

Proceedings

Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests¹

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PREFACE

This proceedings results from a conference held at the Monastery of Vallombrosa, near Florence, Italy, on September 1st - 3rd 1996. The meeting, held under the guidelines of the International Union of Forestry Research Organizations, gathered three IUFRO Working Parties: S7.03.03 (Insects Affecting Reforestation), S7.03.05 (Integrated Control of Scolytid Bark Beetles) and S7.03.07 (Population Dynamics of Forest Insects). Forty-nine participants, from 15 countries, presented 33 papers and 8 posters. These figures understate the contributors' input; considerable sharing of expertise and enthusiasm also occurred between the sessions, and links for present or future co-operation were renewed or established.

The organizers wish to express their gratitude to the Italian colleagues who helped to organize locally the meeting: Prof. Rizio Tiberi and Dr. Franco Cerchiarini (Istituto di Patologia e Zoologia Forestale e Agraria, Universita degli Studi, Firenze), Dr. Andrea Battisti and Mr. Massimo Faccoli (Istituto di Entomologia Agraria, Universita` degli Studi, Padova).

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Table of Contents

Pheromone mass trapping: Does it protect windfalls from attack by <i>Ips typographus</i> L. (Coleoptera: Scolytidae)? JEAN-CLAUDE GRÉGOIRE, LAURENT RATY, ALAIN DRUMONT, AND NATHALIE DE WINDT.....	1
Silvicultural methods of <i>Lymantria dispar</i> L. management: effects on <i>Agrilus bilineatus</i> (Weber) populations. ROSE-MARIE MUZIKA, ANDREW LIEBHOLD, AND KURT GOTTSCHALK.....	9
Augmentation of <i>Dendroctonus frontalis</i> parasitoid effectiveness by artificial diet. F.M. STEPHEN, M.P. LIH, AND L.E. BROWNE.....	15
Spruce aphid population dynamics in relation to canopy character: scope for cultural regulation. K.R. DAY AND H. ARMOUR.....	23
Integrating Tree Felling with Application of an Inhibitor Pheromone for Suppressing Southern Pine Beetle Infestations. SCOTT M. SALOM, RONALD F. BILLINGS, C. WAYNE BERISFORD, STEPHEN R. CLARKE, Q.C. MCCLELLAN, W.W. UPTON, AND M.J. DALUSKY.....	39
A user-friendly PC-based GIS for forest entomology: an attempt to combine existing software. MARIUS GILBERT.....	54
<i>Tomicus piniperda</i> in North America: An Integrated Response to a New Exotic Scolytid. ROBERT A. HAACK, ROBERT K. LAWRENCE, DEBORAH G. MCCULLOUGH, AND CLIFFORD S. SADO.....	62
Preliminary Investigations on the Relationships Between Phloem Phenolic Content of Scots Pine and Maturation Feeding of the Pine Weevil <i>Hylobius Abietis</i> . FRANÇOIS LIEUTIER, JACQUES GARCIA, ANNIE YART, LAETITIA GERARD, CLAUDE-BERNARD MALPHETTES, AND PAUL ROMARY.....	73
Integrated bark beetle control: experiences and problems in Northern Germany. HANS NIEMEYER.....	80
A Molecular Method for Differentiating Sibling Species within the Genus <i>Ips</i> . CHRISTIAN STAUFFER.....	87
Phenolic and Resistance of Scots Pine to Bark Beetles. EVELYNE BOIS, FRANÇOIS LIEUTIER, DANIEL SAUVARD, AND ANNIE YART... 	92

Technology Transfer of Treatments using Verbenone for the Suppression of Southern Pine Beetle Infestations. STEPHEN R. CLARKE, RONALD F. BILLINGS, SCOTT M. SALOM, AND C. WAYNE BERISFORD.....	95
Girdling of crownless Norway spruce snags: a measure against <i>Ips typographus</i> . BEAT FORSTER.....	101
Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety Mountains in Poland. WOJCIECH GRODZKI.....	105
Effects of integrating cultural tactics into the management of the balsam twig aphid <i>Mindarus abietinus</i> Koch (Aphididae: Homoptera) in balsam fir Christmas tree plantations. PAULA K. KLEINTJES.....	112
The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study. B. STAFFAN LINDGREN AND KATHY J. LEWIS.....	122
<i>Tomicus destruens</i> (Wollaston): biology and behaviour in Central Italy. CATIA NANNI AND RIZIERO TIBERI.....	131
Integrating Pheromone and Silvicultural Methods for Managing the Douglas-fir Beetle. DARRELL W. ROSS AND GARY E. DATERMAN.....	135
The attractiveness of pine branches infected with selected wood-colonising fungi to the Large Pine Weevil (<i>Hylobius abietis</i>). IWONA SKRZECZ AND ROGER MOORE.....	146
Spatial and Temporal Attack Dynamics of the Mountain Pine Beetle: Implications for Management. BARBARA J. BENTZ, JESSE A. LOGAN, AND JAMES A. POWELL.....	153
Does drought really enhance <i>Ips typographus</i> epidemics? -A Scandinavian perspective. ERIK CHRISTIANSEN AND ALF BAKKE.....	163
Observations on the Transmission of <i>Ophiostoma ulmi</i> by the Smaller Elm Bark Beetles (<i>Scolytus spp.</i>). M. FACCOLI AND A. BATTISTI.....	172
Intensive silvicultural practices increase the risk of infestation by <i>Dioryctria sylvestrella</i> Ratz (<i>Lepidoptera: Pyralidae</i>), the Maritime pine stem borer. H. JACTEL AND M. KLEINHENTZ.....	177

