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HORSE CHESTNUT SCALE (*PULVINARIA REGALIS*) (HOMOPTERA: COCCIDAE) AND URBAN HOST TREE ENVIRONMENT

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Abstract. The analysis and explanation of the spatial distribution of organisms within a locality are problematic. This study uses a combination of standard analytical methods (Generalized Linear Interactive Modeling [GLIM]) with recently developed spatial statistical techniques (geostatistical analysis), on a model system of insect–plant interactions in an urban setting. Infestations of the horse chestnut scale, *Pulvinaria regalis*, were mapped on three tree species in Oxford, United Kingdom. Various tree parameters were measured, as were aspects of the site in which each tree was growing. Using general linear modeling and geostatistics, the distribution and intensity of scale populations were investigated in relation to these parameters. The trees were separated into those that showed no symptoms of lack of vigor and those that were clearly unhealthy. In both cases, the only parameter that explained much of the variance in the scale egg densities on trees was the impermeability of the substrate surface under the trees, such that as substrates became more impermeable to water and nutrients (for example, as a result of concrete or roadways), the higher were the pest densities on those trees. For the vigorous trees alone, an extra parameter, that of building distance, was also found to be significant, so that trees very close to buildings also showed high pest densities. The spatial dependence of scale insect eggs on trees was found to be anisotropic through the sample area, in the southwest/northeast direction, attributable to wind speed, direction, and canyon effects.

Key words: canyon effects; geostatistics; kriging; plant stress; *Pulvinaria regalis*; scale insects; spatial autocorrelation; urban environments.

INTRODUCTION

For most animals and plants, urban environments represent different habitats to those in which they evolved. Both abiotic and biotic conditions may vary from those found in natural habitats, and organisms living in urban areas might be expected to vary in their fitness as a consequence of how well adapted they are to these evolutionarily novel conditions. Abiotic conditions in urban habitats relative to those in rural areas often include higher wind speeds, due to a “canyon” effect in long open streets, increased temperatures and insolation, lower soil moisture and nutrient flow, and higher levels of aerial pollution (Luria et al. 1990, Kjellgren and Clark 1992). Biotic conditions may include lower plant and animal species diversity, altered natural enemy loads, higher management intensity of plants and animals, and also an increased likelihood of mechanical damage (Fraser and Frankie 1986, Ruzsczyk 1986). One of the consequences of these differences may be an increased variability in vigor of town trees, due to their differing abilities to tolerate these condi-

tions. Variations in vigor may in many cases be related to stresses derived from the trees’ environment (Houston 1984). The relationships between tree vigor, stress, and the growing environment (site) are complex (Speight and Wainhouse 1989, Speight 1996), and the role of vigor and stress respectively in shaping the physiologic responses of trees to environmental factors is currently a matter of debate (Watt 1994). It is nonetheless true that in a general sense town trees are often found to be less healthy than their rural counterparts (Coffelt and Schultz 1993).

Various causes of tree unhealthiness in urban habitats have been suggested. For example, Kjellgren and Clark (1992) report that the growth of town trees can be restricted, predominantly by the chronically high evaporative demand and limited soil resources typical of street habitats. Building and road works frequently limit the amount of water reaching tree roots (Nogueira 1976), and in general, drought conditions are thought to prevail in urban habitats, probably because of the low permeability of ground surfaces to rain water coupled with efficient roadside drainage systems (Houston 1984).

The horse chestnut scale insect, *Pulvinaria regalis* Canard, is a typical urban insect (Speight and Nicol

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TABLE 1. Summary of measurements made on trees during the Oxford Survey.

Category	Measurement type	Code
Tree species	Name	SPS
Location	Map XY coordinate	XY
Height of tree	Absolute	HGT
Diameter at breast height	Absolute	DBH
Evidence of low vigor	Yes or no†	VIG
Distance to nearest infested tree	Absolute	INFE
Distance to nearest road	Absolute	ROAD
Distance to nearest building	Absolute‡	BLDG
Impermeability of ground under canopy	Percentage§	IMP
Level of adult/egg infestation	Score from 0 to 10	EGG
Density of nymphs on leaves	Absolute¶	NYM

† Low vigor was assessed by recording the incidence on each tree of the following phenomena: (a) crown dieback, (b) branch or twig dieback, (c) dead branches, (d) rot holes, (e) and fungal fruiting bodies. If one or more of these features was observed, then low vigor was scored as "yes."

‡ A building was defined as any large man-made structure such as a house or office block, but garden walls were excluded.

§ Impermeability under the tree was assessed by eye, in terms of the type of ground cover. Paving slabs, tarmac, and concrete were considered to be impermeable to water and nutrients, whereas soil, grass, or gravel overlying soil were considered to be permeable. If, for example, a tree was growing next to a road but with one-half of the area under its canopy in grass or soil, then the impermeability was scored as 50%.

|| Adult and accompanying egg mass infestations on each tree were scored using an "eyeball" estimate of bark covered. A tree devoid of any scales received a score of zero, while one with 100% of its bark covered by scales and egg masses received a score of 10. Infestations between these limits were graded at intervals of 10%.

¶ From each tree, a random sample of 10 leaves was collected at the time of the survey. The size (area) of each leaf was measured using a leaf-area analyzer, and all scale insect nymphs settled on both upper and lower leaf surfaces were counted. A measure of mean nymph density per square centimeter of leaf surface per tree could then be calculated.

1985), which is rarely, if ever, found in rural areas in the United Kingdom (UK). The species was first encountered in the UK in the late 1960s (Harris 1970), and is now fairly widespread in England and Wales (Speight and Nicol 1985). This species has also been reported as an urban problem in Belgium (Merlin et al. 1988), in France (Meirleire 1984), and in Germany (Sengonca and Faber 1995). The infestations of adult females and their egg masses are unsightly, and the effect on the growth of host trees by the feeding of nymphs can be severe (Speight 1991). Because of its huge fecundity (Speight 1994) and ability to spread rapidly through urban areas as highly mobile first instar crawlers, the overall impact of this species both as an eyesore and also as a growth-retarding agent can be considerable. However, infestations in towns in southern England are patchy, with some host trees badly infested and others little affected.

This paper describes the results of work conducted to investigate possible causes of *P. regalis* infestation in urban trees in Oxford, England. It uses survey data to examine the role of various environmental parameters in predicting the distribution of *P. regalis* infestations, and employs a combination of analytical approaches from generalized linear interactive modeling to spatial statistics.

METHODS

Survey methods

Infestations of *P. regalis* on town trees were surveyed in Oxford in June 1990, at a period when adult

females with the remnants of their egg masses were most in evidence, but after egg hatch and nymphal colonization of leaves. A small-scale pilot survey was carried out initially, with surveyors being trained in the techniques to standardize record keeping and score assessments. Two people made up each team in the full survey, and double scoring was used to reduce observer bias. The categories assessed during the survey are presented in Table 1.

