Cabbage whiteflies colonise *Brassica* vegetables primarily from distant, upwind source habitats

Martin Ludwig[1]* (iD), Hella Ludwig[2] (iD), Christopher Conrad[3], Thorsten Dahms[3] & Rainer Meyhöfer[1] (iD)

[1]*Institute of Horticultural Production Systems, Section Phytomedicine, Gottfried Wilhelm Leibniz Universität Hannover, Herrenhäuser Str. 2, D-30419, Hannover, Germany, [2]Department of Crop Sciences, Agroecology, Georg-August-Universität, Grisebachstr. 6, D-37077, Göttingen, Germany, and [3]Instute of Geography, Remote Sensing Unit, Julius-Maximilians-Universität Würzburg, Campus Hubland Nord 86, D-97074, Würzburg, Germany*

Abstract

The occurrence of species in rapidly changing environments, such as agricultural landscapes, is affected by their ability to recolonise habitats. Knowledge of the landscape scale affecting colonisation is essential for large-scale pest management. Colonisation by insects can be affected on multiple landscape scales, as different morphs of a species may have specific dispersal abilities. The cabbage white-fly, *Aleyrodes proletella* (L.) (Hemiptera: Aleyrodidae), a major pest of *Brassica* vegetables, is known to colonise *Brassica* vegetables primarily from fields of oilseed rape, *Brassica napus* L. (Brassicaceae). We used field mapping and remote sensing to characterise the relevant scales for colonisation of Brussels sprouts by cabbage whiteflies. Surprisingly, oilseed rape fields in wide landscapes (2–8 km around study sites) explained colonisation better than oilseed rape areas in local landscapes (200–1 000 m around study sites). The explained variance increased when additional weight was given to upwind source habitats, indicating wind transport of whitefly colonisers. Low importance of local compared to wide landscape source habitats can be explained by the flight behaviour of whitefly morphs. Migratory morphs show phototactic attraction but are attracted by hosts only during the later phases of flight. Therefore, they ignore host plants close to their origin and disperse several kilometres. Trivial flight morphs rarely move more than a few hundred metres. In conclusion, as most whitefly colonisers reached *Brassica* vegetables from source habitats at a distance of 2–8 km, predictions on pest pressure and landscape-scale whitefly management should consider these distances. In contrast, oilseed rape fields in the local landscape, which usually worry farmers, had little effect.

Introduction

Colonisation processes affect aspects of species community dynamics, including pest outbreaks and species survival, particularly in rapidly changing habitats such as agricultural landscapes (Wissinger, 1997; Tscharntke et al., 2005). Dispersal is a major driver of colonisation and defined as the movement of organisms away from their parental source to other locations (Lewis et al., 2013). It thereby includes movement on different scales, within as well as among populations and habitats. In terms of insect flights, so-called 'trivial flights' can be distinguished from 'migratory flights' (Danthanarayana, 1986; Johnson, 1969). Trivial flights, also called vegetative or appetitive flights, are random short-distance flights usually associated with feeding, mating, or oviposition behaviour inside habitats (Danthanarayana, 1986). In contrast, migratory flights cover relatively long distances and are, with exception of the late phase of flight, undistracted by stimuli referring to everyday ('trivial') needs (Johnson, 1969). Migratory flights often are associated with changes among habitats and with colonisation of new habitats (Danthanarayana, 1986). Knowledge on the spatial dimension at which dispersal affects colonisation is important for the management of wild animal populations in the context of conservation, utilisation, or crop protection (Mazzi & Dorn, 2012).

*Correspondence: Martin Ludwig, Institute of Horticultural Production Systems, Section Phytomedicine, Gottfried Wilhelm Leibniz Universität Hannover, Herrenhäuser Str. 2, D-30419 Hannover, Germany. E-mail: ludwig@ipp.uni-hannover.de

