1 The effect of spatial variation for 2 predicting aphid outbreaks

3 Christian Damgaard, Marianne Bruus, Jørgen Aagaard Axelsen

4 Department of Bioscience, Aarhus University, Vejløvej 25, 8600 Silkeborg, Denmark

5

6 4400 words, 2 tables, and 5 figures.

7

8 Corresponding author: Christian Damgaard, cfid@bios.au.dk, +45-30183153

9 Abstract

10 In order to improve forecasting of pest epidemics, it is important to know the spatial scale at which specific
 11 forecasts are reliable. To investigate the spatial scale of aphid outbreaks, we have developed a spatio-
 12 temporal stochastic aphid population growth model, and fitted the model to empirical spatial time-series
 13 aphid population data using a Bayesian hierarchical fitting procedure. Furthermore, detailed spatial data of
 14 the initial phases of population growth was investigated in a semivariogram. Our results suggest that there
 15 is limited spatial variation in the initial occurrence probability at a spatial scale of 10 km. Consequently, the
 16 results support the hypothesis that initial aphid population sizes and outbreaks may be predicted in fields
 17 within a 10 km radius. For farmers, this may imply that they can rely their decision of whether to spray
 18 against aphids on observations made by other nearby farmers or by the consultancy service.

19 *Keywords:* Aphid population model; spatial and temporal model; hierarchical models

20

21 Introduction

22 Insect pests are responsible for serious negative effects on food production. The common cereal aphids,
 23 the Cherry oat aphid (*Rhopalosiphum padi*), the Grain aphid (*Sitobion avenae*) and the Rose-grain aphid
 24 (*Metopolophium dirrhodum*), are known to cause considerable losses to winter wheat in large parts of the
 25 world, and these species have been estimated to cause losses of 700.000 tons per year in Europe due to
 26 direct damage (Wellings et al. 1989). On top of this figure comes the indirect damage due to virus
 27 transmission and sooty mold caused by the excretion of honeydew (Larsson 2005). Therefore, there is a
 28 great interest in controlling aphids in winter wheat, and a number of simulation models have been
 29 developed to predict the population development of these pests (e.g. Ciss et al. 2014; Duffy et al. 2017;
 30 Holst & Ruggle 1997; Klueken et al. 2009). Furthermore, some population dynamic models have been
 31 combined with modules on economy and pesticide choices to produce decision support systems with the
 32 aim of helping farmers optimizing the timing of pesticide applications. Such decision support systems
 33 include CPO in Denmark (Hagelskjær & Jørgensen 2003) and GETLAUS (Gosselke et al. 2001) in Germany. In
 34 a review of decision support systems, (Axelsen et al. 2012) concluded that farmers generally do not use
 35 decision support systems, and one of the reasons is that they do not find it worth the effort to spend time
 36 on estimating aphid input densities. Instead, many farmers perform precautionary insecticide treatments,
 37 which may not be economically sound.

38 The grain aphid is the most numerous aphid in winter wheat (Hansen 2003) in Denmark. In temperate
 39 regions, it overwinters on grasses as eggs. When temperatures rise in spring, the eggs hatch into unwinged
 40 females, which reproduce parthenogenetically. In the second or third generation, the majority of aphids are
 41 winged individuals, which migrate into the cereal fields. The formation of winged individuals is initiated by
 42 a complex combination of crowding (i.e. high densities), light and temperature (Hansen 2003). Despite high
 43 temperatures, crowding may be prevented by adverse temperatures, precipitation, predators and
 44 parasites. Once in the cereal fields, temperature is the key driver for aphid population growth, as shown by
 45 Jones (1979). However, population growth may be modified by heavy rainfall, wind, parasites, disease and
 46 predators (Hansen 2003; Jones 1979; Nakata 1995). Plantegenest et al. (2001) showed that not including
 47 the effects of parasitoids and especially fungal diseases may cause over-estimates of aphid population
 48 growth. Wang et al. (2015) and Chabert & Sarthou (2017) found that fertilizer input may increase aphid
 49 populations. A few papers have studied the impact of heavy rainfall on aphid populations. In cotton fields,
 50 Chamuene et al. (2018) found that in some, but not all cases rain incidents of less than 50 mm significantly
 51 increased the mortality of the aphid *Aphis gossypii*. A nine-year study of soybean fields found significant
 52 effects of precipitation patterns on the population dynamics of *Aphis glycines* (Stack Whitney et al. 2016).

