



Landscape epidemiology of an insect-vectored plant-pathogenic bacterium: *Candidatus Liberibacter solanacearum* in carrots in Finland

Anne I. Nissinen^{a,*}, Lauri Jauhiainen^b, Hannu Ojanen^a, Minna Haapalainen^c, Atro Virtanen^d, Wopke van der Werf^e

^a Natural Resources Institute Finland (Luke), Production Systems, Tietotie, FI-31600 Jokioinen, Finland

^b Natural Resources Institute Finland (Luke), Natural Resources, Tietotie, FI-31600 Jokioinen, Finland

^c Department of Agricultural Sciences, University of Helsinki, P.O. Box 27, FI-00014, Finland

^d Finnish Food Authority, P.O. Box 100, FI-00027, Finland

^e Wageningen University, Centre for Crop Systems Analysis, P.O. Box 430, 6700 AK Wageningen, the Netherlands

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ABSTRACT

Crop diseases may be affected by landscape composition, but limited quantitative information is available. We studied the effects of landscape factors on the incidence of the psyllid-transmitted bacterium *Candidatus Liberibacter solanacearum* (CLso) haplotype C in carrots in Finland. Samples were collected from 104 carrot fields in 2013 and 2014. The relationship between CLso incidence and landscape data was analysed using logistic regression. The probability of CLso infection significantly increased with increasing area of carrot cultivation, up to a 10 km radius. Spruce biomass (spruce is the winter shelter of the main vector, *Triozia apicalis*,) within 200 m distance from the field edges affected CLso infection in landscapes with a low to medium area proportion of carrot cultivation but not in landscapes with a high proportion of carrot fields. Disease incidence was higher on clay soils than on mineral soils. The findings illustrate the importance of movement of the vector between carrot and spruce and highlight this disease as a landscape-scale disease syndrome, which needs to be managed also at the landscape level. Moderating the proportion of carrot fields in a carrot production landscape could be a key to manage the disease by breaking the epidemic cycle at the landscape level.

1. Introduction

Disease management in agricultural systems is often regarded as a field level activity and responsibility of individual growers. However, it is also well-known that landscape variables (later referred as factors), such as the occurrence of overwintering disease reservoirs, have a large effect on disease occurrence (Plantegenest et al., 2007). Therefore, actions of different growers are not independent of one another, and thus an area-wide coordinated response may be needed for effective disease control (Parsa et al., 2014; Schneider et al., 2021). While there is an extensive literature on the existence of landscape effects on crop diseases, few studies measure the size and spatial range of the landscape effect. The scarcity of quantitative data on landscape effects on crop diseases contrasts with the many studies that have been conducted to measure and further model landscape effects on the biological control of invertebrate pests in agriculture (e.g. Alexandridis et al., 2021). Insight into landscape effects on crop diseases is required to enable landscape

management to control diseases and motivate stakeholders to consider landscape level management options. Landscape management may help to reach a key target of the European agricultural policy: to reduce the use of chemical pesticides (European Commission, 2020).

The economic impacts of insect-vectored bacterial diseases are increasing worldwide (Perilla-Henao and Casteel, 2016). These diseases include citrus Huanglongbing, caused by several species within the genus *Candidatus Liberibacter*, and vectored by psyllid vectors such as *Diaphorina citri* and *Triozia erytrae* (Bove, 2006; Dala-Paula et al., 2019), and the diseases caused by *Xylella fastidiosa*, (e.g. the pauca strain causing dieback of olive trees) (Schneider et al., 2020). Such insect-transmitted plant pathogens may extend their geographic range towards currently cooler regions under climate change (Boland et al., 2004; Juroszek and von Tiedemann, 2013; Roos et al., 2011). As the dispersal of these pathogens is dependent on the movement of the vector, it is important to know the spatial range of the vector movement. Some studies of landscape effects on aphid-virus interactions, virus

* Correspondence to: Natural Resources Institute Finland (Luke), Production Systems, Juntantie 154, FI-77600 Suonenjoki.

E-mail address: anne.nissinen@luke.fi (A.I. Nissinen).

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dispersal and control are available (e.g. Angelella et al., 2016; Clafflin et al., 2017; Pleydell et al., 2018), however, there are few studies on psyllids, psyllid-transmitted bacteria and movement of the psyllid vectors (Gutiérrez Illán et al., 2020; Thébaud et al., 2009). Despite the large and growing economic relevance of plant pathogenic bacteria, there is overall little information on the spatial scale of movement of their vectors.

Candidatus Liberibacter solanacearum (CLso) is a psyllid-transmitted, non-culturable α -proteobacterium that causes serious physiological disorders in several solanaceous and apiaceous plants (Munyanzeza, 2012; Alfaro-Fernández et al., 2017). Haplotypes C, D and E of this pathogen are associated with apiaceous crops in Europe, primarily carrots, but also including celery (*Apium graveolens*), parsley (*Petroselinum crispum*), and parsnip (*Pastinaca sativa* subsp. *sativa*) (Munyanzeza et al., 2010a; Alfaro-Fernández et al., 2017). Haplotypes D and E are transmitted by the psyllid *B. trigonica* in the Mediterranean countries (Teresani et al., 2014; Antolinez et al., 2017a; b). Haplotype C was first detected in carrots and carrot psyllids in Finland (Munyanzeza et al., 2010a; b) and is transmitted by the psyllid *Trioza apicalis* (Nissinen et al., 2014). CLso haplotypes A and B are associated with diseases on several solanaceous crops in which they are transmitted by the psyllid *Bactericera cockerelli* (Munyanzeza, 2012). These two haplotypes and their vector do not occur in Europe.

CLso has been detected in carrot seed (Bertolini et al., 2015; Monger and Jeffries, 2017), but while one study reported transmission from the seed to the seedling (Bertolini et al., 2015), other studies have not confirmed this finding (Loiseau et al., 2017; Carminati et al., 2019; Nissinen et al., 2021), indicating that seeds, even if infected, are not an important source of infection of seedlings in the field (Nissinen et al., 2021).

Psyllids have been shown to transmit CLso from carrot to carrot (Antolinez et al., 2017a; b). CLso is transmitted by psyllids in a propagative-circulative manner, i.e. the bacteria replicate and systemically colonize the vector insect tissues prior to transmission via salivary glands (Cicero et al., 2017). In one region of Finland, CLso was found in over 60% of field-collected *T. apicalis* (Nissinen et al., 2014). Furthermore, field surveys in Finland in 2011–2014 suggested that CLso was established in several regions, which in turn suggested that this bacterium may be capable of overwintering in *T. apicalis* (Haapalainen et al., 2017). Overwintering of *Candidatus Phytoplasma* spp. in their psyllid vectors (*Cacopsylla* sp.) has been previously observed (Candian et al., 2020; Thébaud et al., 2009). A recent analysis of spatial and temporal dynamics of CLso infection and of *T. apicalis* feeding damage in the field in Finland supports the theory that primary infections are vector-borne (Nissinen et al., 2021).

Carrot psyllid, *T. apicalis*, is a univoltine species, which overwinters as adults on Norway spruce (*Picea abies*) (Rygg, 1977; Valterová et al., 1997; Kristoffersen and Anderbrant, 2007), because carrots do not survive over the winter in the Nordic conditions (Rygg, 1977). However, overwintering on conifers is also widely known among other psyllid species. The *T. apicalis* adults migrate from their overwintering sites to carrots in late May or early June (Laská, 1974; Rygg, 1977; Tiilikkala et al., 1996). The eggs are laid on carrot leaves, and the highest numbers of nymphs are observed in the middle of August. Thereafter, the emergence of new adults starts, and these adults move to spruce in the autumn (Rygg, 1977). These adults disperse back to carrot next spring, providing a pathway for transmission of CLso from one carrot field to another, if the bacteria are maintained within the vector over winter. Previously, retention and even increase of '*Candidatus Phytoplasma prunorum*' in its host-alternating psyllid vector, *Cacopsylla pruni*, was shown during the overwintering period on conifers (Thébaud et al., 2009). Overwintering bacteriferous *T. apicalis* are a plausible pathway for bridging the gap between carrot crops in subsequent years. However, the distance of movement and the flight capacity of the *T. apicalis* are not precisely known. Results from a previous inventory of overwintering sites suggest that the maximum dispersal distance is at least 1 km

(Kristoffersen and Anderbrant, 2007).