The survey covered an area of Oxford which included the main shopping area, colleges and university departments, and extended for 1.6 km (one mile) east to west and 1.6 km (one mile) north to south, with a total area of ~250 ha. Only the three main tree species known to be hosts for *Pulvinaria regalis* (Speight 1991) were included in the survey; namely horse chestnut (*Aesculus hippocastanum* L.), lime (*Tilia cordata* Miller), and sycamore (*Acer pseudoplatanus* L.), though egg masses occurring on other species were noted. All trees, whatever their age, of the three species within the survey area were recorded, numbering 233 in total.

Analysis

Traditional multiple regression approaches to the analysis of data generated by this type of survey are fraught with problems of correlation between variables, and multiplicity of *P* values. Nonetheless, surveys are often the only form of investigation possible in the early stages of ecological studies, and they provide vital evidence for the creation of hypotheses about cau-

sality that may be subsequently investigated in experimental investigations. Scatterplots of the survey data suggested that the trees were not evenly distributed. Spatial distributions of trees were therefore tested for overdispersion at two levels of organization; the entire population, and infested specimens only. Local frequencies of trees in each class were determined by superimposing a 100×100 m grid on the survey area. In each case cells containing no trees were discounted, then the observed frequency distribution of trees in the grid was compared to that expected from a Poisson distribution (G test for goodness-of-fit), lumping across categories where demanded by low expected values. To ensure independence from cell demarcation, the tests were repeated with the grid displaced through 50 m on each axis. Test results indicated that the distributions of trees in both classes were significantly overdispersed (all trees: $G = 32.7/36.4$, $P < 0.001$, $df = 4$; infested trees $G = 28.5/31.8$, $P < 0.001$, $df = 4$).

Two measures of *P. regalis* infestation level were provided by the survey (egg code and nymph density), but because they were highly correlated ($P < 0.001$), only the egg code variable was employed in analysis. The nymph density data was considered to be less appropriate since eggs are indicative of the surviving scale populations on each tree, without the extra complication of potential immigration and emigration of crawlers. Prior to commencing analysis, the number of independent variables (see Table 1) was reduced to decrease the problems of multiplicity of P values. Correlated pairs of independent variables such as tree height and diameter were identified, and only the member of the pair explaining the higher proportion of variance in a simple multiple regression was included in the final model.

A Poisson error structure was assumed for data (based on counts), and this was substantiated during the analysis by model checking procedures. The scale parameter was also calculated and used to compensate for overdispersion where necessary. Variables entered into the final GLIM regression model were: species (SPS), diameter (DBH), distance from nearest infested tree (INFEST), distance to nearest road (ROAD), percentage impermeability of ground surface under tree canopy (IMP), vigor estimate of tree (VIG), and distance from nearest building (BLDG). In the case of the final parameter, any building farther than 50 m from a tree was constrained in the GLIM analysis to be at 50 m; this was carried out to reduce the overemphasis on a few, distant, outlying data points wherein no building influence could be envisaged.

The GLIM analysis was carried out using standard model criticisms. Residuals were plotted against fitted values and explanatory variables during the process, and these plots were examined for any recognizable pattern. A Poisson error structure was established as the most appropriate. Compensation for overdispersion was carried out at the model-fitting stage. Variables

were entered into the model simultaneously, and then adjusted and sequential ss were compared to simplify the final model by excluding variables with marginal significance (e.g., $0.01 < P < 0.05$), with a critical value of $P < 0.001$ being set for variable inclusion in the final model. The choice of $P < 0.001$ rather than a higher level of significance meant that only the very important variables were considered.

Geostatistical tools were used to explore the spatial component of the data. They allow the exploration and quantification of the spatial continuity of a geo-referenced data set. A more complete description of these tools is presented in Isaaks and Srivastava (1989) and Cressie (1993). A conflict between the GLIM analysis and the spatial statistics might be identified, in that errors from both protocols may be related. This is unavoidable, but the reason for performing the two types of analysis on the same data set was to explore different aspects of the same phenomenon. Normally, in work of this nature, spatial relationships are completely ignored.

The principle of spatial continuity is based on the premise that pairs of random variables, only short distances apart, are likely to have values that are more similar to each other than those of other pairs of the same variables that are farther apart from each other (Isaaks and Srivastava, 1989). Different tools exist in geostatistics to explore and quantify the spatial continuity of a data set, which include \mathbf{h} -scatterplots, semivariograms, non-ergotic correlograms (N-E correlogram) and non-ergotic covariance measures (Rossi et al. 1992). The semivariogram is a crucial tool used in geostatistics to describe the spatial continuity of a data set. Let $z(\mathbf{x}_i)$ be an observation at location x_i and $z(\mathbf{x}_i + \mathbf{h})$ an observation at location $x_i + \mathbf{h}$ (\mathbf{h} can be a scalar or a vector); a classical estimator of the semivariance at lag \mathbf{h} is given as

$$\gamma(\mathbf{h}) = \frac{\sum_{i=1}^{N(\mathbf{h})} [z(\mathbf{x}_i) - z(\mathbf{x}_i + \mathbf{h})]^2}{2N(\mathbf{h})}$$

where $N(\mathbf{h})$ is the number of data points separated in space by a lag of \mathbf{h} . The most widely used geostatistical techniques assume that the random process is stationary; it is assumed that neither the expectation of the process nor its variogram are dependent on location. Furthermore, if the semivariogram is only a function of distance \mathbf{h} and is independent of direction, the process is said to be isotropic, otherwise, it is anisotropic. Usually, as suggested above, data from locations that are close together give values that are more similar than data separated by larger distances. For this reason, the semivariance is usually small at small lags, and increases with lag. In most cases, there is a lag value beyond which it does not increase any more (spatial dependence is no longer perceptible); this lag value is called range, and the corresponding semivariogram pla-