53 In laboratory experiments, Mann et al. (1995) found that the loss of *Sitobion avenae* from oat plants was
54 correlated with rain intensity and duration, and increased when combined with wind gusts. Jones (1979)
55 observed that heavy rainfall before the ears appear may reduce aphid numbers on cereals, and that
56 information about rainfall may complement the prediction of population size based on temperature.

57 In order to optimize the decision support systems, large efforts have been spent on improving model
58 performance in relation to weather parameters and natural regulation. These efforts have without doubt
59 improved the models, but taking into consideration that aphid populations develop exponentially, and that
60 the population can double in 55 hours at 20°C (Dedryver et al. 2010), it is critical that the initial densities
61 are determined at high precision in order to predict the epidemic development. However, surprisingly little
62 efforts have been devoted to obtaining quick and reliable estimates of the initial densities, although several
63 methods have been developed to estimate the density of aphids in cereals. For instance, Elliott et al. (1990)
64 developed binomial sequential sampling plans that require rather larger efforts at low densities to produce
65 reliable estimates, and Hansen (1991), who suggested to investigate aphid presence/absence on 50 or 100
66 tillers and used an equation to convert to aphids per tiller. Both methods take some time, and come up
67 with assessments of average densities with some uncertainties. The uncertainties are predefined in the
68 sequential sampling plan and the required uncertainty level is decisive for the number of plants to
69 investigate. When counting presence/absence on a number of straws, the uncertainty can be calculated
70 before being used in simulation models and decision support systems. However, none of the models and
71 decision support systems appear to use uncertainty in their projections of aphid population development,
72 and in turn relate uncertainties to the output. Given that aphids show exponential population growth,
73 uncertainties in the estimate of initial densities can cause large uncertainties to the projections of the aphid
74 population density some weeks later. This uncertainty should ideally be reflected in the suggestions
75 produced by a decision support system.

76 To predict the spatial and temporal development of aphid outbreaks it is important to sample and model
77 population data that encompasses both spatial and temporal dimensions. In this study, we have sampled
78 aphid populations in a spatial setup during both the initial and the epidemic phase to fit a population
79 growth model. More specifically, we have developed a spatio-temporal stochastic aphid population growth
80 model and fitted the model to empirical spatial time-series aphid population data using a Bayesian
81 hierarchical fitting procedure. Such Bayesian hierarchical population models have successfully been applied
82 on a number of pest cases, e.g. the population dynamics of coffee berry borer infestation (Ruiz-Cárdenas et
83 al. 2009). The fitted spatio-temporal population growth model may be used to generalize existing

deterministic aphid forecasting models with the effect of stochastic spatial variation. Furthermore, we use the fitted model and complementary spatial statistics to investigate the hypothesis that initial aphid population sizes and outbreaks may be predicted in fields within a 10 km radius of the nearest aphid-monitoring site.

Materials and Methods

Field sites and aphid sampling

The occurrence probability of the grain aphid, *Sitobion avenae*, i.e. the percentage wheat straws with aphids (correlated with both number of aphids per straw, and number of aphids per area (Feng et al. 1993; Hansen 2003; Hein et al. 1995)), was recorded in twelve wheat fields in central Jutland, Denmark, in 2016 and 2017. The wheat fields (=sites) were laid out in hierarchical geographic design with three regions of four sites. In Denmark, aphids are monitored in the official aphid-sampling programme (Observation Web, <https://www.landbrugsinfo.dk/planteavl/plantevaern/varslingregistrerings-net/-sider/startside.aspx>). In the current project, we used an Observation Web field as centre site for each of the three regions, and within each region, three other sites (fields), positioned approximately three, six and ten kilometers away (Fig. 1), were studied. As a consequence of the proximity of some of the Observation Web fields, the three regions overlap to some extent. At each site, the occurrence probability of aphids on individual plants were recorded and the occurrence probability was used as a proxy for the aphid population size, based on the fact that percentage straws with aphids is highly correlated with the number of aphids per square meter (Feng et al. 1993; Hansen 2003; Hein et al. 1995).