T. apicalis has been recorded as a carrot pest for approximately 100 years in Finland, Sweden, Norway, and Germany (Lundblad, 1929; Bey, 1931; Tiilikkala et al., 1996; Rygg, 1977), and for several decades in the Czech Republic and Switzerland (Láska, 1974; Burckhardt and Freuler, 2000). The geographical distribution of *T. apicalis* is even wider, including Denmark and the UK (Ossiannilsson, 1992), however, in Denmark there are no reports of psyllid damages in carrot since the early 1900s (Rostrup, 1921) and in the UK this psyllid is a rare species. Most forests in the Denmark and UK consist of broadleaved tree species that are not suitable for overwintering of *T. apicalis* (Rygg, 1977). This may suggest that finding suitable overwintering sites at a reachable distance from the summer host is a crucial factor for the build-up of *T. apicalis* populations and subsequent plant health problems associated with CLso in apiaceous crop species. The severity of carrot psyllid damage in carrots has increased in Finland and in Norway over the last two decades (Munyanzeza et al., 2014; Nissinen et al., 2020). Climate change can enhance the disease development in the fields as CLso titres in carrots increase with temperature (Nissinen et al., 2021). However, it is unknown whether the occurrence of CLso in carrot fields is related to landscape factors, such as the proximity of other carrot fields or the proximity of winter shelter plants like spruce trees.

Finding spatial relationships at the landscape level might provide an explanation for the current severity of CLso in Finland, and it might also provide clues for disease management. Finding solutions for management is critical because rapid damage formation caused by *T. apicalis*, and heavy reliance on pyrethroids for several decades have driven carrot growers to spray insecticides for vector control at ever shorter intervals, down to three days between sprays, creating a situation that is considered environmentally unsustainable and unprofitable.

The aim of this study was to quantify landscape effects on CLso occurrence in carrot fields. To determine the relationship between habitat connectedness for vectors and disease, the area of carrot fields was defined at different distances from the carrot fields evaluated for the presence of CLso in 2013–2014, as well as the amount of possible overwintering habitats in the surroundings of the fields based on GIS analyses from spatial databases. In addition, soil type of the carrot fields was taken into consideration, because of farmers' reports that the psyllid damage is often concentrated in parts of the field with a higher clay content in the soil (personal communication A. Hyytiäinen 4 July 2016). Logistic regression was used to analyse this data as it concerned the probability of a binary event (CLso present /absent in a location) and a set of explanatory variables (Hastings et al., 2005).

We tested the following hypotheses: 1) CLso incidence increases if carrot cultivation area increases, 2) the incidence increases if spruce branch biomass in the area increases, 3) the incidence increases if there is carrot as well as spruce in the area (interaction), 4) the incidence increases if the soil type is clay rather than sandy or organic (peat), 5) the incidence increases if the landscape has a long-term history of carrot cultivation, 6) the incidence varies by year and 7) the incidence is affected by the amount of deciduous trees in the area.

2. Materials and methods

The occurrence of CLso infection in carrots was studied in 104 randomly selected carrot fields on commercial farms in all the main carrot cultivation areas of Finland in 2013–2014: 77 fields were selected in 2013 and 27 different fields in 2014 (Appendix A.1). Each of the fields was classified as infested with CLso or not infested with CLso. To check for presence of CLso, in each field, samples of four plants from three foliar symptom categories were collected: plants with no signs of the vector or the bacterium, plants with leaf-curling symptoms (indicating vector presence) but no leaf discoloration, and plants with leaf-curling symptoms and discoloration indicating potential infection with CLso (Haapalainen et al., 2017). If fewer than four plants with symptoms of each category were found, only those plants were collected. If no foliar

symptoms of insect feeding or infection with CLso were observed during the survey of the field, only four symptomless plants were collected. The carrot samples were tested for presence of CLso by conventional PCR assay with primers OA2 and Lsc2, as described previously (Liefting et al., 2009; Haapalainen et al., 2017). We classified a field as "positive" if any of the collected plants gave a positive PCR result and as negative if no CLso was detected.

We used logistic regression to analyse the data because the data represent independent binary responses (no disease/disease), and fields were assumed to be spatially independent (i.e. they were spread over a large area). In the logistic model the probability for disease follows the equation:

$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_5$ where p is the probability a field is found infected given the values of five predictor variables x_i and six parameters $\beta_0 - \beta_5$. These five predictor variables were (1) carrot area in the landscape around the field; (2) year (2013 as reference; parameter indicates the effect of 2014 relative to 2013); (3) biomass of branches of conifer trees in the landscape around the field; (4) biomass of branches of deciduous trees in the landscape around the field; and (5) soil type (details provided below). The model assumes a linear relationship between the predictor variables ($x_1 \dots x_5$) and the response (p), using a logit-link function, i.e. $\ln\left(\frac{p}{1-p}\right)$.

The first predictor variable, carrot cultivation intensity (the number of carrot fields and their total area) in the surroundings of each field in the previous year, was calculated using data from the Finnish Food Authority (Ruokavirasto) database (<https://www.ruokavirasto.fi/tieto-toa-meista/avointieto/tiedonluovutukset/peltoohkoaineisto/>). To explore the distance over which carrot cultivation exerts an influence on CLso incidence in the following year, carrot cultivation intensity was quantified within radii of 500 m, 1 km, 2 km, 3 km, 4 km, 5 km and 10 km from the centre of each field in each year. The predictive power of regressions for different landscape radii was compared. The number of carrot cultivation years since 2006 in each field was calculated from the same database and used as an alternative rather than an extra regressor because of high correlation of this variable with the area proportion of carrot in the landscape ($r = 0.61, 0.91, 0.89, 0.89, 0.91, 0.92$ and 0.93 for radii 0.5, 1, 2, 3, 4, 5 and 10 km, respectively; $P < 0.001$). The second predictor variable, biomass of Norway spruce branches, was also

quantified at radii of 500 m, 1 km, 2 km, 3 km, 4 km, 5 km, 10 km radii from the centre of each field as well as from the same distance from the field edges (Fig. 1). These data were calculated from the Finnish multi-source forest inventory database (<https://kartta.luke.fi/index-en.html>) using ArcGIS Pro. The branch biomass was used instead of trunk biomass, since the psyllids overwinter at the base of the needles (33), i.e. the branch biomass represent better the availability of overwintering sites. As a third predictor variable, the branch biomass of deciduous trees within radii of 100 m, 200 m, 500 m, 1 km and 2 km from the field edges was calculated. Finally, soil types at the centre of each field were received from the Geological Survey of Finland's spatial database superficial deposits of Finland 1:200 000 (sediment polygon) (<https://hakku.gtk.fi/en/locations/search>). Soil types in the fields were classified in three classes: organic soil (thin or deep peat layer, 23 fields), clay (11 fields) and moraine deposits (coarse and fine-grained sediments without clay, 70 fields).

In the first analysis step, we analysed the relationship between the incidence of CLso and the carrot cultivation intensity in the preceding year. We considered two variables to express the intensity: number of carrot fields and total carrot area, and considered seven different radii, for a total of 14 analyses. In addition to the metric for carrot intensity, the year of measurement was included as a categorical variable:

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2$$

Where β_0 is the intercept, x_1 is the intensity within the considered radius (either area in hectares or number of fields), and x_2 is a categorical variable for year ($x_2 = 0$ for 2013 and $x_2 = 1$ for 2014). Different values of x_1 were used for different scales (i.e. values of x_1 increased when radius increased, and unit of measurement for area and numbers of fields are not the same).

