeed that cereal aphid parasitism (both primary and hyperparasitism) was enhanced with the surface of non-crop areas (Zhao et al. 2014). This may explain the negative effect of grasslands at 1000 m detected on *R. padi* colonization rate. Alternatively, this negative effect of grasslands could reflect a dilution effect, grasslands providing an alternative target for the colonization, or reflect the effect of landscape structure on aphid landing rates as grasslands are strongly correlated with hedgerows in our two study sites (Pearson correlation coefficient $r = 0.91$).

Though the observed proportion of viruliferous aphids was low (5.25 %), it was consistent with previous observations of viruliferous *R. padi* caught in suction traps in the northern half of France (Fabre et al. 2005). These authors found that the percentage of viruliferous aphids ranged between 2 and 10 %, increasing with the ratio of land covered by cereals to land covered by maize. By contrast, when we inferred the host plant of aphids that transmitted BYDV to the seedlings, we found all but one originated from maize. This is all more surprising because maize is known to provide lower concentration of BYD viruses than

other crops (Hammond et al. 1983; Plumb 1990). However, this observation relied on a low number of aphids, which in addition originated mainly from maize. At the regional scale, the proportion of seedlings infected by BYD virus was, however, higher in PVS, where the colonization rate was lower and the proportion of land covered by small-grain cereals was higher. This is consistent with the results obtained by Fabre et al. (2005). During the survey, BYD prevalence in *R. padi* was too low to assess accurately the influence of landscape on transmission of BYD viruses. The approach we used here could, however, be of use in studying the influence of landscape on the dynamics of other plant diseases.

Conclusion

In this study, we monitored the colonization of wheat seedlings by the aphid *R. padi* in autumn and analysed it in relation to the composition of the surrounding landscape. We also used an original approach to simultaneously assess the host plant of origin and the viruliferous potential of the migrants in order to assess the influence of landscape features on an epidemiological risk. The study allowed us addressing both theoretical and applied questions on how landscape affects the intensity of crop colonization. Taken together, our results indicate that crop areas, especially sown with maize, were the main sources of *R. padi* colonizing wheat fields during our survey. We detected significant influence of landscape variables at both local and landscape scales. Reducing epidemiological risk of crop plants through landscape management therefore requires considering the local and landscape scales. Such studies monitoring simultaneously colonization and infestation rates, as well as the origin of migrants, in other vector-transmitted plant diseases are useful aids in designing habitat manipulation strategies to improve crop protection. Such strategies can help in reducing pesticide use while maintaining crop yields.

Authors' contributions

AG, CAD and MP designed research in collaboration with VB and JB. AG, JFLG, PL, CAD and MP conducted the sampling, which was supervised by AG. BG and JB performed the landscape analyses. AG, BG and NP analysed the data. AG, BG, CAD and MP drafted the complete manuscript, with NP, PL, VB and JB commenting and contributing to discussions on the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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