In 2016, aphid occurrence was recorded for five samples of either 80 or 100 wheat plants at each site on May 24, June 6, June 13, June 20, June 27, July 4, and July 11. The five samples within a site were taken along a transect with at least 50m between samples. Site-specific degree-days were calculated from the average day temperature at the weather station closest to each site with a base temperature of 5 degrees Celsius. Furthermore, the intensity of precipitation events at the different sites was recorded daily by a weather station placed at each field (Agrimex® Rosenborg 35980).

In order to complement the result of the spatial variation of the initial phases of aphid outbreaks obtained in the spatial modelling of the aphid occurrence data sampled in 2016, aphid occurrence was recorded more intensively at the same twelve sites in the beginning of the growth period the following year and analyzed in a semivariogram. In 2017, aphid occurrence was recorded for ten samples of 50 wheat plants at

each site on May 30 and June 7. The ten samples within a site were laid out along three transects with at least 50m between all plots, and the exact geographical position of each sample was determined.

Statistical modelling of the aphid population

The spatio-temporal aphid occurrence data is modelled using Bayesian hierarchical methods (Clark & Gelfand 2006). The observed number of straws with at least one aphid at site i and plot k at degree-day t is denoted $y_{i,k,t}$ and is assumed to be binomially distributed with $n_{i,k,t}$, the number of straws sampled, and $p_{i,t}$, the occurrence probability that a straw has at least one aphid at site i at degree-day t ,

$$y_{i,k,t} \sim \text{Bin}(n_{i,k,t}, p_{i,t}) \quad (1).$$

The site-specific occurrence probability is modelled using an exponential function of degree-day t ,

$$p_{i,t} = p_{i,0} \text{Exp}(r_0 + r_1 t + r_2 t^2 + \epsilon_i) \quad (2),$$

where $p_{i,0}$ is the occurrence probability on a fixed initial day, r_0 , r_1 , and r_2 are population growth parameters, and ϵ_i are Gaussian distributed site-specific random effects, $\epsilon_i \sim \text{Gau}(0, \sigma_p^2)$.

The n site-specific initial occurrence probabilities are assumed to arise from a Gaussian process model,

$$p_{i,0} \sim \text{Gau}(\mu_0, \Sigma), \quad \Sigma = \begin{pmatrix} \sigma_0^2 & \cdots & \sigma_0^2 \rho(d_{1,n}) \\ \vdots & \ddots & \vdots \\ \sigma_0^2 \rho(d_{n,1}) & \cdots & \sigma_0^2 \end{pmatrix} \quad (3),$$

where μ_0 is the mean initial occurrence probability, σ_0^2 is the variance, and $\rho(d_{i,j}) = \rho_0 \text{Exp}(-\frac{d_{i,j}}{\alpha})$ with $d_{i,j}$ being the distance between site i and site j , α is the scale of the spatial effect that is set to 10 km, and ρ_0 is a parameter that measures the spatial covariance (Haran 2011; Ovaskainen et al. 2016). The covariance matrix by definition has to be positive definite, which puts upper and lower bounds on ρ_0 .

The prior distributions of all parameters were assumed to be uniform except the two scale parameters that were assumed to be inverse gamma distributed, $\sigma_p \sim \text{Invgam}(0.1, 0.1)$ and $\sigma_0 \sim \text{Invgam}(0.1, 0.1)$. The joint Bayesian posterior distribution of the parameters and the two latent variable vectors, $p_{i,0}$ and ϵ_i , each of dimension n , were calculated using Markov Chain Monte Carlo (MCMC), Metropolis-Hastings, simulations

135 with a multivariate normal candidate distribution and using a MCMC run of 300,000 iterations after a burn-
136 in period.