In the second analysis step, different proxies for spruce branch biomass were added to the model, as well as the biomass of spruce branches-by-carrot cultivation interaction, carrot cultivation years since 2006 and soil type (clay soils, coarse mineral soils, and organic soils). Carrot cultivation years since 2006 and biomass of spruce branches-by-carrot cultivation interaction were not included in the final model because their effects were not statistically significant. In addition, the number of carrot cultivation years since 2006 was correlated with carrot



Fig. 1. Illustration of two landscapes differing in the amount of spruce branch biomass in a radius of 500 m from the edges of a carrot field inspected for the occurrence of *Candidatus Liberibacter solanacearum*. The landscape in A) had a high biomass of spruce branches while the landscape in B) had a low spruce tree biomass in the surroundings of the carrot field.

cultivation intensity in the landscape, resulting in a multicollinearity problem.

As a third step, we explored whether the best model found in the second step can be improved by adding the effect of the biomass of deciduous tree branches to the previously defined best models at different scales. We thereby found a high correlation between the biomass of Norway spruce and deciduous tree branches. Finally soil type was added as a categorical predictor.

Results of the finally estimated models are presented as odds ratios (OR) associated with a change in an independent variable. The ‘odds’ of an event are defined as the probability of the outcome event occurring divided by the probability of the event not occurring. Now the event is the incidence of CLso. An ‘odds ratio’ is one set of odds divided by another. If the value of the estimated parameter is b_i , the odds of CLso is increased by a factor $\exp(b_i)$ if x_i is increased by one unit. If a positive relationship was found, the odds ratio will be larger than 1, indicating that the probability of CLso in the field is increased. If the 95% confidence interval of the OR does not include the value of 1.00, a statistically significant positive relationship for occurrence of CLso is indicated. Models were fitted using SAS procedure LOGISTIC (SAS, 2013).

3. Results

The relationship between the incidence of CLso in a focal field and the area of carrot cultivation in the landscape around that field in the previous year was significant ($P < 0.05$) or highly significant ($P < 0.001$) at the larger scales, from 3 km upwards, but not at smaller scales of 3 km or less (Table 1), indicating that CLso is more prevalent in landscapes with widespread carrot cultivation. Likewise, strong relationships were found between CLso incidence and the number of carrot fields in the wider area (within 3–10 km).

The interaction between the biomass of spruce branches and the area of carrot cultivation was not statistically significant at any combination of scales ($p > 0.10$ always), and therefore only the main effects were further explored. The area of carrot cultivation and the number of carrot fields were compared to find the better predictor. The models with area of carrot cultivation had the higher log likelihood as compared to models with number of carrot fields (e.g. for a radius of 5 km: -6.8 vs. -9.5) and carrot cultivation area was therefore used for further model estimation. The estimated probability, \hat{p} , for the CLso intensity variable in relation to total cropping area within 5 km is illustrated in Fig. 2 A. Parameter values for the fitted model are: $b_0 = -0.3522 \pm 0.7238$ (intercept), $b_1 = 0.0676 \pm 0.0234$ ($P < 0.01$) (effect of carrot area), and $b_2 = 0.5561 \pm 0.2651$ ($P < 0.04$) (2014 vs 2013). Model fit confirmed that CLso incidence increases with the cultivation intensity of carrot in the preceding year. This landscape effect extended over a large distance, and is estimable at distances up to 10 km.

The effect of spruce branch biomass nearby the carrot fields was tested by adding biomass calculated at radii of 100 m, 200 m, 500 m, 1 km and 2 km from the field edges and at radii of 500 m, 1 km, 2 km, 3 km, 4 km, 5 km, 10 km from the middle point of each field (i.e. using the same spatial scales as for the carrot cultivation area). The biomass within 200 m distance from the field edges was the best explanatory

variable (Table 2).

CLso incidence increased as spruce branch biomass increased in the surroundings of the field. The increase due to spruce in the area was particularly relevant if the carrot area in the surroundings was low or moderate (Fig. 2B,C). When the carrot cultivation area in the surroundings of the fields was high (Fig. 2D), adding the spruce branch biomass to the model did not increase the estimated probability of CLso by much because the probability was already very high (0.8–0.9), even if the branch biomass dropped to zero.

The difference in CLso incidence between coarse mineral soils and peat soils was not significant (OR 1.22, 95%CI 0.36–4.14). However, the difference between clay and peat soils was significant at a level of 5% (OR 8.56, 95%CI 1.03–75.46), which supports the fourth hypothesis: CLso incidence increased if the soil type was clayey rather than peaty. The difference between clay and coarse mineral soil was marginally significant (OR 7.00, 95%CI 0.67–73.07).

In the third step of analysis, biomass of deciduous trees was added to the model to test the expectation that deciduous trees would not be related to CLso incidence because the vector psyllid *T. apicalis* does not overwinter on them. Biomass of deciduous trees had statistically a marginally significant effect ($P = 0.06$ – 0.09), depending on the radius at which the biomass was calculated from the field edges, and CLso occurrence decreased with increasing biomass of deciduous trees near the carrot field. At the same time, the effect of biomass of spruce branches, also included in the model, almost doubled. These two biomass variables are highly correlated (Spearman’s rank-order correlation coefficient: $r = 0.77$, $P < 0.001$) and thus the separate effects of spruce and deciduous trees could not be identified from the dataset due to collinearity. After removing the biomass of spruce branches from the model, the biomass of deciduous trees did not have a significant effect ($P = 0.82$), but without deciduous trees in the model, spruce had a significant effect. These results indicated that the biomass of deciduous trees did not have a biologically meaningful relationship with CLso occurrence and therefore the effect was removed from the model in agreement with the initial hypothesis that deciduous trees do not affect the incidence of CLso.

In conclusion, the probability of CLso infection significantly increased with increasing area of carrot cultivation area, up to a 10 km radius. Further, spruce biomass within 200 m distance from the field edges affected CLso infection in landscapes with a low to medium area proportion of carrot cultivation. Disease incidence was higher on clay soils than on mineral or peaty soils.

4. Discussion

Results of this data analysis show that the incidence of CLso in carrot fields is related to two landscape factors: the carrot cultivation area in the previous year up to 10 km radius and the biomass of spruce branches in the surroundings of the field, which indicates the importance of connectivity in the landscape. The relationship of CLso with both the prevalence of the host plant, carrot, and the winter shelter plant of the vector *T. apicalis* indicates that the pathogen is circulating within the landscapes between the carrot crops via the vector which overwinters on

Table 1

Odds ratios (OR) for the carrot cultivation area and the number of carrot fields at different distances from the inspected fields. If $OR > 1\%$ and 95% confidence interval did not include a value of 1.00, a statistically significant positive relationship for occurrence of ‘*Candidatus Liberibacter solanacearum*’ was found.

radius	The area of carrot fields				The number of carrot fields			
	OR*	95%L	95%U	P-value	OR	95%L	95%U	P-value
500 m	0.96	0.85	1.08	0.50	1.21	0.81	1.79	0.35
1 km	0.98	0.89	1.07	0.60	1.04	0.84	1.28	0.71
2 km	1.03	0.97	1.09	0.41	1.13	0.96	1.32	0.15
3 km	1.05	1.00	1.10	0.04	1.19	1.05	1.34	< 0.01
4 km	1.07	1.02	1.11	< 0.01	1.23	1.10	1.37	< 0.001
5 km	1.07	1.03	1.11	< 0.01	1.22	1.10	1.34	< 0.001
10 km	1.07	1.04	1.10	< 0.001	1.18	1.10	1.27	< 0.001