In this study, we investigated colonisation of young Brussels sprout plants by the cabbage whitefly, *Aleyrodes proletella* (L.) (Hemiptera: Aleyrodidae), a serious pest in *Brassica* vegetable fields, such as kale, Savoy cabbage, and Brussels sprouts (Pelgrom et al., 2015). The cabbage whitefly prefers Brassicaceae plants but also occurs on plants of the Asteraceae and Papaveraceae families (Bährmann, 2002). The worldwide spread of cabbage whitefly and its importance as a vegetable pest have increased dramatically in the last few decades (El-Helaly et al., 1972; de Barro & Carver, 1997; Pelgrom et al., 2015). Furthermore, the species has developed resistance to pyrethroid insecticides (Springate & Colvin, 2012). The increasing abundance of cabbage whiteflies in Europe may be related to increased production of oilseed rape, *Brassica napus* L. (Brassicaceae), in the last few decades (Dixon, 2007). Cabbage whiteflies use winter oilseed rape fields for hibernation and as a spring reproduction habitat when *Brassica* vegetables are unavailable ('green bridge'; Dixon, 2007; den Belder et al., 2008). In early summer, when oilseed rape fields mature, whiteflies disperse to the surrounding landscape due to a decrease in host quality (Richter & Hirthe, 2014). At this time of the year, newly planted *Brassica* vegetables are available as alternative hosts. Therefore, oilseed rape fields are an important source of whiteflies that colonise *Brassica* vegetable fields (Richter & Hirthe, 2014).

Dispersal ability largely determines the relevant scale for colonisation processes. Whiteflies have been traditionally seen as weak fliers, unable to actively fly more than a few hundred metres (Byrne & Bellows, 1991). Thus, the availability of source habitats within the local landscape seems to be a key factor for the successful colonisation of a habitat and population built-up. Accordingly, oilseed rape fields at distances up to 1 000 m affect colonisation by cabbage whiteflies (Ludwig et al., 2018; Ludwig & Meyhöfer, 2016). However, the importance of more distant source habitats is unknown. Studies on the sweet potato whitefly, *Bemisia tabaci* (Gennadius), show a bimodal dispersal pattern with peaks at 100 and 2 000 m distances from the dispersal source (Byrne et al., 1996). Byrne et al. (1996) concluded that the different peaks of the sweet potato whitefly result from two morphs differing in their specific ability and willingness to fly, namely the so-called 'trivial flight morph' (100 m peak) and the 'migratory flight morph' (2 000 m peak). Migratory and host-finding behaviour of aphids and whiteflies are similar. During migratory flights they are attracted by UV or white skylight and thereby ignore host cues (Isaacs et al., 1999; Döring, 2014). Subsequent host finding is similar to behaviour during trivial flights and characterised by attraction to green and yellow surfaces (Isaacs et al., 1999; Blackmer et al., 1994), whereas some species additionally respond to

olfactory cues (Butler, 1938; Döring, 2014). Finally, host suitability is evaluated by probing the plant after landing (Noldus et al., 1986).

Similar to the sweet potato whitefly, the cabbage whitefly has two morphs with different specific flight abilities (Iheagwam, 1977). Consequently, cabbage whiteflies colonising *Brassica* vegetables may either be (1) migratory morphs derived from source habitats (particularly oilseed rape fields) up to several kilometres away, or (2) trivial flight morphs derived from source habitats in the local landscape at a few hundred metres distance. Upwind source habitats should be of utmost importance for wind-dispersed migratory morphs to colonise *Brassica* vegetables (Figure 1; Naranjo et al., 2010). In contrast, colonisation by trivial flight morphs should be independent of prevailing wind directions as they fly in calm conditions close to the ground and find their hosts by random landing on green surfaces (Byrne & Bellows, 1991). On the other hand, downwind source habitats could be of importance if cabbage whiteflies follow olfactory cues (Figure 1; Butler, 1938; Pasek, 1988; Bleeker et al., 2009). Consequently, colonisation by whiteflies might be affected simultaneously on multiple landscape scales.

To answer the question of how colonisation is affected by distance of oilseed rape fields, we compared the variance in colonisation of young Brussels sprout plants by the cabbage whitefly explained by individual landscape radii (200–8 000 m). First, we hypothesised that colonisation of *Brassica* vegetables by the cabbage whitefly depends on
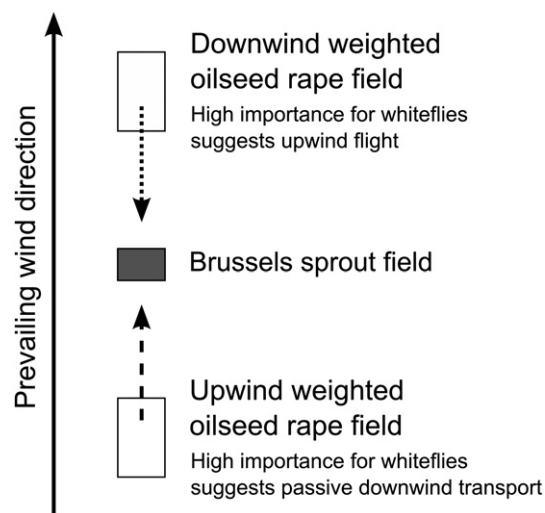