137 Plots of the sampling chains of all parameters and latent variables were inspected in order to check the
138 mixing properties of the used sampling procedure, and whether the burn-in period was sufficient.
139 Additionally, the overall fitting properties of the model were checked by inspecting the regularity and
140 shape of the marginal distribution of all parameters as well as the distribution of the deviance ($=$
141 $-2 \log L(Y|\theta)$). The efficiency of the MCMC procedure was assessed by inspecting the evolution in the
142 deviance.

143 Statistical inferences on the parameters were based on the marginal posterior distribution of the
144 parameters.

145 All calculations were done using *Mathematica* version 10 (Wolfram 2015).

146 Results

147 The observed spatio-temporal mean occurrence probability of *S. avenae* in 2016 (Fig. 2) was fitted to the
148 spatial growth model. The burn-in period of the MCMC was relatively long (600,000 iterations), but after
149 the deviance had stabilized, the fitting properties of the models were judged to be acceptable based on
150 visual inspections of the mixing properties of the parameters and the latent variables.

151 The deterministic part of the population growth model (eqn 1.) seemed to adequately model the dynamics
152 of aphid occurrence probabilities as a function of degree days from June 1 2016 to July 1 2016 (Fig. 3) when
153 shape and mode of the expected outbreak was visually compared to the observed spatio-temporal mean
154 occurrence probability data in the same period (Fig. 2). Furthermore, there were no apparent pattern
155 among the latent variables that model the among-site variation in population growth, ϵ_i (Fig. 4), which
156 indicate that there were no systematic regional effects influencing growth apart from degree days.

157 The marginal posterior distributions of the parameters of interest are summarized in Table 1 by their
158 percentiles. The parameters were generally uncorrelated, except for, as expected, the estimates of the
159 population growth parameters r_0 , r_1 and r_2 , which were highly correlated (Table 2).

160 The posterior marginal distribution of the parameter that measures the effect of geographic distance on
161 the spatial covariance, ρ_0 , is left-skewed towards the upper boundary and significantly larger than zero
162 (Table 1), and the site-specific initial occurrence probabilities are consequently positively correlated among
163 the sites at the spatial scale of 10 km. However, the importance of this positive correlation for the among-
164 site variation in aphid outbreaks has to be evaluated in relation to the estimated among-site variation in
165 the initial occurrence probability as modelled by σ_0 , and population growth as modelled by σ_p (Table 1).

166 The rainfall of the 2016 season is presented in the electronic supplement. Incidents of heavy rain were
167 observed in late May and in June, especially in the Viborg region, with incidents of up to 25 mm per day.
168 However, if the observed rain records at the sites were manually scored according to severity and
169 compared to the latent variables that model the among-site variation in population growth, ϵ_i , then there
170 was no significant relationship between the heavy rain score and population growth rate (results not
171 shown, $P = 0.89$).

172 The variation in aphid occurrence among sampling plots as a function of the geographical distance among
173 plots on May 30 and June 7 2017 is shown as a semi-variogram (Fig. 5). Generally, the variation among plots
174 is relative low at the two sampling days, although the variation seems to increase irregularly with time
175 when assessed from only two samples in time. There is a slight indication that the variation among plots
176 increases with the distance among plots at the second sampling.

177 Discussion

178 The site-specific initial occurrence probabilities were found to be positively correlated among the sites at
179 the spatial scale of 10 km. However, when the spatial variation in the initial occurrence probability was
180 examined in more detail the following year, the spatial variation among plots in the beginning of the aphid
181 outbreaks did not seem to increase much with among-plot distance. This indicates that there was only
182 limited spatial effects, i.e. that the initial epidemic development was more or less in synchrony over
183 distances up to and above 10 km. Since the parameter that measures the effect of geographic distance on
184 the spatial covariance, ρ_0 , also depends on the spatial variation in the following aphid epidemic estimated
185 from the 2016 data set, we tend to put more weight on the more detailed investigation in 2017, and
186 conclude that our investigation suggest that there is limited spatial variation in the initial occurrence
187 probability. Consequently, the overall results support the working hypothesis that initial aphid population
188 sizes and outbreaks may be predicted for fields within a 10 km radius of the aphid-monitoring site. For

189 farmers, this may imply that they can rely their decision of whether to spray against aphids on observations
190 made within a distance of up to 10 km.