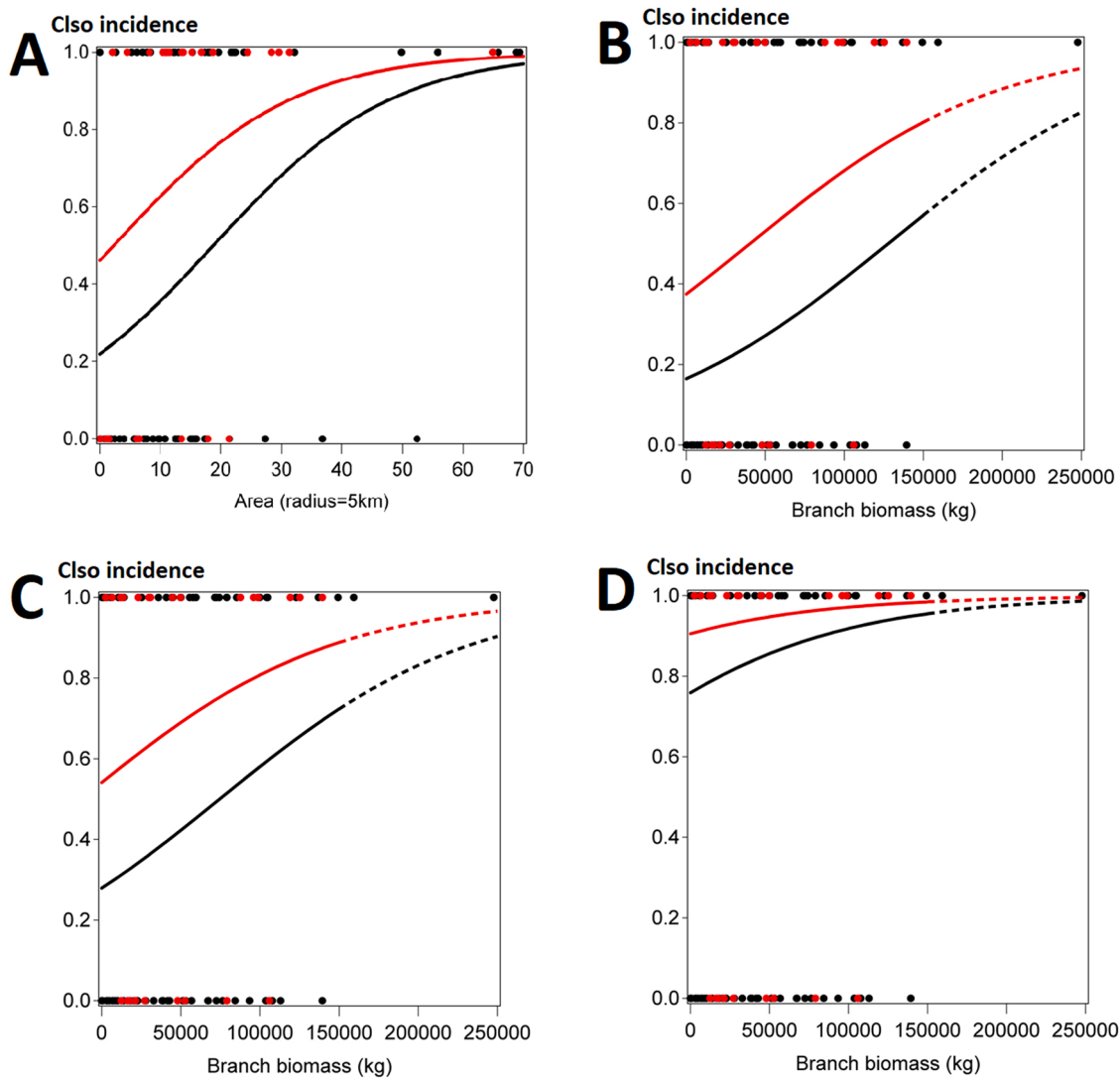


Fig. 2. Observed and fitted incidence (presence/absence) of *Candidatus Liberibacter solanacearum* in carrots A) in relation to the total cultivation area (ha) of carrot within a 5 km radius around the field centre in the preceding year and for the average spruce branch mass within 200 m from the edges of the field, and in relation to the total spruce branch mass within 200 m from the edges of the field parcels, when the surrounding carrot area is B) 5 ha, C) 15 ha, or D) 45 ha. Black data points and the black fitted line are for 2013 while red points and the red fitted line are for 2014. Each data point represents a single field. The fitted lines in each panels B-D take into account the different areas of carrot production in the preceding year and its effect on CLso incidence. The dotted part of the line is based only on a few observations.

Table 2

Odds ratios (OR) for the effect of spruce branch biomass at different distances from the inspected fields on the incidence of CLso. Significant effects were found at all distances from the edge of the focal fields except the shortest of 100 m, indicating landscape scale effects of Norway spruce on the incidence of CLso.

Branch biomass				
radius of circles	OR*	95%L	95%U	P-value
100 m	1.18	0.95	1.47	0.14
200 m	1.24	1.06	1.44	< 0.01
500 m	1.03	1.01	1.06	0.02
1 km	1.01	1.00	1.02	0.04
2 km	1.00	1.00	1.01	0.03

spruce. The psyllids multiply on carrot and the bacteria multiply in the carrot and in the psyllids, which then overwinter on the spruce trees and the next year colonize newly sown carrot fields. The carrot cultivation area had a significant effect on CLso incidence at distances from 3 km to 10 km, but not at shorter distances from the focal field. The wideness of the area within which the significant effects were found may suggest

that the vector can move several kilometres between the winter shelter plant (spruce) and the summer host (carrot). It may also indicate that the effect of carrot cultivation proportion becomes particularly important for the circulation of CLso in landscapes if carrot is grown on a high proportion of a large area, where an increase in spruce branch biomass did not further increase the probability of CLso occurrence in carrot fields. This suggests that carrot cultivation area determines the landscape level cycling of the pathogen. This is plausible as smaller areas of carrot cultivation surrounded by greater areas without carrot may experience more "spill-over" of bacteriferous vectors without sufficient bacteriferous vectors returning (cf. Skelsey et al., 2005). The small scale of the effect of spruce branch mass seems at odds with the much wider scale at which carrot cultivation affects CLso. The difference in the spatial scale of the carrot and spruce effects may be related to differences in the spatial pattern of carrots and spruce in Finland. The carrots are distributed in pockets of arable land that occur as islands in areas that have high coverage of spruce. Thus, the carrot in the landscape is the true limiting factor for the disease occurring. On the other hand, spruce is available anywhere in Finland, and its influence on CLso is mainly

when there are a lot of spruce really close to the field. Finally, the large scale of the carrot effect can also be a statistical phenomenon in the sense that carrot cultivation area over a bigger landscape circle gives a more robust estimate of carrot prevalence in an area than carrot cultivation area in a smaller circle around the local field. More work is needed to further elucidate the mechanisms underlying the differences in spatial scale of the effects of carrot area and spruce branch mass.

The flight capacity of *T. apicalis* is not well known. However, in a previous study we found substantial differences in psyllid pressure between carrot fields (Haapalainen et al., 2018a). Psyllid pressure dropped close to zero within 7 kilometres distance from the field with the highest psyllid density. In comparison, another psyllid species, *Diaphorina citri*, the vector of citrus greening (Huanglongbing), is capable of flying 2 km in search for necessary resources (Lewis-Rosenblum et al., 2015). Dispersal of *D. citri* was observed up to 2.3 km in a dense forest in Florida, and the maximum flight duration of *D. citri* was consistent with a flight distance of 2.4 km (Martini et al., 2013, 2014).