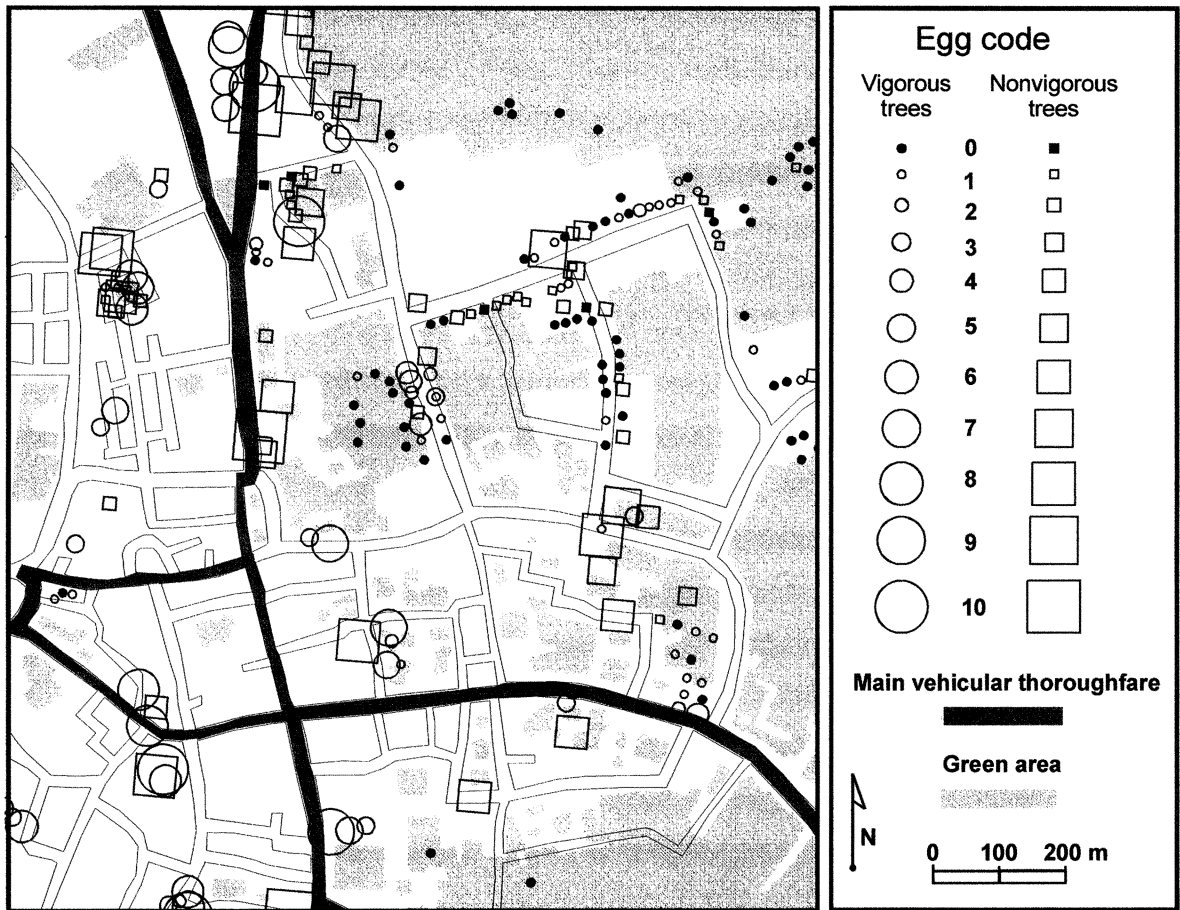


FIG. 1. Street map of central Oxford, showing the distribution of sampled trees, together with a representation of their vigor and scale insect egg infestation. Dark shaded streets indicate the major roads used by heavy traffic, and light shaded areas indicate the green areas.

teau is referred to as the sill. In stationary processes, and when the study-area radius is large when compared to the range, sill value is equal to the process variance. When the lag is zero, the semivariance is, by definition, always zero. In reality, however, semivariograms often tend to a positive value when lag is zero; this is called the nugget effect. There are two explanations for this effect; firstly, measurement errors may create "white noise" that is added to the semivariogram, and secondly, it can be due to variations at a smaller scale than the smallest *h*.

Geostatistical studies are never straightforward; results of each step in the analysis guide the choice of methods that will produce meaningful results in the next step (Rossi et al. 1992). In the present study, interactive exploratory variography and modeling were performed using the software package Variowin (Pannatier, 1996). The geostatistical analysis had two main goals. The first was to provide the best egg density surface map and the second was to explore the spatial distribution of the data. Two separate techniques were

employed, ordinary kriging, and spatial dependence analysis.

The estimation tool known as ordinary kriging takes account of the estimated range, sill, and directional anisotropy in a model that is used for spatial interpolation. These surfaces provide visual (mapped) descriptions of the geographical distribution of populations (Maurer 1994). They allow complex patterns such as those revealed in multivariate analyses to be displayed in a simple, intuitive format, and illustrate patterns related to statistical trends.

RESULTS

The distribution of sample trees in central Oxford is shown in Fig. 1, with the density of eggs on each tree indicated by the relative size of the markers at each location. Circular markers indicate the positions of vigorous trees, while squares indicate the positions of nonvigorous trees. The majority of trees were found along roadsides or in town squares, so that the samples were nonuniformly distributed. The spatial continuity be-

tween points can be seen to change markedly from one area to another such that in the northwest, southwest, and northeast part of the map, the spatial continuity of infestation levels appears to be fairly good. On the other hand, in the middle of the map, it can be observed that highly attacked trees are close to unattacked ones. These discontinuities may have a strong influence on the quantitative analysis of the general spatial continuity of the egg counts. Explanations for this nonuniform distribution were then sought.

The final GLIM model accounted for over one-half of the total variance in the data ($r^2 = 0.508$) and showed differences in the response of trees scored as "vigorous" and those scored "not vigorous" to the average impermeability of the ground around them and the distance to the nearest building:

$$\text{Low vigor: } \ln \text{ EGGs} = 0.3909 + 0.01375(\text{IMP}) \quad (1)$$

$$\text{High vigor: } \ln \text{ EGGs} = 0.5581 + 0.01375(\text{IMP}) \\ - 0.0532(\text{BLDG}). \quad (2)$$

The estimated scale parameter from the model was 2.268; had it exceeded a value of ~ 3 , then a different transformation would have been sought, but as it was, it was considered to provide a reasonable approximation to Poisson errors (Crawley 1993).

Significance was investigated using rescaled chi-squared tests. In the model (Eqs. 1 and 2), the effect of impermeability was highly significant for both vigorous and nonvigorous trees ($\chi^2 = 44.89$, $df = 1$, $P < 0.001$), while that of building distance was significant for the vigorous category ($\chi^2 = 14.02$, $df = 1$, $P < 0.001$) but not for the nonvigorous ($\chi^2 = 0.48$, $df = 1$). Assuming that trees very close to buildings were likely to be influenced adversely, the interaction between vigor and building distance was also obtained; the building distance–vigor interaction was significant ($\chi^2 = 18.86$, $df = 1$). The slopes for high and low vigor were not significantly different from one another ($\chi^2 = 0.42$, $df = 1$). Other variables were excluded from the model by the analysis, such that tree species, dbh, and road distance had no significant effect. Examination of Eqs. 1 and 2 reveals that low vigor trees were in general more infested by scale insects at any given level of substrate impermeability, except when vigorous trees were very close to a building (~ 3 m). Only then did they have predicted egg codes greater than a nonvigorous tree on the same site. Fig. 2 shows the model predictions of the distributions of scale insect eggs. In very close proximity to a building, otherwise-vigorous trees may be stressed by shade and/or root compaction. It is important to note that there were no detectable significant links directly between lack of vigor symptoms in the trees and the soil impermeability from the survey data, indicating the operation of other factors causing deterioration of tree health, such as age, wounding and/or disease.