Figure 1 Diagram illustrating the high importance of upwind source habitats for passively downwind dispersed arthropods (dashed arrow) and the high importance of downwind source habitats for arthropods with (olfactory oriented) upwind flight (dotted arrow).

the amount of oilseed rape as a source habitat in the local landscape, due to the typical dispersal behaviour by trivial flights, as well as in the wide landscape, due to migratory flights. Therefore, a model simultaneously considering oilseed rape area at these two spatial scales should explain the colonisation pattern better than a model considering only one of these scales. As the exact distance covered by cabbage whiteflies in trivial and migratory flights is unknown, different radii for the local (200–1 000 m) and wide landscapes (2 000–8 000 m) were tested. Second, we hypothesised that downwind transport is of importance for dispersal on wide landscape scale. Thus, giving additional weight to upwind source fields at the wide landscape scale should increase the model's explanatory power and thereby indirectly support this hypothesis. Third, we hypothesised that olfactory orientation towards host plants plays a role in trivial flights by the cabbage whitefly. Consequently, giving additional weight to downwind source fields at the local landscape scale should further improve the model's explanatory power and thereby indirectly support the third hypothesis.

Materials and methods

Field survey

Eighteen Brussels sprout fields on organic horticultural farms located in northwest North Rhine-Westphalia and southern Lower Saxony, Germany, were selected (southwestern and north-eastern corner of the study region in UTM-coordinates, respectively: east: 459004, north: 5686565; east: 611046, and north: 586746). Farmers grew a large variety of vegetables, including Brussels sprouts (planted from late April to early June) and other *Brassica* vegetables. The agricultural landscapes surrounding the study sites (Brussels sprout fields) differed in land use and represented a gradient in the area of oilseed rape, for example, 0–20 and 0.5–11% oilseed rape at 200 and 8 000 m radii around the study sites, respectively. A weather station (PCE-FWS 20; PCE Instruments, Meschede, Germany) recorded wind directions at 15-min intervals on each study site.

Colonisation of Brussels sprouts by cabbage whiteflies was sampled on sentinel plants exposed at all study sites in early July 2012 at the peak of cabbage whitefly early summer migration (Ludwig et al., 2014, 2018). Sentinel plants were potted organically cultivated Brussels sprout plants free of pests and natural enemies. They were standardised in terms of soil type [mixture of 1.7 g water-storing granulate (Broadleaf P4; AgriPol, Bournmoor, UK) per l potting soil], age (3–4 weeks), and variety (*Brassica oleracea* L. var. *gemmifera* cv. 'Topline F1') and were selected randomly. Twenty sentinel plants were exposed per study site close to

the farmer's Brussels sprout plants (max. 5 m distance). The plants were placed in two groups of 10 plants, each separated by at least 50 m, whereas in two exceptions all 20 plants were placed as single group. After 2 weeks, eggs and nymphs of cabbage whiteflies were counted on all leaves of the sentinel plants (mean number of leaves per plant $\pm$ SD = 7.7 $\pm$ 1.9).

Landscape survey by manual mapping and remote sensing

To quantify the position and area covered by oilseed rape fields within 8-km radii around study sites, we manually mapped the local agricultural landscape (1-km radius) around study sites on the ground and used relatively less time-consuming remote sensing methods to assess land use in radii of 8 km. Agricultural land use types were grouped into 10 crop type classes (Table S1). These data, in addition to forest and urban areas mapped on the basis of satellite images, were digitised using ESRI ArcGIS v.10 (Environmental Systems Research Institute, Redlands, CA, USA).

In a further step, these results were used as reference data to determine land use in the wide landscape (up to 8 km) using satellite images and remote sensing methods. The reference data objects were separated into training data (70%) to train the classification algorithm 'Random Forests' and validation set (30%) for final validation of the classification (Breiman, 2001; Table S1). 'Random forests' is a machine-learning method that is widely used to classify remote sensing data (Pal, 2005) including the identification of different crops (Conrad et al., 2014).