In an inventory of overwintering sites, the highest numbers of *T. apicalis* in conifer trees were found within 250 m from carrot fields, indicating that the psyllids colonizing the spruce trees were most likely from the nearby carrot fields (Kristoffersen and Anderbrant, 2007). The observations in this study and in a Swedish study (Kristoffersen and Anderbrant, 2007) suggest that *T. apicalis* migrate short distances from their summer host to winter shelter plants. In Switzerland, the autumn migration of *T. apicalis* continued up to November (Burckhardt and Freuler, 2000). Personal observations by Nissinen suggest that the autumn migration from carrots to spruce can continue until October in Finland. This, in turn, may suggest that low day time temperatures restrict the psyllids' flight capacity to the overwintering sites. In line with this, during winter, evidence was found only of short distance flight of the Asian citrus psyllid, *Diaphorina citri*, (Hall and Hentz, 2011). In the case of *T. apicalis*, the carrot fields are situated at different distances from the overwintering sites in the following year, due to the crop rotation. Therefore, psyllids may have to search for the summer host over a greater distance than they flew in the autumn to the winter host, which may be facilitated by the higher day temperature during the summer migration (late May–July). This in turn may explain why the carrot cultivation area has a significant effect on the CLso occurrence within 3–10 km distance, while the spruce area is only significant up to 200 m.

The positive effect of the biomass of spruce in the landscape is in accordance with the previous observations of *T. apicalis* overwintering on conifers (Rygg, 1977; Valterová et al., 1997; Kristoffersen and Anderbrant, 2007), and it may explain why the populations of *T. apicalis* have so far not developed to damaging levels in Denmark and the UK, where the connectedness between carrot and spruce trees is lower than in Finland, Sweden and Norway. In Finland, finding overwintering sites is not a limiting factor in the carrot psyllid life cycle, because over 70% of the land area is covered by forests, and Norway spruce is one of the most common tree species, also in crop-dominated areas.

Herbaceous seminatural habitat elements near the fields, such as ditch banks and road verges, were not quantified in this study, because previous studies showed that *T. apicalis* was not able to hibernate on herbaceous plants i.e. on carrots (Rygg, 1977) or on Poaceae (Valterová et al., 1997). Previously, CLso infection was found in some cow parsley plants (Haapalainen et al., 2018b). However, genetic studies revealed that CLso in cow parsley and the associated psyllid species, *Trioza anthrisci*, represent different strains than the bacteria in *T. apicalis* and in cultivated plants (Haapalainen et al., 2018b). Thus, *T. apicalis* and *T. anthrisci* form separate populations on their own host plants (Haapalainen et al., 2018b).

Soil type had a significant effect on CLso occurrence, with CLso being more prevalent on clayey than peaty or mineral soils. This could be due to a slower early development of carrot in the heavier clay soils compared to sandy or organic soils which warm up more quickly in the spring. Smaller carrots are more prone to develop severe symptoms in

response to psyllid feeding than larger carrot plants (Nissinen et al., 2007, 2012) and the effect of the bacterial inoculum delivered by a psyllid is relatively greater in a smaller carrot. Similarly, yellowing viruses in sugarbeet are translocated to sink tissues, but leaves formed before the plant gets infected are not affected by the disease, making the plant more tolerant if it is affected at a later growth stage (De Koeijer and van der Werf, 1995). Furthermore, in the case of sugarbeet viruses, the spread within the field is greatly facilitated if the first (primary) infections occur on young plants, because vectors build larger populations on younger plants than on older plants that exhibit mature plant resistance (Williams et al., 1999). It is also likely that plant size affects vector movement in the canopy (Nemecek, 1993).

Observations supporting these hypotheses have been previously done on potato with the psyllid *Bactericera cockerelli* and the American haplotypes of CLso. The most severe symptoms of zebra chip disease developed in plants exposed to the psyllids at an early growth stage, suggesting that the shoot structures may become less palatable for the potato psyllid feeding at the later growth stages (Gao et al., 2009). Furthermore, the amount of CLso transmitted to the plant by a psyllid can affect the plant response. The CLso titre varies largely between individual specimens of carrot psyllid, and in the carrot seedlings exposed to psyllids with low titre of CLso the bacterial multiplication was limited and the plants did not develop disease symptoms (Nissinen et al., 2014). Previously, potatoes exposed to potato psyllids bearing a low CLso titre were observed to express mild symptoms, in contrast to the lethal disease following exposure to psyllids with a high CLso titre (Alvarado et al., 2012).

What lessons can be learned from this study for *T. apicalis* control? In Finland, forest areas are large, and forestry is an important sector of industry. Therefore, removing spruce trees from carrot growing landscapes is not an option for psyllid control. However, if the carrot growers own the land between the fields, they could benefit from planting deciduous trees between the fields, i.e. increasing the distance from carrot field to the vectors' overwintering sites. As the results of this study suggest, the vector *T. apicalis* may be capable of reaching the summer hosts up to 5–10 km distance from the overwintering sites. If the carrots are grown in a cluster of several farms, and high psyllid pressure frequently occurs, insect-excluding netting covering the crop is an effective control option, which efficiently prevents the spread of CLso (Nissinen et al., 2020). Another option could be regional crop rotation (Helenius, 1995), to interfere with the vector population growth by removing the summer host from an area in cycles of a few years. Such an approach may be difficult to achieve if the land in an area is owned by multiple farmers who would have to coordinate their carrot growing decisions. It might, however, be possible in contract production where the contractor can define the production area for each year. In line with this, the biggest carrot growers actively seek new fields in areas with no previous carrot cultivation history, to reduce the need for carrot psyllid control.

Previously, in studies concerning pathosystem of *Candidatus Phytoplasma prunorum* and a host-alternating psyllid, *Cacopsylla pruni*, *C. pruni* showed lower infection rates on its summer host (Thébaud et al., 2009) whereas, the vector transmission ability was at its peak after the 8 months latent period i.e. when the psyllids returned from overwintering sites on conifers to *Prunus* spp. (Thébaud et al., 2009). *C. pruni* was found to migrate several kilometres from its summer hosts, *Prunus* spp., to overwintering sites on conifers in the mountains. These results suggest that overwintering hosts and migration have a high impact on the infectiveness of the vector (Thébaud et al., 2009). Similarly, a continued increase of '*Candidatus Phytoplasma mali*' was observed in *C. melanonura* during its stay on shelter plants and persistent infectivity without an intermediate reacquisition of the phytoplasma (Candian et al., 2020). Thébaud et al. (2009) suggest that this original transmission cycle may exist among other univoltine psyllid species overwintering as adults on conifers, and indeed the above-mentioned pathosystems greatly resemble that of CLso and *T. apicalis* in northern

Europe. These examples may indicate that the time spent on overwintering hosts and migration impact the infectiveness of a psyllid vector bearing a bacterial plant pathogen. Therefore overwintering conditions of psyllid vectors should be studied to better understand the epidemiology of these pathosystems. Furthermore, disturbing the connectedness between psyllid vectors' winter shelter plant and summer host could be an option to manage the pathogen dispersal. Regional crop rotation could break this connectedness for an annual crop, such as carrot, and studying the landscape epidemiology can provide the spatial scale at which the regional crop rotation should be managed.