Exploratory Data Analysis (EDA; Tukey 1977) of

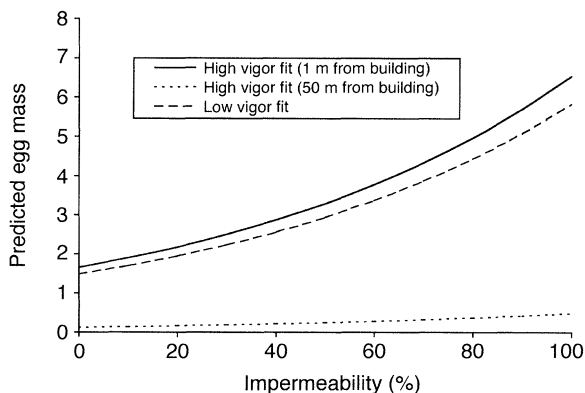


FIG. 2. Predicted values of egg masses (back transformed) derived from GLIM analysis (Eqs. 1 and 2). Two extremes of building distance (1 m and 50 m) for vigorous trees are shown to compare with nonvigorous trees, showing that the trees in the latter category always have higher infestations except when very close indeed to buildings.

the *Pulvinaria* data set provided useful information. Firstly, the data exhibited a strongly left-skewed distribution. These effects were corrected, as prescribed by Tukey (1977), by application of a logarithmic transformation ($Z' = \log Z + 1$). Secondly, spatial continuity measured by directional semivariograms was found to be anisotropic (east–northeast direction), and sills were larger than data variances. Combination of these two observations were considered to be evidence of global nonstationarity, and would indicate presence of a spatial trend in the data. There are two ways to take account of a spatial trend, either by trying to identify the trend or alternatively by using a variogram estimator that filters local mean (non-ergodic correlograms). In the present case, a planar regression was found significant ($P < 0.001$) and standardized residuals were therefore used for further computations. Spatial dependence measured by semivariograms of these residuals was still anisotropic (east–northeast direction), but sills were equal to data variance. A two-dimensional anisotropic model was built and used to perform ordinary kriging of these standardized residuals. Results were then added to the trend surface and back transformed to provide the egg density distribution maps presented in Fig. 3. The interpolated surface resulting from the kriging is presented in Fig. 3. Both two-dimensional and three-dimensional surfaces of the egg densities are presented, which indicate highest egg densities in the southwest and northwest area of the map.

The spatial continuity of the transformed egg counts was found to be anisotropic. This spatial dependence could have been a consequence of significant factors in the GLIM analysis since they were also spatially autocorrelated. In order to separate the dispersal spatial continuity from the regressor spatial continuity, GLIM analysis standardized residuals were used instead of

the egg counts for further calculations. One major problem was encountered. The distance to building parameter used in the model is intrinsically spatial, i.e., it depends on the relative position of sample points and buildings. For example, in the case of an east–west egg gradient with a building to the west, the correlation between egg counts and distance to building will be excellent and standardized residuals will be spatially independent. If however, the building is to the north or south, in the middle of the egg gradient, the correlation will be low and standardized residuals will be highly spatially dependent. In the present study, there was an east–west trend in the transformed egg counts (Fig. 4a; $P < 0.001$), showing that the trees are over-dispersed. Buildings were clustered in the city, but in no particular direction relative to trees, and so to avoid such a bias, further statistics were performed on standardized residuals of the GLIM model that did not include the distance to building.

The standardized residuals exhibited a strongly left-skewed distribution and these effects were corrected, by application of a logarithmic transformation ($Z' = \log Z + 2$). Again spatial continuity measured by directional semivariograms was found to be anisotropic (east–northeast direction), and sills were larger than data variances. Planar regression standardized residuals were used for directional semivariogram estimation. A semivariogram surface (Fig. 4b) was estimated as well as semivariograms in the two main axes (Fig. 4c). The semivariogram surface summarizes semivariogram estimations for all the combinations of distances and directions within ± 500 m in X and Y directions.

The significant factors from the GLIM analysis were spatially autocorrelated. The impermeability was spatially dependent up to 200 m with a nugget of 30% of the variance, whilst the vigor of the trees was spatially dependent up to 150 m with a nugget of 60% of the total variance. Finally, the distance to buildings was spatially dependent up to 150 m with a nugget of 5% of the total variance. The planar regression computed on the GLIM analysis log-transformed standardized residuals was significant (Fig. 4a, $P < 0.001$), and indicated the presence of an east–northeast decreasing gradient. Directional semivariograms showed a strong directional anisotropy with a range of >500 m in the east–northeast direction, with a lower anisotropy up to 200 m in the north–northwest direction (Figs. 4b and c).