The classification of pixel-based satellite image units into land use types was performed as follows. Five Landsat 7 Enhanced Thematic Mapper Plus sensor scenes were used for the classification (acquisition day number in 2012: 66, 146, 199, 247, and 279). Clouds were masked out using a threshold on the blue band and the 'normalised difference vegetation index' (NDVI). As classifications do not require an atmospheric correction (Song et al., 2001), this step was applied to the top-of-atmosphere reflectance data. Four spectral bands (blue, green, red, and near-infrared), as well as the vegetation indices 'soil-adjusted vegetation index' (SAVI), NDVI and the 'simple ratio' (SR) were utilised as input for the classification (Table S2). Due to cloud coverage and the 'scan line correction error' (SLC) (Wulder et al., 2014), we classified and merged multiple Landsat scene combinations to cover the entire study area. In the final class decision for a single pixel, the classification with more input scenes was prioritised over the classification based on fewer Landsat scenes to ensure that the full potential of the multi-temporal dataset was used and that the major part of the study area was classified. The resulting post-classification map was clumped using

'ENVI' v.4.8 (Exelis Visual Information Solutions, Boulder, CO, USA) to ensure spectral coherency.

The final land cover map was validated using the validation set described above. The classification accuracies were calculated according to Congalton (1991) and are shown in Table S3. Overall accuracy was 79.89% (kappa coefficient = 0.76), whereas the accuracies of the class of interest (oilseed rape) were higher (producer's accuracy = 89.51% and user's accuracy = 88.96%; Table S3).

Data preparation

Data analysed in this study are included in the Supporting Information (Table S6). As recording wind data failed at two study sites and no remote sensing landscape data were available from another study site, all data analyses were conducted with 15 of the initial 18 study sites. The mean number of egg clutches laid per leaf within a 2-week exposure time at each study site was used as a measure of colonisation. Thereby, egg clutches that hatched during the exposure time were included (4.7 nymphs corresponded to one clutch; Ludwig, 2017).

The percentage area covered by oilseed rape within circular areas around the study sites was calculated at 16 radii ranging from 200 to 1 000 m in 100-m steps (local landscape) and from 2 to 8 km in 1-km steps (wide landscape) to investigate the importance of oilseed rape fields as source habitats at different radii. Data recorded by personal mapping were used to ensure the highest accuracy for the nine local landscape radii, whereas the data obtained from satellite image analysis were used for the seven wide landscape radii, allowing us to consider the wide-scale landscapes (which could not be mapped manually). The data generated from the satellite images at the 1-km radius and those from personal mapping were highly correlated (r = 0.92).

To weigh the contribution of the oilseed rape areas according to their location relative to the study sites and prevailing wind directions, the circular landscape areas were separated into eight wind direction sectors (N, NE, E, SE, S, SW, W, and NW; Figure 2). To account for a greater importance of upwind source habitats in cases of passive wind dispersal (Figure 1), we first calculated the proportion of wind events (>0.3 m s^{-1}) blowing from each of the eight sectors towards the study site during the time the sentinel plants were exposed. Second, the percentage oilseed rape area per sector was multiplied by the proportion of wind events blowing towards the study site. The sum of the resulting eight values (one value per sector) produced an area index with increased weight for upwind located habitats, hereafter referred to as 'upwind weighted' area (Table S4). To account for a greater importance of downwind source habitats in cases of attraction by wind-transported odours (Figure 1), we weighted the area of the three habitat categories accordingly: percentage of oilseed rape area per sector was multiplied by the proportion of wind events blowing from the study site towards the sector. The sum of these resulting eight values produced an area index with increased weight for downwind located source habitats, hereafter referred to as 'downwind weighted' area.