In line with our results, *Bactericera cockerelli* was previously found to be more abundant in landscapes with high host connectivity and low crop diversity (Gutiérrez Illán et al., 2020). High connectivity between different solanaceous crops and large natural areas which contain wild hosts used for overwintering can enhance populations of this vector (Gutiérrez Illán et al., 2020). In a broader context, the results of this study confirm the notion that low diversity landscapes promote the aggravation of pest and disease problems and a need for greater control measures, up to the point that such measures may no longer work, due to pesticide resistance. Indeed, some Finnish carrot growers are at the brink of giving up on carrots or dramatically changing their practices. The remedy is straightforward but difficult to attain: diversification. In several cases, it has been shown that increase in crop cultivation area in the surroundings increases abundance of pest insects (Hokkanen, 2000; Zaller et al., 2008; Lundblad et al., 2016). Also, pyrethroid resistance in pollen beetles was significantly affected by total proportion of oilseed rape in the region over a short term (Riggi et al., 2016). Therefore, a regional management program was suggested to control this problem (Riggi et al., 2016). Diversification would dilute the crop species in the wider landscape and thus make recolonization of a new crop after the winter less efficient for the same reason that intercrops mitigate plant disease epidemics due to host dilution (Zhu et al., 2000; Boudreau, 2013; Zhang et al., 2019). In line with this, O'Rourke and Jones (2011) observed that specialist insects were more affected by land use changes than generalists, and they predicted that landscape diversification will reduce insecticide use. However, achieving host dilution at the landscape level is challenging, because it negates the scale benefits attained when cropping practices are concentrated in the vicinity of the associated industries that are part of the same supply chain, a phenomenon known as agglomeration economies. Such agglomeration economies work up to the point where the concentration mechanism itself causes problems that can best be solved by diversification and spreading out (De Roest et al., 2018). Carrot growers in Finland are now moving into that direction. They diversify crop choice in areas with a history of carrots, they adapt their cropping practices (e.g. by use of insect-exclusion netting), and they spread out carrot cultivation over wider areas without a history of carrot cultivation and without a large reservoir of CLso. Similar remedies could be used elsewhere to overcome the devastating problems that find their origin in a lack of crop diversity at landscape level, promoting circulation of pests and pathogens.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108137.

References

- Alexandridis, N., Marion, G., Chaplin-Kramer, R., Dainese, M., Ekroos, J., Grab, H., Jonsson, M., Karp, D.S., Meyer, C., O'Rourke, M.E., Pontarp, M., Poveda, K., Seppelt, R., Smith, H.G., Martin, E.A., Clough, Y., 2021. Models of natural pest control: Towards predictions across agricultural landscapes. *Biol. Control* 163, 104761 <https://doi.org/10.1016/j.biocontrol.2021.104761>.
- Alfaro-Fernández, A., Hernández-Llopis, D., Font, M.I., 2017. Haplotypes of 'Candidatus Liberibacter solanacearum' identified in Umbelliferous crops in Spain. *Eur. J. Plant. Pathol.* 149, 127–131. <https://doi.org/10.1007/s10658-017-1172-2>.
- Alvarado, V.Y., Odokonyero, D., Duncan, O., Mirkov, T.E., Scholthof, H.B., 2012. Molecular and physiological properties associated with zebra complex disease in potatoes and its relation with *Candidatus Liberibacter* contents in psyllid vectors. *PLoS One* 7 (5), e37345. <https://doi.org/10.1371/journal.pone.0037345>.
- Angelella, G.M., Holland, J.D., Kaplan, I., 2016. Landscape composition is more important than local management for crop virus-insect vector interactions. *Agr. Ecosyst. Environ.* 233, 253–261. <https://doi.org/10.1016/j.agee.2016.09.019>.
- Antolínez, C.A., Fereres, A., Moreno, A., 2017a. Risk assessment of 'Candidatus Liberibacter solanacearum' transmission by the psyllids *Bactericera trigonica* and *B. tremblayi* from Apiaceae crops to potato. *Sci. Rep.* 7, 45534. <https://doi.org/10.1038/srep45534>.
- Antolínez, C., Fereres, A., Moreno, A., 2017b. Sex-specific probing behaviour of the carrot psyllid *Bactericera trigonica* and its implication in the transmission of 'Candidatus Liberibacter solanacearum'. *Eur. J. Plant. Pathol.* 147, 627–637. <https://doi.org/10.1007/s10658-016-1031-6>.
- Bertolini, E., Teresani, G.R., Loiseau, M., Tanaka, F.A.O., Barbé, S., Martínez, C., Gentil, P., López, M.M., Cambra, M., 2015. Transmission of 'Candidatus Liberibacter solanacearum' in carrot seeds. *Plant. Pathol.* 64, 276–285. <https://doi.org/10.1111/ppa.12245>.
- Bey, N.S., 1931. Untersuchungen über Möhrenblattsäuger. *Z. Angew. Entomol.* 18, 175–188.
- Boland, G.J., Melzer, M.S., Hopkin, A., Higgins, V., Nassuth, A., 2004. Climate change and plant diseases in Ontario. *Can. J. Plant. Pathol.* 26 (3), 335–350. <https://doi.org/10.1080/07060660409507151>.
- Boudreau, M.A., 2013. Diseases in intercropping systems. *Annu. Rev. Phytopathol.* 51, 499–519. <https://doi.org/10.1146/annurev-phyto-082712-102246>.
- Bove, J.M., 2006. Huanglongbing: a destructive, newly-emerging, century-old disease of citrus. *J. Plant. Pathol.* 88, 7–37. <https://doi.org/10.4454/jpp.v88i1.828>.
- Burckhardt, D., Freuler, J., 2000. Jumping plant-lice (Hemiptera, Psyllodea) from sticky traps in carrot fields in Valais. In: *Sch. Entomol. Ges.* 73. Mit, Switzerland, pp. 191–209.
- Candian, V., Monti, M., Tedeschi, R., 2020. Temporal dynamics of 'Ca. Phytoplasma mali' load in the insect vector *Cacopsylla melanoneura*. *Insects* 11 (9), 592. <https://doi.org/10.3390/insects11090592>.
- Carminati, G., Satta, E., Paltrinieri, S., Bertaccini, A., 2019. Simultaneous evaluation of 'Candidatus Phytoplasma' and 'Candidatus Liberibacter solanacearum' seed transmission in carrot. *Phytopathog. Moll.* 9, 141–142.
- Cicero, J.M., Fisher, T.W., Qureshi, J.A., Stansly, P.A., Brown, J.K., 2017. Colonization and intrusive invasion of potato psyllid by 'Candidatus Liberibacter solanacearum'. *Phytopathology* 107, 36–49.
- Clafin, S.B., Jones, L.E., Thaler, J.S., Power, A.G., Lewis, O., 2017. Crop-dominated landscapes have higher vector-borne plant virus prevalence. *J. Appl. Ecol.* 54, 1190–1198. <https://doi.org/10.1111/1365-2664.12831>.
- Dala-Paula, B.M., Plotto, A., Bai, J.H., Manthey, J.A., Baldwin, E.A., Ferrarezi, R.S., Gloria, M.B., 2019. Effect of huanglongbing or greening disease on orange juice quality, a review. *Front. Plant. Sci.* <https://doi.org/10.3389/fpls.2018.01976>.
- De Koeijer, K.J., van der Werf, W., 1995. Effects of yellowing viruses on light interception and light use efficiency of the sugarbeet crop. *Crop Prot.* 14, 291–297. [https://doi.org/10.1016/0261-2194\(94\)00003-Q](https://doi.org/10.1016/0261-2194(94)00003-Q).
- De Roest, K., Ferrari, P., Knickel, K., 2018. Specialisation and economies of scale or diversification and economies of scope? Assessing different agricultural development pathways. *J. Rural. Stud.* 59, 222–231. <https://doi.org/10.1016/j.jrurstud.2017.04.013>.
- European Commission, 2020. Farm to Fork Strategy. URL: https://ec.europa.eu/food/system/files/2020-05/f2f_action-plan_2020_strategy-info_en.pdf (2021-6-27).
- Gao, F., Jifon, J., Yang, X., Liu, T.X., 2009. Zebra chip disease incidence on potato is influenced by timing of potato psyllid infestation, but not by the host plants on which they were reared. *Insect Sci.* 16, 399–408. <https://doi.org/10.1111/j.1744-7917.2009.01261.x>.
- Gutiérrez Illán, J., Bloom, E.H., Wohleb, C.H., Wenninger, E.J., Rondon, S.I., Jensen, A. S., Snyder, W.E., Crowder, D.W., 2020. Landscape structure and climate drive population dynamics of an insect vector within intensely managed agroecosystems. *Ecol. Appl.* 30 (5), e02109 <https://doi.org/10.1002/eap.2109>.
- Haapalainen, M., Kivimäki, P., Latvala, S., Rastas, M., Hannukkala, A., Jauhainen, L., Lemmetty, A., Pirhonen, M., Virtanen, A., Nissinen, A.I., 2017. Frequency and