DISCUSSION

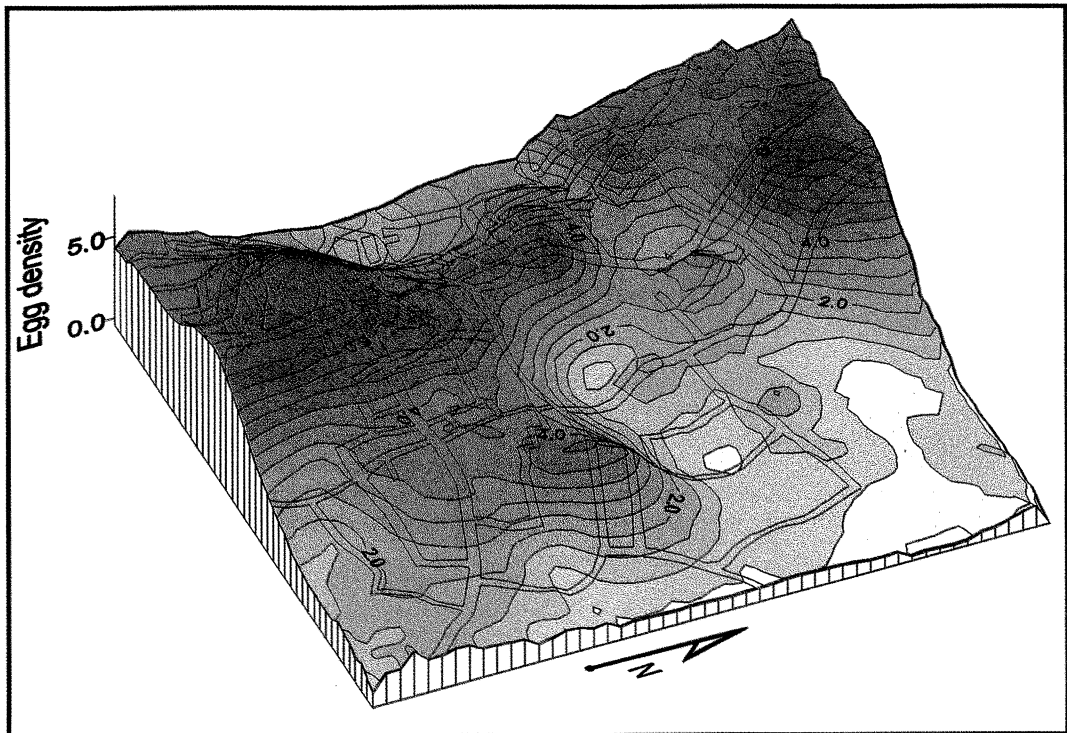
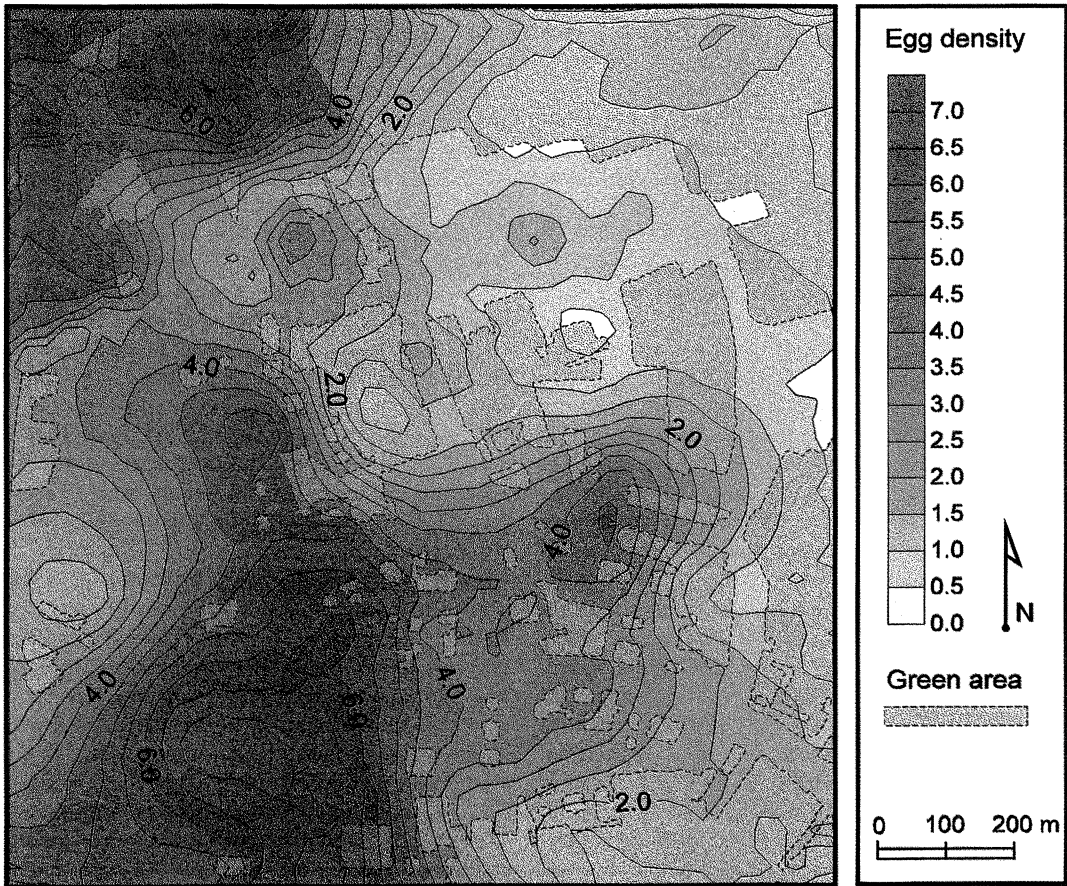
The spatial distribution of high populations of insects in a habitat is rarely random, especially if the host plant

is widespread but discontinuous within the habitat. In fact, because of the fundamental heterogeneity of the environment, most populations are patchily distributed (*sensu* MacArthur and Pianka 1966). In order to explain these distributions, mapping and Geographical Information Systems (GIS) are gathering momentum in the analysis of forest insect outbreak dynamics (Liebhold et al. 1993), though at the moment, interpolative systems do little more than produce pictorial descriptions of distributions, relying on external statistical packages to investigate the quantitative, potentially causal, relationships. The employment of geostatistics offers a particularly appropriate method for this.

In this study, using geostatistical analysis, it was found that the GLIM analysis standardized residuals from the egg counts were spatially dependent. It is concluded that the number of eggs on any particular tree has an influence on the number of eggs on another up to at least 500 m in the east–northeast direction, and ~ 200 m in the north–northwest direction, whatever the soil impermeability or vigor of the tree. In other words, pairs of points separated by a distance >200 m are spatially independent if they are located in the north–northwest direction and are dependent if they are located in the east–northeast direction. Most likely, this influence is due to long distance transport of first instar crawlers in the previous year. Moreover, such a strong directional anisotropy is most likely caused by a directional feature which has an influence on crawler dispersal. The main environmental feature with such a directional influence is likely to be the wind. In Oxford, the main wind direction is west–southwest to southwest (*unpublished meteorological data*, School of Geography, University of Oxford). This direction coincides very well with the correlogram surface (Fig. 4b) and the trend direction (Fig. 4a). *Pulvinaria regalis* fecundity may be very high (Speight 1994), and dispersal is via the first instar crawlers, predominantly within the tree canopy from which they originated, but also by being carried on the wind to other trees. The losses are extremely high at this stage of the life cycle (Speight 1994), but it is clear that the crawlers may be carried relatively long distances in a street “canyon.” This is true especially when vehicular traffic at street level increases air turbulence (DePaul and Sheih 1986), thus increasing the probability of their reaching another suitable host tree before they die.