191 We did not detect any significant effects of heavy rain events on aphid occurrence probability. This is
192 contradictory to the conclusions of Whitney et al. (2016) and the experimental findings by Mann et al.
193 (1995) that heavy rainfall may cause a loss of aphids up to 30 % of the population. The rainfall incidents
194 measured per day in the present study resemble those studied by Chamuene et al. (2018), who found that
195 such incidents may cause increased aphid mortality and hence reduce population growth in some, but not
196 all cases. One reason why we did not see a reduced population increase may be that most rainfall incidents
197 happened after the ears of the winter wheat appeared, as Jones (1979) only found rainfall before ear
198 appearance to affect aphid numbers.

199
200 The simple quadratic function used to model population growth as a function of degree-days performed
201 adequately for modelling the growth in the aphid population from June 1 2016 to July 1 2016. However, the
202 purpose of this simple quadratic model was only to model the deterministic part of the population growth
203 in order to quantify the stochastic variation among sites, and the fitted quadratic model is not suitable for
204 making actual predictions outside the domain of the collected aphid population data. Instead, the
205 deterministic part of the population growth could be the models described by Holst et al. (1997), Ciss et al.
206 (2014), Duffy et al. (2017) or the model element of the aphid modules of decision support systems such as
207 CPO (Hagelskjær & Jørgensen 2003) and GETLAUS (Gosselke et al. 2001).

208
209 Most decision support systems will let the user know if it is appropriate to treat against aphids or not,
210 without telling how certain the “decision” is (e.g. GETLAUS (Gosselke et al. 2001) and CPO (Hagelskjær &
211 Jørgensen 2003). If the output came with uncertainties, such as “It can now with 55% certainty pay off to
212 treat against aphids in your field”, using the decision support system may appear more difficult, because
213 the farmer is left with an uncertain foundation for his decision. However, the output might include
214 information on how to reduce the uncertainty. If the farmer had counted aphids on 50 tillers, the output
215 might tell the farmer that the uncertainty would be reduced if he continued and counted on a higher
216 number of tillers, and he could continue until he was able to take certain decisions. This would require
217 some time, but the farmers would get some knowledge on the importance of spending time on providing
218 the decision support system with good initial aphid density estimates, as spending more time will provide a
219 safer foundation for decisions. Estimates of initial densities can be used to predict peak densities of S.

220 *avenae* (Honek et al. 2017), and good estimates of initial densities will, everything else equal, provide
 221 better estimates of peak densities.
 222
 223 Nevertheless, the farmer might still not be willing to spend the required time on counting aphid, but
 224 counting might be found worth the effort if the result could be used by neighbors, or by all farmers within a
 225 certain area. This would optimize the balance between time input spend on counting aphids and economic
 226 output in terms of higher yield and probably less expenses on pesticide applications.

227 **Tables**

228 Table 1. Marginal posterior distributions of the parameters in the spatio-temporal stochastic aphid
229 population growth model spatial when fitted to 2016 occurrence data. The distributions are summarized by
230 their 2.5%, 50% and 97.5% percentiles.

Parameter	2.5%	50%	97.5%
r_0	0.0147	0.0175	0.0215
r_1	-1.17E-05	1.32E-05	2.87E-05
r_2	-1.17E-07	-8.83E-08	-4.71E-08
σ_p	0.00554	0.00911	0.01677
μ_0	0.000395	0.00786	0.01531
σ_0	0.00509	0.00857	0.01620
ρ_0^2	0.936	1.2185	1.2412

231

232

233 Table 2. Correlation matrix between the parameters r_0 , r_1 , and r_2 in the spatio-temporal stochastic aphid
234 population growth model spatial when fitted to 2016 occurrence data.

	r_0	r_1	r_2
r_0	1	-0.96	0.93
r_1	-0.96	1	0.99
r_2	0.93	0.99	1

235

236

237

Figures

Fig. 1. Twelve wheat fields in the middle of Jutland, Denmark, where aphids were sampled. The wheat field were laid out in hierarchical geographic design with three regions of four fields. Each region had a center field with fields positioned approximately three, six and ten kilometers away.