Statistical analysis

Regression models were used to analyse the effects of oilseed rape area at different scales with and without weighting by wind on colonisation of Brussels sprout. Therefore, the mean number of *A. proletella* egg clutches per leaf calculated for each study site was used as a response variable in all models (see Figure S1 for distribution of the response variable). The response variable was $\log(x + 1)$-transformed, avoiding non-normal error distribution. To identify landscape radii in which oilseed rape mainly affected colonisation by pests, we calculated 32 models containing one of the 32 explanatory variables (nine radii from 200 to 1 000 m for the local scale, once with and once without downwind weighting of oilseed rape area, and seven radii from 2 to 8 km for the wide scale, once with and once without upwind weighting of oilseed rape area). To investigate whether including two spatial scales explained colonisation better than one scale, we calculated models
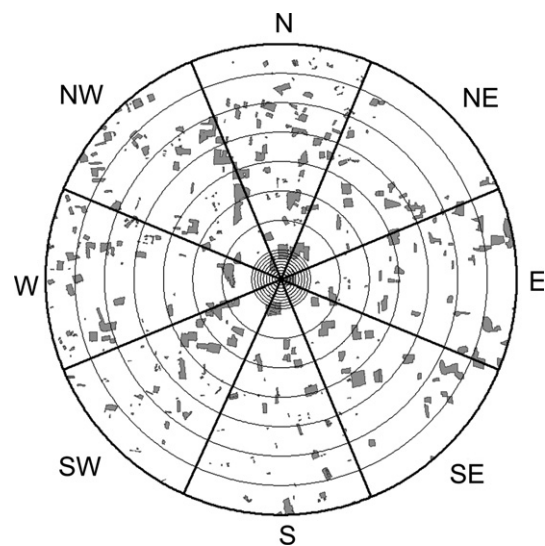

Figure 2 Separation of one of the analysed landscapes into circular areas with various radii around the study site (thin grey circles) and sectors dedicated to wind direction. Grey areas represent oilseed rape fields.

with two explanatory variables (% oilseed rape area on the local and wide scales) covering all possible combinations of local scale (nine radii) and wide scale (seven radii), leading to a total of 63 models. Furthermore, we calculated 189 models in which one or both variables were weighted by wind. Combined explanatory variables were not correlated referred to a threshold of $|r| > 6$. All of these models ($32 + 63 + 189 = 284$) were ranked using Akaike's information criterion corrected for small sample size (AIC_c), which is a measure of relative goodness-of-fit and simplicity of the statistical models for a given data set. The best models in a range of delta $AIC_c \leq 2$ are shown, which are supposed to be of similar quality (Burnham & Anderson, 2002). All analyses were performed in R v.3.3.1 (R Core Team, 2016).

Results

The cabbage whitefly was the most abundant pest species on Brussels sprout plants. Its density reached 0.2–61.4 egg clutches per leaf (median = 15.3, mean = 19.4). No natural enemies specialised in whiteflies – such as the chalcid wasp *Encarsia tricolor* (Förster) or the lady beetle *Clitostethus arcuatus* (Rossi) – were observed, but syrphid larvae and spiders were present. The prevailing wind directions were southern or western (coming from the SE, S, SW, W, and NW) for all study sites. The most frequent wind direction was southwest at 12 of the 15 study sites (80%), whereas north was the least frequent direction at nine study sites (60%).

After comparing all combinations of oilseed rape area at the wide-scale and/or local-scale landscapes with and without weighting by wind, eight of the total 284 models were in the $\Delta AIC_c \leq 2$ range (Table 1). All of these models showed a significant effect of oilseed rape area at the wide scale, but local scale landscapes were not included in any of these best models (see Table S5 for parameter weights of the full set of models).

Five of the eight best models for the wide landscape scale contained upwind weighting of source habitats, including the model with the lowest AIC_c (5-km radius with upwind weighting of oilseed rape area, $R^2 = 0.41$, $P = 0.011$; Figure 3). The comparison of variance explained (R^2) by models with oilseed rape area in different radii with and without weighting by wind as a single explanatory variable showed that upwind weighting of oilseed rape area on a wide landscape scale increased the explained variance of all scales with a radius ≥2 km (Figure 4). Downwind weighting of oilseed rape area on local landscape scale increased explained variance only at the 200-m radius and was not part in any of the models in the $\Delta AIC_c \leq 2$ range.