Wind dispersal by Hemiptera and other insects is well known; the sooty beech scale, *Ultracoelostoma assimile*, disperses in the crawler stage on the wind in New Zealand (Morales et al. 1988), and two close rel-

FIG. 3. Two-dimensional and three-dimensional interpolated surfaces produced by two-dimensional ordinary kriging based on egg counts. The green shaded area indicates the parks, gardens, etc. (the “green” areas of the survey site). Highest densities are located in the southwest and northwest quadrants with a tail extending in a northeasterly heading, probably as result of prevailing winds and traffic concentration.



atives of *P. regalis*, *P. delottoi*, and *Pulvinariella mesembryanthemi* from California spread rapidly in the same life stage on wind currents (Washburn and Frankie 1985). Even the notorious phylloxera aphid, *Daktulosphaira vitifoliae*, which has caused so much damage in grape growing regions of the world, has a crawler stage that is carried by the wind. However, in this case, 20 m seems to be the maximum distance for this transport system (King and Buchanan 1986). Reference to the area map (Fig. 1), to the observed trend (Fig. 4a), and the kriged surfaces (Fig. 3) suggests that scale infestations were concentrated towards the northwest and southwest of the urban survey area, with least infestations in the northeast. Moreover, the interpolated egg density distribution coincides remarkably well with the green regions in the sample area (Fig. 3). These green areas, dominated by gardens, parkland, and playing fields, are described by regions of low impermeability in the GLIM analysis, and provide a different environment for tree growth and perhaps for insect survival, when compared with more normal urban areas, predominantly city streets, shopping centers and car parks. Insect survival has been shown to increase where urban environments provide sheltered, relatively warm, overwintering sites (Miller and Hart 1987, Yoder and Robinson 1990), such as might be expected close to buildings or street lights. Areas devoid of vegetation, leaf litter, exposed soil etc., are also less likely to harbor natural enemies (Fang et al. 1983, Hanks and Denno 1993); in fact, arthropods in cities are likely to consist mainly of species overwintering on the food plant itself (Segebad and Schaefer, 1979).

Determining whether or not a tree is vigorous or under stress is difficult until clearly visible symptoms appear. Subtle changes in plant chemistry may occur in the early stages of stress that benefit sap feeding and defoliating insects, but by the time rots and diebacks become apparent, stress conditions can be assumed to be severe. The likelihood of trees in urban areas being less vigorous than their rural counterparts has often been discussed (Coffelt et al. 1993), and stress in the host tree leading to increased populations of herbivores is well known (for example, Speight 1986, 1996, White 1993). Specific stress-inducing agents include drought (Thomas and Hodkinson 1991, Foggo and Speight 1993), soil nutrients (Stoszek 1988, Thomas and Hodkinson 1991, Potter 1992), root damage (Foggo and Speight 1993), light conditions (Fang et al. 1983), aerial pollution, especially SO₂ (Skuhrava and Skuhrava 1986, Warrington and Whittaker 1990, Nair and Ma-

thew 1992), extremes of geographical range (McClure 1985), and physical damage (Rogers and Grant 1990).

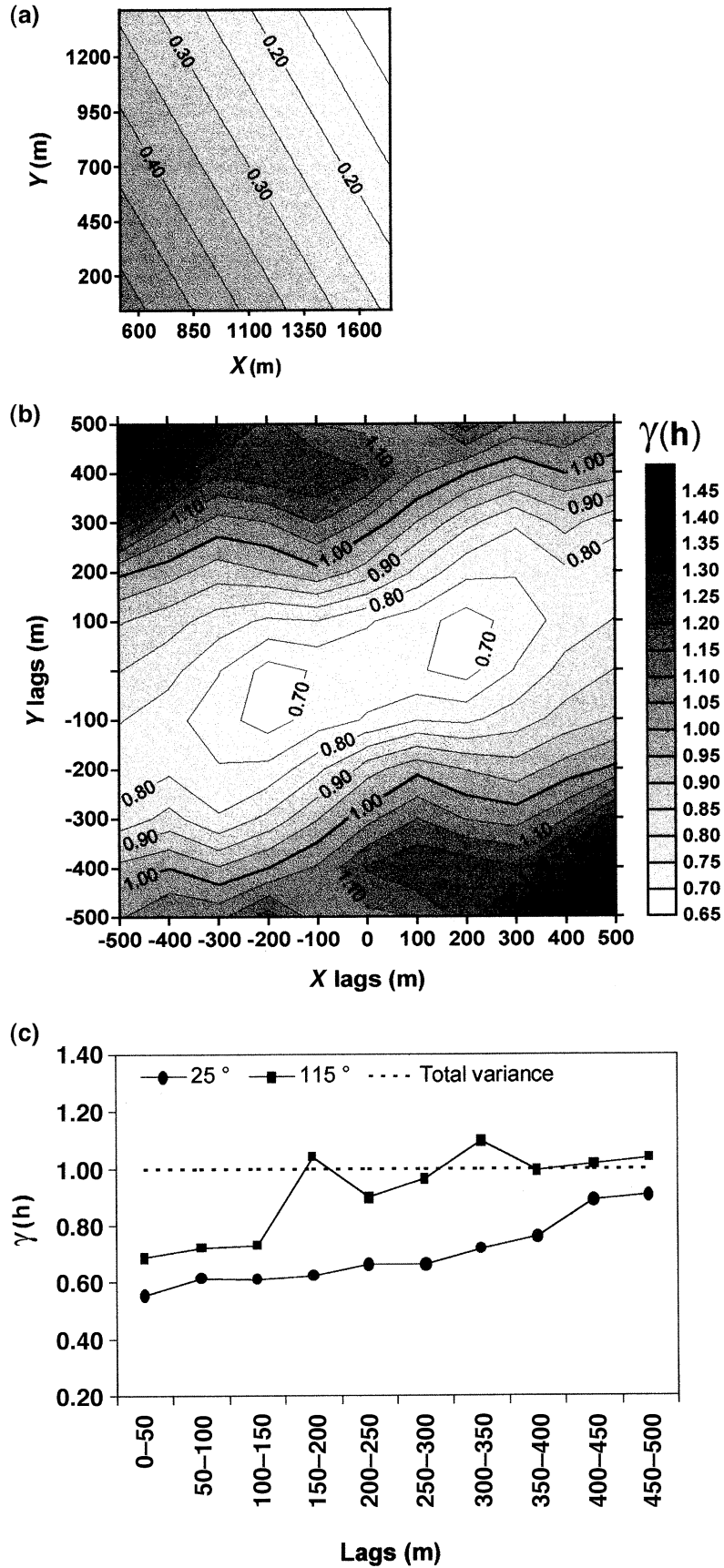
Only two of the environmental parameters measured were found to be important in predicting scale egg numbers for vigorous trees, the impermeability of ground cover under the trees, and their proximity to buildings. Substrate impermeability is of course high, even maximal, close to a building; tree roots will extend under the foundations where no water or nutrients can penetrate vertically. Other stress-inducing conditions close to buildings might be root damage by excavation works, and shade. The latter effect will depend on aspect, time of day, and of course, the size of the building, and is likely to have most influence very close to the tree in question. In any event, the general building effect would appear to be of relatively little importance in influencing tree vigor when compared with impermeability, or more general problems such as rots, diebacks, or simply old age; all common problems with urban trees.