243 Fig. 2. Observed spatio-temporal mean occurrence probability of *S. avenae*. The sites are located in three
244 different regions (Borum, Hammel and Viborg). Each region had a center field (0) with fields positioned
245 approximately three (3), six (6) and ten (10) kilometers away.

246

247

248

249 Fig3. Expected occurrence probability of *S. avenae* at the mean degree-days from June 1 2016 to July 1
 250 2016. The curve is calculated using equation (2), the expected μ_0 , and the joint posterior distribution of r_0 ,
 251 r_1 , and r_2 . The thick line is the median occurrence probability and the two thin lines are the 25% percentile
 252 and 75% percentile of the occurrence probability. The shaded area is the 95% credibility interval of the
 253 occurrence probability.

254

255

256

257 Fig. 4. The distribution of the latent variables that model the among-site variation in population growth, ϵ_i ,
258 at the different sites.

261 Fig. 5. Semivariogram. The variation in aphid occurrence as a function of the geographical distance among
262 sampling plots. Blue points: May 30 2017, yellow points June 7 2017.

References

- Axelsen J.A., Munk L., Sigsgaard L., Ørum J.E., Streibig J.C., Navntoft S., Christensen T., Pedersen A.B., Elkjær K., Korsgaard M. and Bonefeld-Jørgensen E.C. 2012. Udredning om monitorings, varslings- og beslutningsstøttesystemer for skadevoldere i planteproduktionen i landbrug, gartneri og frugtavl., Miljøstyrelsen, Copenhagen, p. 192.
- Chabert A. and Sarthou J.-P. 2017. Practices of conservation agriculture prevail over cropping systems and landscape heterogeneity in understanding the ecosystem service of aphid biocontrol. *Agriculture, Ecosystems & Environment* 249: 70-79.
- Chamuene A., Araujo T.A., Silva G., Costa T.L., Berger P.G. and Picanco M.C. 2018. Performance of the Natural Mortality Factors of *Aphis gossypii* (Hemiptera: Aphididae) as a Function of Cotton Plant Variety and Phenology. *Environ Entomol* 47: 440-447.
- Ciss M., Parisey N., Moreau F., Dedryver C.-A. and Pierre J.-S. 2014. A spatiotemporal model for predicting grain aphid population dynamics and optimizing insecticide sprays at the scale of continental France. *Environmental science and pollution research international* 21: 4819-4827.
- Clark J.S. and Gelfand A.E. (eds). 2006. Hierarchical modelling for the environmental sciences. Oxford University Press, Oxford.
- Dedryver C.A., Le Ralec A. and Fabre F. 2010. The conflicting relationships between aphids and men: a review of aphid damage and control strategies. *C R Biol* 333: 539-553.
- Duffy C., Fealy R. and Fealy R.M. 2017. An improved simulation model to describe the temperature-dependent population dynamics of the grain aphid, *Sitobion avenae*. *Ecological Modelling* 354: 140-171.
- Elliott N.C., Kieckhefer R.W. and Walgenbach D.D. 1990. Binomial Sequential Sampling Methods for Cereal Aphids in Small Grains. *Journal of Economic Entomology* 83: 1381-1387.
- Feng M.G., Nowierski R., M. and Zeng Z. 1993. Binomial sampling plans for the English grain aphid, *Sitobion avenae* (Homoptera: Aphididae) based on an empirical relationship between mean density and proportion of tillers with different tally thresholds of aphids. *Bulletin of Entomological Research* 83: 187-196.
- Gosselke U., Triltsch H., Rossberg D. and Freier B. 2001. GETLAUS01 - the latest version of a model for simulating aphid population dynamics in dependence on antagonists in winter wheat. *Ecological Modelling* 145: 143-157.
- Hagelskjær L. and Jørgensen L.N. 2003. A web-based decision support system for integrated management of cereal pests. *EPPO Bulletin* 33: 467-471.
- Hansen L.M. 1991. Measuring aphid density in spring barley. *Danish J. Pl. Soil. Sci.* 95: 93 - 95.
- Hansen L.M. 2003. Kornbladlus i vinterhvede. Rapport fra Danmarks JordbrugsForskning. Forskningscenter Flakkebjerg.