- occurrence of the carrot pathogen '*Candidatus Liberibacter solanacearum*' haplotype C in Finland. *Plant Pathol.* 66, 559–570. <https://doi.org/10.1111/ppa.12613>.
- Haapalainen, M., Latvala, S., Rastas, M., Wang, J., Hannukkala, A., Pirhonen, M., Nissinen, A.I., 2018a. Carrot pathogen '*Candidatus Liberibacter solanacearum*' haplotype C detected in symptomless potato plants in Finland. *Potato Res.* 61, 31–50. <https://doi.org/10.1007/s11540-017-9350-3>.
- Haapalainen, M., Wang, J., Latvala, S., Lehtonen, M.T., Pirhonen, M., Nissinen, A.I., 2018b. Genetic variation of '*Candidatus Liberibacter solanacearum*' haplotype C and characterization of a novel haplotype from *Trioxa urticae* and stinging nettle. *Phytopathology* 108, 925–934. <https://doi.org/10.1094/PHYTO-12-17-0410-R>.
- Hall, D.G., Hentz, M.G., 2011. Seasonal flight activity by the Asian citrus psyllid in east central Florida. *Entomol. Exp. Appl.* 139, 75–85. <https://doi.org/10.1111/j.1570-7458.2011.01108.x>.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.* 8, 91–101. <https://doi.org/10.1111/j.1461-0248.2004.00687.x>.
- Helenius, J., 1995. Regional crop rotations for Ecological Pest Management (EPM) at landscape level. In *Integrated Crop Protection: Towards Sustainability?* British Crop Protection Council Symposium Proceedings. 63, 255–260.
- Hokkanen, H.M., 2000. The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. *Entomol. Exp. Et. Appl.* 9, 141–149. <https://doi.org/10.1046/j.1570-7458.2000.00652.x>.
- Juroszek, P., von Tiedemann, A., 2013a. Plant diseases, insect pests and weeds in a changing global climate: a review of approaches, challenges, research gaps, key studies and concepts. *J. Agric. Sci.* 151, 163–188. <https://doi.org/10.1017/S0021859612000500>.
- Kristoffersen, L., Anderbrant, O., 2007. Carrot psyllid (*Trioxa apicalis*) winter habitats - insights in shelter plant preference and migratory capacity. *J. Appl. Entomol.* 131, 174–178. <https://doi.org/10.1111/j.1439-0418.2007.01149.x>.
- Láska, P., 1974. Studie über den Möhrenblattfloh (*Trioxa apicalis* Först.) (Triozidae, Homoptera). *Acta Sci. Nat. Acad. Sci. Bohemoslov.* 8, 1–44.
- Lewis-Rosenblum, H., Martini, X., Tiwari, S., Stelinski, L.L., 2015. Seasonal movement patterns and long-range dispersal of Asian citrus psyllid in Florida citrus. *J. Econ. Entomol.* 208, 3–10. <https://doi.org/10.1093/jee/tou008>.
- Liefting, L.W., Weir, B.S., Pennycook, S.R., Clover, G.R.G., 2009. '*Candidatus Liberibacter solanacearum*', a liberibacter associated with plants in the family Solanaceae. *Int. J. Syst. Evol. Microbiol.* 59, 2274–2276. <https://doi.org/10.1099/ijls.0.007377-0>.
- Loiseau, M., Renaudin, I., Cousseu-Suhard, P., Lucas, P.M., Forveille, A., Gentit, P., 2017. Lack of evidence of vertical transmission of '*Candidatus Liberibacter solanacearum*' by carrot seeds suggests that seed is not a major transmission pathway. *Plant Dis.* 101, 2104–2109. <https://doi.org/10.1094/PDIS-04-17-0531-RE>.
- Lundblad, O., 1929. Morotbladlöpnan *Trioxa viridula* Zett. Dess biologi och uppträdande som skadedjur i Sverige. Meddelande N:o 350 från Centralanstalten för försöksväsendet på jordbruksområdet. *Lantbr. Avd.* 55, 1–45.
- Martini, X., Addison, T., Fleming, B., Jackson, I., Pelz-Stelinski, K., Stelinski, L.L., 2013. Occurrence of *Diaphorina citri* (Hemiptera: Liviidae) in an unexpected ecosystem: the Lake Kissimmee State Park Forest, Florida. *Florida Entomol.* 96, 658–660. <https://doi.org/10.1653/024.096.0240>.
- Martini, X., Hoyte, A., Stelinski, L.L., 2014. Abdominal color of the Asian citrus psyllid (Hemiptera: Liviidae) is associated with flight capabilities. *Ann. Entomol. Soc. Am.* 107, 842–847. <https://doi.org/10.1603/AN14028>.
- Monger, W.A., Jeffries, C.J., 2017. A survey of '*Candidatus Liberibacter solanacearum*' in historical seed from collections of carrot and related Apiaceae species. *Eur. J. Plant. Pathol.* 150, 803–815. <https://doi.org/10.1007/s10658-017-1322-6>.
- Munyanze, J.E., 2012. Zebra chip disease of potato: biology, epidemiology, and management. *Am. J. Potato Res.* 89, 329–350. <https://doi.org/10.1007/s12230-012-9262-3>.
- Munyanze, J.E., Fisher, T.W., Sengoda, V.G., Garcynski, S.F., Nissinen, A., Lemmetty, A., 2010a. First report of '*Candidatus Liberibacter solanacearum*' associated with psyllid-affected carrots in Europe. *Plant Dis.* 94, 639. <https://doi.org/10.1094/PDIS-94-5-0639A>.
- Munyanze, J.E., Fisher, T.W., Sengoda, V.G., Garczynski, S.F., Nissinen, A., Lemmetty, A., 2010b. Association of '*Candidatus Liberibacter solanacearum*' with the psyllid, *Trioxa apicalis* (Hemiptera: Triozidae). *Eur. J. Econ. Entomol.* 103, 1060–1070. <https://doi.org/10.1603/EC10027>.
- Munyanze, J.E., Sengoda, V.G., Sundheim, L., Meadow, R., 2014. Survey of '*Candidatus Liberibacter solanacearum*' in carrot crops affected by the Psyllid *Trioxa apicalis* (Hemiptera: Triozidae). *Nor. J. Plant. Pathol.* 96, 397–402. <https://doi.org/10.4454/JPP.V96I2.019>.
- Nemecek, T., 1993. The role of aphid behavior in the epidemiology of potato virus Y: a simulation study. Swiss Federal Institute of Technology Zurich, Obersiggental, Switzerland. 232 p. (Ph.D. thesis).
- Nissinen, A.I., Haapalainen, M., Jauhiainen, L., Lindman, M., Pirhonen, M., 2014. Different symptoms in carrots caused by male and female carrot psyllid feeding and infection by '*Candidatus Liberibacter solanacearum*'. *Plant Pathol.* 63, 812–820. <https://doi.org/10.1111/ppa.12144>.
- Nissinen, A.I., Haapalainen, M., Ojanen, H., Pirhonen, M., Jauhiainen, L., 2021. Spreading of *Trioxa apicalis* and development of '*Candidatus Liberibacter solanacearum*' infection on carrot in the field conditions. *Ann. Appl. Biol.* 178, 39–50. <https://doi.org/10.1111/aab.12644>.
- Nissinen, A.I., Lemmetty, A., Pihlava, J.M., Jauhiainen, L., Munyanze, J.E., Vanhala, P., 2012. Effects of carrot psyllid (*Trioxa apicalis*) feeding on carrot yield and content of sugars and phenolic compounds. *Ann. Appl. Biol.* 161, 68–80. <https://doi.org/10.1111/j.1744-7348.2012.00551.x>.