Only ground impermeability under the canopy was shown to be an important predictor of egg densities on both vigorous and nonvigorous trees. Because of severe restrictions on water flow, drainage, nutrient cycling, and soil conditions under concrete, tarmac, paving slabs, and buildings will undoubtedly be less than optimal for plant growth. In other studies, it has been found that trees growing in urban sites where nutrient and water flow are restricted by paving have reduced growth rates and high vapor pressure deficits when compared with trees in parks (Kjelgren and Clark 1993). Oxygen tension in soil beneath these trees must also be low, tending towards anaerobic conditions and reduced root performance.

These results clearly support the view that the site conditions in which a tree is growing can fundamentally influence its susceptibility to insect herbivory. Sap-feeding scale insect populations are in many cases limited by food quantity and quality, by intraspecific competition for these parameters, and also for space (Denno et al. 1995). The influence of parasitoids and predators is less important in population regulation of *P. regalis* (Speight, unpublished). Hence, any improvement in the food supply will promote individual success and population increase. Planting trees in urban areas where soil/root conditions are radically altered and normal performance prevented will significantly reduce the vigor of the host trees and encourage herbivory. Many other authors discuss the potential for higher population levels of herbivorous insects in urban areas

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FIG. 4. (a) Trend calculated on the basis of the log-transformed GLIM analysis standardized residuals, showing an east-northeast decreasing gradient $Z = 0.657 - (2.4 \times 10^{-4})X - (1.4 \times 10^{-4})Y$, $P < 0.001$, $df = 231$. (b) Semivariogram surface of the log-transformed GLIM analysis standardized residuals after trend removal, showing strong directional anisotropy in the east-northeast direction (range >500 m in the 25° direction and estimated to 200 m in the 115° direction). (c) Semivariogram of log-transformed GLIM analysis standardized residuals after trend removal, showing the two main anisotropy axes and a spatial dependence of respectively 45% and 35% of the total variance for the first lag in the 25° and 115° directions.



compared with rural ones, though the causal agents vary. Thus, the scale insect *Pseudaulacaspis pentagona* infests host trees in parking grounds and along roadsides, but is not found in woodlands (Hanks and Denno 1993), which is exactly the situation found with *P. regalis*. Higher insect population densities on trees in towns have been attributed to various causes. For example, larch aphids in China are thought to increase in urban habitats due to high light conditions and reductions in natural enemy complexes (Fang et al. 1983), and lepidopteran wood borers show highest infestation levels in urban areas where mechanical damage to trees from various anthropogenic sources is severe (Rogers and Grant 1990). Combinations of conditions likely to be more prevalent in urban habitats promote insect attack and tree damage; plants growing in soils of low nitrogen status and subject to drought stress are most effective hosts for various defoliators and miners (Thomas and Hodkinson 1991, Foggo and Speight 1993), while the impact of aphids on host trees seems to be greatest on trees effected by drought and compounded by high levels of sulphur dioxide pollution (Warrington and Whittaker 1990).

The associations between tree environment and herbivory levels on the trees are clearly complex and multifaceted. From a management perspective however, the signs are simple enough; trees cultivated in sites likely to stress them should be avoided if insect pests are to be reduced or avoided. Furthermore, as the geostatistics have shown, extra environmental factors such as easy dispersal of propagules or colonizers by wind, aided by urban corridors, can exacerbate such pest problems; management tactics might include the establishment of trees at risk in the lee of windbreaks, or in isolation from infection or infestation sources.

Finally, the analysis of the *Pulvinaria regalis* data in this study validates the use and further development of spatial statistics as a tool for the investigation of patterns of insect abundance in a patchy landscape. In essence, the systems are simple (especially with up-to-date computer software), robust, and are able to reveal new information about the distribution of data which standard multivariate statistics ignore. Though this study has been a fairly small scale one, using individual trees as sample units, it has provided a convenient model with which to test both mapping and interpolation methods, as well as variography. It is entirely possible to use the same techniques on wider ranging and much larger data sets which cover whole forests or even geographical regions. Further data collection is required to provide for more development and verification of this type of spatial statistics in both pure and applied ecology. Existing data may benefit from reanalysis using these new protocols.

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LITERATURE CITED

- Coffelt, M. A., P. B. Schultz, and D. D. Wolf. 1993. Impact of late-season orangestriped oakworm (Lepidoptera: Saturniidae) defoliation on oak growth and vigor. *Environmental Entomology* **22**(6):1318-1324.
- Crawley, M. J. 1993. *GLIM for ecologists*. Blackwell Scientific, Oxford, UK.
- Cressie, N. A. C. 1993. *Statistics for spatial data*. John Wiley and Sons, New York, USA.
- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interaction in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* **40**:297-332.
- DePaul, F. T., C. M. Sheih. 1986. Measurements of wind velocities in a street canyon. *Atmospheric Environment* **20**(3):455-460.
- Fang, S. Y., H. Zhong, and Y. M. Ling. 1983. An investigation on larch aphids in the botanical garden of Heilongjiang Province. *Journal of North Eastern Forestry Institute, China*. **11**(4):36-41.
- Foggo, A., and M. R. Speight. 1993. Root damage and water stress: treatments affecting the exploitation of the buds of common ash *Fraxinus excelsior* by the larvae of the ash bud moth *Prays fraxinella*. *Oecologia* **96**(1):134-139.
- Fraser, J. B., and G. W. Frankie. 1986. An ecological comparison of spiders from urban and natural habitats in California (USA). *Hilgardia* **54**(3):1-24.
- Hanks, L. M., and R. F. Denno. 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology* **74**:1081-1091.
- Harris, K. M. 1970. Horse chestnut scale. *Arboricultural Association Journal* **1**:257-262.
- Houston, D. R. 1984. Stress related to diseases. *Arboricultural Journal* **8**:137-149.
- Isaaks, E. H., and R. M. Srivastava. 1989. *An introduction to applied geostatistics*. Oxford University Press, New York, New York, USA.
- King, P. D., and G. A. Buchanan. 1986. The dispersal of phylloxera crawlers and spread of phylloxera (*Daktulosphaira vitifoliae*) infestations in New Zealand and Australian vineyards. *American Journal of Enology and Viticulture* **37**(1):26-33.
- Kjelgren, R. K., and J. R. Clark. 1992. Microclimates and tree growth in three urban spaces. *Journal of Environmental Horticulture* **10**:139-145.
- Kjelgren, R. K., and J. R. Clark. 1993. Growth and water relations of *Liquidamber styraciflua* L. in an urban park and plaza. *Trees: structure and function*. **7**(4):195-201.
- Liebhold, A. M., R. E. Rossi, and W. P. Kemp. 1993. Geostatistics and geographic information systems in applied insect ecology. *Annual Review of Entomology* **38**:303-327.
- Luria, M., R. Weisinger, and M. Peleg. 1990. Carbon monoxide levels at the centre of city roads in Jerusalem (Israel). *Atmospheric Environment Part B, Urban Atmosphere* **24**(1):35-42.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603-609.
- Maurer, B. A. 1994. *Geographical population analysis: tool for the analysis of biodiversity*. Methods in Ecology, Blackwell Scientific, Oxford, UK.
- McClure, M. S. 1985. Patterns of abundance, survivorship, and fecundity of *Nuculaspis tsugae* (Homoptera: Diaspididae) on *Tsuga* species in Japan in relation to elevation. *Environmental Entomology* **14**(4):413-415.