298 Haran M. 2011. Gaussian random field models for spatial data. In: Brooks S. P., Gelman A. E., Jones G. L. and
299 Meng X.-L. (eds), Handbook of Markov chain Monte Carlo. CRC, Boca Raton.

300 Hein G.L., Elliot N.C., Michels Jr G.J. and Kieckhefer R.W. 1995. A general method for estimating cereal
301 aphid populations in small grain fields based on frequency of occurrence. The Canadian Entomologist 127:
302 59-63.

303 Holst N. and Ruggle P. 1997. A physiologically based model of pest–natural enemy interactions.
304 Experimental & Applied Acarology 21: 325-341.

305 Honek A., Martinkova Z., Dixon A.F.G. and Saska P. 2017. Annual predictions of the peak numbers of
306 Sitobion avenae infesting winter wheat. Journal of Applied Entomology 141: 352-362.

307 Jones M.G. 1979. Abundance of Aphids on Cereals from Before 1973 to 1977. Journal of Applied Ecology 16:
308 1-22.

309 Klueken A.M., Hau B., Freier B., Friesland H., Kleinhenz B. and Poehling H.-M. 2009. Comparison and
310 validation of population models for cereal aphids. Journal of Plant Diseases and Protection 116: 129-140.

311 Larsson H. 2005. A crop loss model and economic thresholds for the grain aphid, Sitobion avenae (F.), in
312 winter wheat in southern Sweden. Crop Protection 24: 397-405.

313 MANN J.A., TATCHELL G.M., DUPUCH M.J., HARRINGTON R., CLARK S.J. and McCARTNEY H.A. 1995.
314 Movement of apterous Sitobion avenae (Homoptera: Aphididae) in response to leaf disturbances caused by
315 wind and rain. Annals of Applied Biology 126: 417-427.

316 Nakata T. 1995. Population Fluctuations of Aphids and Their Natural Enemies on Potato in Hokkaido, Japan.
317 Applied Entomology and Zoology 30: 129-138.

318 Ovaskainen O., Roy D.B., Fox R. and Anderson B.J. 2016. Uncovering hidden spatial structure in species
319 communities with spatially explicit joint species distribution models. Methods in Ecology and Evolution 7:
320 428-436.

321 Plantegenest M., Pierre J.S., Dedryver C.A. and Kindlmann P. 2001. Assessment of the relative impact of
322 different natural enemies on population dynamics of the grain aphid Sitobion avenae in the field. Ecological
323 Entomology 26: 404-410.

324 Ruiz-Cárdenas R., Assunção R.M. and Demétrio C.G.B. 2009. Spatio-temporal modelling of coffee berry
325 borer infestation patterns accounting for inflation of zeroes and missing values. Scientia Agricola 66: 100-
326 109.

327 Stack Whitney K., Meehan T.D., Kucharik C.J., Zhu J., Townsend P.A., Hamilton K. and Gratton C. 2016.
328 Explicit modeling of abiotic and landscape factors reveals precipitation and forests associated with aphid
329 abundance. Ecol Appl 26: 2598-2608.

- 330 Wang L., Hui C., Sandhu H.S., Li Z. and Zhao Z. 2015. Population dynamics and associated factors of cereal
 331 aphids and armyworms under global change. Sci Rep 5: 18801.
- 332 Wellings P.W., Ward S.A., Dixon A.F.G. and Rabbinge R. (eds). 1989. Crop loss assessment. Elsevier, NL.
- 333 Wolfram S. 2015. Mathematica. Wolfram Research, Inc., Champaign, USA.

334

335

Electronic Supplement

Rainfall at the three study sites in 2016