Table 1 Minimum adequate models ($\Delta AIC_c \leq 2$ range) explaining colonisation of young Brussels sprout plants by cabbage whiteflies. All possible combinations of oilseed rape area on the wide landscape scale (2–8 km radius, with and without upwind weighting) and on the local landscape scale (200–1 000 m radius, with and without downwind weighting) were used as explanatory variables in the full models, but no models including the local landscape scale were present in the $\Delta AIC_c \leq 2$ range. AIC_c = Akaike's information criterion corrected for small sample size; weighting = weighting of oilseed rape area by wind direction; + = with weighting; − = without weighting

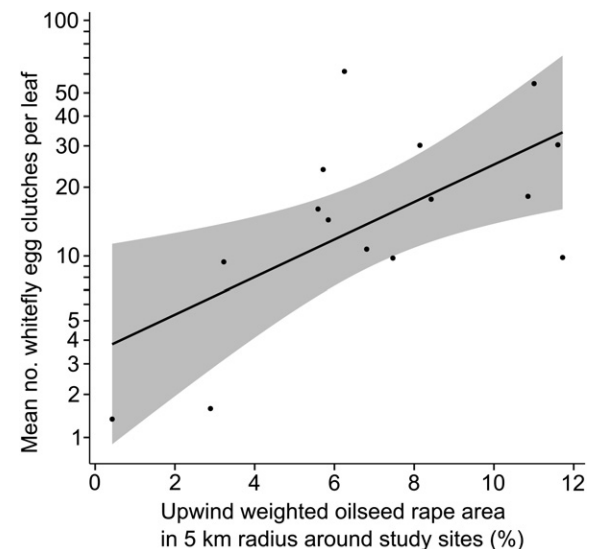| Radius (km)	Weighting	Estimate	P	R^2	ΔAIC_c
5	+	0.176	0.011	0.41	0.00
7	+	0.194	0.016	0.37	0.90
5	−	0.171	0.018	0.36	1.17
6	+	0.178	0.018	0.36	1.17
4	+	0.152	0.020	0.35	1.35
7	−	0.191	0.023	0.34	1.63
6	−	0.177	0.026	0.33	1.87
8	+	0.187	0.026	0.33	1.90

Figure 3 Increase in whitefly colonisation of sentinel plants with increasing oilseed rape area. Black dots represent colonisation of sentinel plants of the different study sites measured as mean number of whitefly clutches per leaf. The black line represents the model predictions, the grey shading around the line a confidence interval of 0.95.

Discussion

We calculated the number of whitefly egg clutches laid on sentinel plants' leaves within 2 weeks as a measure for colonisation based on counted egg clutches and nymphs. This measure might slightly underestimate the effective
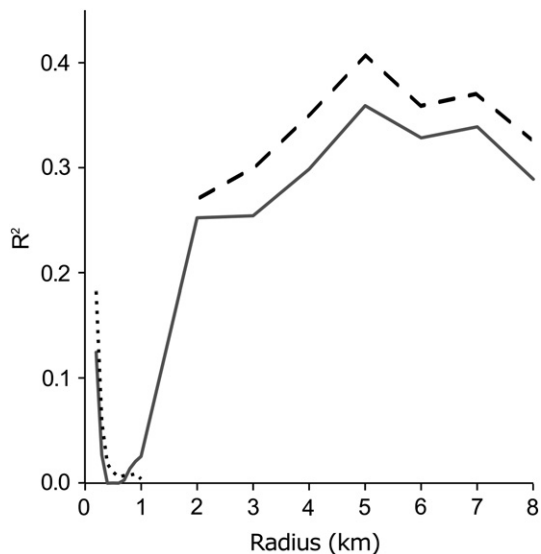
Figure 4 Explained variance (R^2) of cabbage whitefly colonisation of Brussels sprouts by the percentage of oilseed rape area (i.e., source habitat) in 16 radii resulting from separate models for each radius. Continuous grey line = local and wide landscape scale without weighting by wind; dashed line = wide landscape scale with upwind weighted oilseed rape area; dotted line = local landscape scale with downwind weighted oilseed rape area.

colonisation, as some egg clutches or larvae may have been fed by predators (sentinel plants were not protected from predators). However, only some generalist predators were present on the sentinel plants, which have only weak effects on cabbage whitefly numbers (van Rijn et al., 2008). Specialised predators were not observed, whereas larvae infested with parasitoids were counted along with unparasitized larvae.

Our results show that the area of oilseed rape fields (source habitats) within 5-km radii around the study sites explained 36% of the variance in colonisation of young Brussels sprout plants by the cabbage whitefly. The explained variance increased (to a maximum of 41%) when source habitats were upwind weighted. In contrast, oilseed rape area at the local landscape scale showed no or only a weak effect on colonisation of young Brussels sprout plants by the cabbage whitefly. These findings highlight the importance of source habitats on a wide landscape scale for even weak fliers such as whiteflies (Byrne & Bellows, 1991) and reveal the importance of passive downwind transport for dispersal.