- Nissinen, A.I., Pihlava, J.M., Latvala, S., Jauhiainen, L., 2020. Assessment of the efficiency of different control programs to reduce *Trioxa apicalis* Först. (Triozidae: Hemiptera) feeding damage and the spread of '*Candidatus Liberibacter solanacearum*' on carrots (*Daucus carota* ssp. *sativus* L.). *Ann. Appl. Biol.* 177, 166–177. <https://doi.org/10.1111/aab.12603>.
- Nissinen, A., Vanhala, P., Holopainen, J.K., Tiilikkala, K., 2007. Short feeding period of carrot psyllid (*Trioxa apicalis*) females at early growth stages of carrot reduces yield and causes leaf discoloration. *Entomol. Exp. Appl.* 125, 277–283. <https://doi.org/10.1111/j.1570-7458.2007.00628.x>.
- Lundblad, O., Rundlöf, M., G.Smith, H., Bommarco, R., 2016. Historical change and drivers of insect pest abundances in red clover seed production. *Agric. Ecosyst. Environ.* 233, 318–324. <https://doi.org/10.1016/j.agee.2016.09.025>.
- O'Rourke, M.E., Jones, L.E., 2011. Analysis of landscape-scale insect pest dynamics and pesticide use: an empirical and modeling study. *Ecol. Appl.* 21, 3199–3210. <https://doi.org/10.1890/10-1180.1>.
- Ossiannilsson, F., 1992. The Psylloidea (Homoptera) of Fennoscandia and Denmark, Leiden, New York, Köln. Brill.
- Parsa, S., Morse, S., Bonifacio, A., Chancellor, T.C.B., Condori, B., Crespo-Pérez, V., Hobbs, S.L.A., Kroschel, J., Ba, M.N., Rebaudo, F., Sherwood, S.G., Vanek, S.J., Faye, E., Herrera, M.A., Dangles, O., 2014. Obstacles to integrated pest management adoption in developing countries. *P. Natl. Acad. Sci. USA* 111 (10), 3889–3894. <https://doi.org/10.1073/pnas.1312693111>. (<https://doi.org/10.1073/pnas.1312693111>).
- Perilla-Henao, L., Casteel, C.L., 2016. Vector-borne bacterial plant pathogens: interactions with Hemipteran insects and plants. *Front. Plant. Sci.* 7, 1163. <https://doi.org/10.3389/fpls.2016.01163>.
- Plantegenest, M., Le May, C., Fabre, F., 2007. Landscape epidemiology of plant diseases. *J. R. S. Interface* 4, 963–972. <https://doi.org/10.1098/rsif.2007.1114>.
- Pleydell, D.R.J., Soubeyrand, S., Dallet, S., Labonne, G., Chadœuf, J., Jacquot, E., Thébaud, G., 2018. Estimation of the dispersal distances of an aphid-borne virus in a patchy landscape. *PLOS Comput. Biol.* 14 (4), e1006085. <https://doi.org/10.1371/journal.pcbi.1006085>.
- Riggi, L.G., Gagic, V., Bommarco, R., Eklom, B., 2016. Insecticide resistance in pollen beetles over 7 years – a landscape approach. *Pest. Manag. Sci.* 72, 780–786. <https://doi.org/10.1002/ps.4052>.
- Roos, J., Hopkins, R., Kvarnheden, A., Dixelius, C., 2011. The impact of global warming on plant diseases and insect vectors in Sweden. *Eur. J. Plant Pathol.* 129, 9–19. <https://doi.org/10.1007/s10658-010-9692-z>.
- Rostrup, S., 1921. Gulerods-Krusesygge, forarsaget af Gulerods-Bladluppen (*Trioxa viridula*). *Tidsskr. Landbr. Plant.* 27, 617–630.
- Rygg, T., 1977. Biological investigations on the carrot psyllid *Trioxa apicalis* Förster (Homoptera, Triozidae). *Meldinger fra Norges Landbrukshøgskole*, 56, 1–20.
- SAS Institute Inc. 2013. SAS/STAT® 13.1 User's Guide. Cary, NC: SAS Institute Inc. <https://support.sas.com/documentation/onlinedoc/stat/131/logistic.pdf>.
- Schneider, K., van der Werf, W., Cendoya, M., Mourits, M., Navas-Cortés, J.A., Vicent, A., Oude Lansink, A., 2020. Impact of *Xylella fastidiosa* subspecies *pauca* in European olives. *Proc. Natl. Acad. Sci.* 117 (17), 9250–9259. <https://doi.org/10.1073/pnas.1912206117>.
- Schneider, K., Skevas, I., Oude Lansink, A.J.G.M., 2021. Spatial spillovers on input-specific inefficiency of Dutch. *Arable Farms J. Agr. Econ.* 72, 224–243. <https://doi.org/10.1111/1477-9552.12400>.
- Skelsey, P., Rossing, W.A.H., Kessel, G.J.T., Powell, J.A., van der Werf, W., 2005. Influence of host diversity on development of epidemics: an evaluation and elaboration of mixture theory. *Phytopathology* 95, 328–338. <https://doi.org/10.1094/PHYTO-95-0328>.
- Teresani, G.R., Bertolini, E., Alfaro-Fernandez, A., Martinez, C., Tanaka, F.A.O., Kitajima, E.W., Rosello, M., Sanjuan, S., Ferrandiz, J.C., Lopez, M.M., Cambra, M., Font, M.I., 2014. Association of '*Candidatus Liberibacter solanacearum*' with a vegetative disorder of celery in Spain and development of a real-time PCR method for its detection. *Phytopathology* 104, 804–811. <https://doi.org/10.1094/PHYTO-07-13-0182-R>.
- Thébaud, G., Yvon, M., Alary, R., Sauvion, N., Labonne, G., 2009. Efficient transmission of '*Candidatus Phytoplasma prunorum*' is delayed by eight months due to a long latency in its host-alternating vector. *Phytopathology* 99, 265–273. <https://doi.org/10.1094/PHYTO-99-3-0265>.
- Tiilikkala, K., Ketola, J., Taivalmaa, S.L., 1996. Monitoring and threshold value for control of the carrot psyllid. *Integrated Control in Field Vegetable Crops. IOBC/WPRS Bulletin* 19(11), 18–24.
- Valterová, I., Nehlin, G., Borg-Karlson, A.K., 1997. Host plant chemistry and preferences in egg-laying *Trioxa apicalis* (Homoptera, Psylloidea). *Biochem. Syst. Ecol.* 25, 477–491. [https://doi.org/10.1016/S0305-1978\(97\)00028-8](https://doi.org/10.1016/S0305-1978(97)00028-8).
- Williams, I.S., van der Werf, W., Dewar, A.M., Dixon, A.F.G., 1999. Factors affecting the relative abundance of two coexisting aphid species on sugar beet. *Agr. For. Entomol.* 1, 119–125. <https://doi.org/10.1046/j.1461-9563.1999.00017.x>.
- Zaller, J.G., Moser, D., Drapela, T., Schmöger, C., Frank, T., 2008. Effect of within-field and landscape factors on insect damage in winter oilseed rape. *Agric., Ecosyst. Environ.* 123, 233–238. <https://doi.org/10.1016/j.agee.2007.07.002>.
- Zhang, C.C., Dong, Y., Tang, L., Zheng, Y., Makowski, D., Yu, Y., Zhang, F.S., van der Werf, W., 2019. Intercropping cereals with faba bean reduces plant disease incidence regardless of fertilizer input: a meta-analysis. *Eur. J. Plant Pathol.* 154, 931–942. <https://doi.org/10.1007/s10658-019-01711-4>.
- Zhu, Y.Y., Chen, H.R., Fan, J.H., Wang, Y.Y., Li, Y., Chen, J.B., Fan, J.X., Yang, S.S., Hu, L.P., Leung, H., Mewk, T.W., Teng, P.S., Wang, Z.H., Mundt, C.C., 2000. Genetic diversity and disease control in rice, 718–22 *Nature* 406. <https://doi.org/10.1038/35021046>.