- Meirleire, H. 1984. *Pulvinaria* scales of ornamental trees; two species that should not be confused. *Phytoma* **354**:37–38.
- Merlin, J., J. C. Grégoire, M. Dolmans, M. R. Speight, J. M. Pasteels, and C. Verstraeten. 1988. Preliminary comparison of two scale insect species on broad-leaved trees in western Europe. *Mededelingen Van De Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **53**:1153–1158.
- Miller, F. D., and E. R. Hart. 1987. Overwintering survivorship of pupae of the mimosa webworm, *Homadaula anisocentra* (Lepidoptera: Plutellidae) in an urban landscape. *Ecological Entomology* **12**(1):41–50.
- Morales, C. F., M. G. Hill, and A. K. Walker. 1988. Life history of the sooty beech scale (*Ultracoelostoma assimile*) (Maskell), (Hemiptera, Margarodidae) in New Zealand *Nothofagus* forests. *New Zealand Entomologist* **11**:24–37.
- Nair, K. S. S., and G. Mathew. 1992. Biology, infestation characteristics and impact of the bagworm, *Pteroma plagiophleps* Hamps in forest plantations of *Paraserianthes falcata*. *Entomon* **17**(1–2):1–13.
- Nogueira, C. D. S. 1976. The phytosanitary problem with pines in Estoril. *Anal. do Instituto Superior de Agronomia* **36**:203–240.
- Pannatier, Y. 1996. VARIOWIN: Software for Spatial Data Analysis in 2D. Springer-Verlag, New York, New York, USA.
- Potter, D. A. 1992. Abundance and mortality of a specialist leafminer in response to experimental shading and fertilisation of American holly. *Oecologia* **91**(1):14–22.
- Rogers, L. E., and J. F. Grant. 1990. Infestation levels of dogwood borer (Lepidoptera: Sesiidae) larvae on dogwood trees in selected habitats in Tennessee. *Journal of Entomological Science* **25**:481–485.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological Monographs* **62**:277–314.
- Ruszczuk, A. 1986. Mortality of *Papilio scamander scamander* (Lepidoptera: Papilionidae) pupae in four districts of Porto Alegre (southern Brazil) and the causes of superabundance of some butterflies in urban areas. *Revista Brasileira de Biologia* **46**(3):567–580.
- Segebade, R., and M. Schaefer. 1979. On the ecology of arthropods in urban districts and their surroundings II. Plant galls and leaf mines. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz* **52**(8):117–121.
- Sengonca, C., and T. Faber. 1995. Beobachtungen über die neu eingeschleppte Schildlausart *Pulvinaria regalis* Canard am Park- und Alleebäumen in einigen Stadtgebieten im nördlichen Rheinland. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **102**(2):121–127.
- Speight, M. R. 1986. Environmental influences on host plant susceptibility to insect attack. Insects and the plant surface. Pages 309–316 in B. Juniper and T. R. E. Southwood, editors. Edward Arnold, London, UK.
- . 1991. The impact of leaf feeding by nymphs of the horse chestnut scale insect, *Pulvinaria regalis* Canard (Hom., Coccidae) on young host trees. *Journal of Applied Entomology* **112**:389–399.
- . 1994. Reproductive capacity of horse chestnut scale insect, *Pulvinaria regalis* Canard (Hom., Coccidae). *Journal of Applied Entomology* **118**:59–67.
- . 1996. The relationship between host tree stresses and insect attack in tropical forest plantations and its relevance to pest management. Impact of diseases and insect pests in tropical forests. Pages 363–372 in K. S. S. Nair, J. K. Sharma, and R. V. Varma, editors. International Union of Forest Research Organisations (IUFRO) Symposium, Kerala Forest Research Institute, Peechi, India 1993.
- Speight, M. R., and M. Nicol. 1985. Horse chestnut scale—another problem for urban trees? *Antenna* **9**(4):175–178.
- Speight, M. R., and D. Wainhouse. 1989. Ecology and management of forest insects. Oxford Science Publications, Clarendon Press, Oxford, UK.
- Stoszek, K. J. 1988. Forest under stress and insect outbreaks. *Northwest Environmental Journal* **4**(2):247–261.
- Thomas, A. T., and I. D. Hodkinson. 1991. Nitrogen, water stress and the feeding efficiency of lepidopteran herbivores. *Journal of Applied Ecology* **28**:703–720.
- Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, Massachusetts USA.
- Warrington, S., and J. B. Whittaker. 1990. Interactions between Sitka spruce, the green spruce aphid, sulphur dioxide pollution and drought. *Environmental Pollution* **65**:363–370.
- Washburn, J. O., and G. W. Frankie. 1985. Biological studies of iceplant scales, *Pulvinariella mesembryanthemi* and *Pulvinaria delotti* (Homoptera: Coccidae) in California (USA). *Hilgardia* **53**(2):1–27.
- Watt, A. D. 1994. The relevance of the stress hypothesis to insects feeding on foliage. Pages 63–70 in S. R. Leather, A. D. Watt, N. J. Mills and K. F. A. Walters, editors. Individuals, populations and patterns in ecology. Intercept, Hampshire, UK.
- White, T. C. R. 1993. The inadequate environment—nitrogen and the abundance of animals. Springer, Berlin, Germany.
- Yoder, K. M., and W. H. Robinson. 1990. Seasonal abundance and habits of the boxelder bug, *Boisea trivittata* (Say), in an urban environment. *Proceedings of the Entomological Society of Washington* **92**(4):802–807.