The low proportion of explained variability in whitefly colonisation by oilseed rape area in the local landscape and the steep increase in explained variation from radii of 700 m to 2 km suggest that landscapes up to 700 m play a negligible role, whereas landscapes ≥700 m are particularly

important for whitefly colonisation. Analogous results from an analysis using circle-shaped landscape areas for the local landscape and ring-shaped landscape areas for the wide landscape confirmed these findings. This leads to the question why source habitats in a wide-scale landscape are more important for colonising *Brassica* vegetable fields compared to that of local-scale source habitats. A possible reason is that cabbage whitefly migratory morphs are the main colonisers of *Brassica* vegetable fields. Trivial flight morphs fly for a very short time only (19 s on average; Iheagwam, 1977) and immediately land on green surfaces (Blackmer et al., 1994). Therefore, they may only be able to reach a new habitat if it directly borders their source habitat. In our study, we presumably did not detect colonisation by trivial flight morphs, as none of the Brussels sprout fields studied directly adjoined an oilseed rape field (the minimal distance was >100 m, with one exception of >40 m but shielded by field hedges). In contrast, migratory whitefly morphs fly for 15 min on average (Iheagwam, 1977). They show positive phototactic behaviour and ignore visual host cues during the first phase of their flight (Isaacs et al., 1999; Iheagwam, 1977), which can cover 2–7 km (Cohen et al., 1988; Byrne et al., 1996). This behaviour, which is similar to dispersal strategy of other insects such as aphids (Döring, 2014), can be meaningful in order to avoid exploitation of the local resources as a consequence of population growth or decrease in resource availability. Consequently, most migratory morphs may not colonise Brussels sprout fields close to their source habitat, as their specific flight behaviour leads them directly to a height at which they are transported by the prevailing wind. Thus, whitefly populations of the wide landscape's oilseed rape fields may colonise Brussels sprout fields independently from whitefly populations in the local landscape.

Consequently, these results do not confirm our first hypothesis, stating that a model involving two spatial scales (considering the two morphs) explains colonisation by the cabbage whitefly better than a model considering only one spatial scale. All eight of our best models contained only wide-scale landscape variables, indicating that the wide landscape was the most important for colonisation of Brussels sprouts by cabbage whiteflies, whereas the local landscape seemed to be almost negligible.

The second hypothesis stated that wind transport is important for a wide-landscape-scale dispersal of the cabbage whitefly and, consequently, models including upwind weighted oilseed rape area explained colonisation particularly well. Three of the eight best models considered oilseed rape area without weighting by wind; thus, there is no solid proof for high importance of wind effects during colonisation by cabbage whitefly. On the other hand, the five

models including upwind weighting of oilseed rape area always had a lower AIC_c and explained more variance than equivalent models without weighting by wind. The importance of wind transport in dispersal has been suggested previously for other whitefly species (Byrne et al., 1996; Bährmann, 2002). Sweet potato whitefly dispersal can peak 2 km downwind from the source habitat whereas single individuals travel distances of 7 km (Cohen et al., 1988; Byrne et al., 1996). For aphids, passive wind transport of even hundreds of kilometres is reported, whereas flights of <20 km are seen as local movement (Loxdale et al., 1993).

Although optical orientation is most important, olfactory orientation can also be used by whiteflies to find host plants (Butler, 1938; Vaishampayan et al., 1975; Bleeker et al., 2009). Therefore, we hypothesised that cabbage whiteflies are attracted by Brussels sprout fields from nearby downwind oilseed rape fields (which decrease in host plant quality as they mature). This hypothesis was not confirmed, as oilseed rape areas at the local scale (200 m radius) had, if any, a negative effect on colonisation of Brussels sprout. In addition, the quality of oilseed rape host plants is generally weak in July but oilseed rape plants with delayed development (often found on lanes inside the fields) may be suitable cabbage whitefly hosts. An effect of decreasing colonisation with increasing downwind source habitat area was found for pollen beetles, which use olfactory cues to locate hosts (Moser et al., 2009). The authors explained that lower numbers of herbivores reach a study site when alternative source habitats are along their way. However, the role of olfactory orientation is not well investigated in whiteflies. The cabbage whitefly was found to orientate towards the scent of crushed cabbage leaves (Butler, 1938), but no orientation towards the scent of intact cabbage leaves could be detected (P Hondelmann, pers. comm.). The most important host location cues for whiteflies are visual (Vaishampayan et al., 1975; Mound, 1962), but olfactory stimuli affect pre-alighting host selection behaviour (Vaishampayan et al., 1975; Bleeker et al., 2009).

Besides oilseed rape fields, less widespread source habitats may also affect colonisation. Furthermore, colonisation of the sentinel plants may be altered by aspects of the colonised field, such as field size or farming practice, which were largely standardised in our study by selecting small to medium sized organic farms only. Predictions on whitefly pest pressure could be further refined by implementing these aspects as well as other environmental factors, such as temperature or rainfall (Naranjo et al., 2010; Ludwig et al., 2018). These predictions may be useful to develop integrated plant protection strategies (Meyhöfer & Ludwig, 2016).

Conclusions

The combination of wind and landscape configuration data as well as determining the most important landscape scale (5-km radius) using satellite images in our study is an important step to gauge colonisation of cabbage plants by the cabbage whitefly. We combined wind and landscape configuration data by upwind weighting of source habitats (i.e., oilseed rape fields) on a wide landscape scale (assuming wind dispersal) and downwind weighting of source habitats on a local landscape scale (assuming olfactory orientation during host finding). The wide landscape radii of 2–8 km explained colonisation best, particularly when source habitats were upwind weighted, indicating wind transport by whitefly colonisers. Local landscapes (up to 1-km radius) were only slightly important for colonisation by cabbage whiteflies. This can be explained by the specific flight behaviour of migratory morphs, ignoring potential host plants close to their place of origin and dispersing over a distance of several kilometres. Thus, predictions on pest pressure and landscape-scale whitefly management need to consider large landscape scales. In contrast, oilseed rape fields at moderate distances of up to 1 km, about which farmers usually are most concerned, are relatively negligible for colonisation. Brussels sprout fields directly bordered by oilseed rape fields were not part of the study and may be an exception from the observed pattern (M Ludwig, pers. obs.). Predictions could be further refined by implementing further local and environmental factors.

Apart from its relevance in crop protection, the combined use of wind and landscape effects is of interest for landscape ecological science, as they represent further development of the common nested circles method (Thies & Tscharntke, 1999). The combination of wind and landscape effects is useful to predict not only pest outbreaks but also colonisation by other arthropods affected by wind, either by downwind transport of small arthropods, such as aphids, whiteflies, or ballooning spiders (Compton, 2002; Schmidt & Tscharntke, 2005), or for upwind-oriented olfactory searchers, such as pollen beetles or parasitoid wasps (Moser et al., 2009; Steinberg et al., 1993).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Overview of the crop type classes and the number of objects used for training and validation.

Table S2. Overview of the calculated vegetation indices. The bands of the Landsat Enhanced Thematic Mapper Plus sensor were named according to the part of the spectra they represent (e.g., BLUE = 0.45-0.52 μm; GREEN = 0.53-0.61 μm; RED = 0.63-0.69 μm; NIR (nearinfrared) = 0.78-0.90 μm; L = 0.5). SAVI = Soil-adjusted Vegetation Index; NDVI = Normalised Difference Vegetation Index; SR = Simple Ratio.

Table S3. Accuracy table showing the producer's accuracy (percentage of the elements of a class that are correctly dedicated to that class), the user's accuracy (percentage of the elements dedicated to a class that really belong to that class), the overall accuracy, and the Kappa coefficient (Congalton,).

Table S4. Example for the weighting by wind direction, giving higher weight to upwind oilseed rape area in a landscape of 2-km radius around the study site.

Table S5. Relative variable importance (parameter weights) for explanatory variables, based on AIC_c values for the full set of 284 models. Weighting: upwind = giving more weight to upwind oilseed rape fields; downwind = giving more weight to downwind oilseed rape fields.

Figure S1. Distribution of the response variable: mean number of whitefly egg clutches per leaf. Additionally, the mean number of whitefly egg clutches per leaf for each of the 15 study sites is shown (black dots). Their position on the y-axis is jittered around the frequency of 1.

Table S6. Response variable and explanatory variables used in the models.