Spatio-temporal geostatistical analysis for <i>Ips typographus</i> monitoring catches in two Romanian forest districts. LAURENT RATY, CONSTANTIN CIORNEI, AND VASILE MIHALCIUC.....	191
Impact of natural enemies on <i>Tomicus piniperda</i> offspring production. L.M. SCHROEDER.....	204
Phenolic Compounds as Predictors of Norway Spruce Resistance to Bark Beetles. FRANÇOIS LIEUTIER, FRANCK BRIGNOLAS, DANIEL SAUVARD, CHRISTOPHE GALET, ANNIE YART, MARTINE BRUNET, ERIK CHRISTIANSEN, HALVOR SOLHEIM, AND ALAN BERRYMAN.....	215
<i>Cryphalus piceae</i> and silver fir decline in Vallombrosa forest. FRANCO CERCHIARINI, AND RIZIERO TIBERI.....	217
Japanese Phoretic Mites and Their Hyperphoretic Fungi Associated with Flying Adults of the Spruce Beetle (<i>Ips Typographus Japonicus Nijima</i>) (Col., Scolytidae). JOHN C. MOSER, THELMA J. PERRY, AND KIMOTO FURUTA.....	220
Current research on genetic resistance to white pine weevil in British Columbia. RENE I. ALFARO.....	222
Mass Attack by <i>Tomicus piniperda</i> L. (Col., Scolytidae) on <i>Pinus yunnanensis</i> Tree in the Kunming Region, Southwestern China. HUI YE.....	225
Uncommon cases of damage to young coniferous trees by several curculionoidea species, and possible ecological reasons. A.V. GOUROV AND V. TAGLIAPIETRA.....	228

Spatio-temporal geostatistical analysis of *Ips typographus* monitoring catches in two Romanian forest districts.

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ABSTRACT Systematic trapping and monitoring of the spruce bark beetle *Ips typographus* has been carried out extensively in the Romanian Carpathians since 1984, using pheromone traps. We present here a geostatistical analysis of catches performed in two contiguous Romanian forest districts, Rastolita and Lunca Bradului. Numbers of insects caught per trap between 1987 and 1994 were aggregated over each year. These data presented very good spatial, and good temporal auto-correlation. Because of their strongly left skewed distribution, analyses were performed on logarithm of the catches. Data were spatially detrended by a median-polish, that produced spatially isotropic residuals. Isolated spatial outliers were Winsorized through robust krigings based on omni-directional variograms, and performed separately over each year. A global spatio-temporal (anisotropic) variogram was then fitted to Winsorized data, and kriging estimates were built. It was possible to estimate catch logarithm, using spatial kriging, with relative precision ranging around 10%, taking into account results of only the current year. More interestingly, spatio-temporal kriging also performed well to forecast logarithmic catch, using results from three previous years. In spatio-temporal kriging, auto-correlation between measurements spaced too closely introduced a loss of information. A theoretical analysis of the spatio-temporal variogram showed that, when kriging neighbourhood is limited in terms of number of data used to forecast next-year catches (thus when computation effort is limited), an optimal trap density may be calculated.

KEY WORDS *Ips typographus*, Romania, geostatistics, interpolation, forecast, monitoring

THE SPRUCE BARK BEETLE, *Ips typographus* (Coleoptera: Scolytidae), is a semi-aggressive bark beetle that can kill extensive areas of spruce by the burrowing activities of its larvae, particularly after natural, weather-linked, phenomena such as drought and windthrow. Loss of vigour due to stressing agents such as these is a very common precursor to serious pest outbreaks (Speight 1996). Control of this pest species is very difficult; sanitation management of forests can reduce the impact of *Ips typographus*, though the sheer magnitude of the outbreaks can render the operation unfeasible.

In the Romanian Carpathians (Moldavia and Transylvania), systematic trapping and monitoring program of the spruce bark beetle has been carried out very extensively since 1984. Pheromone-baited traps are now placed in virtually every forest likely to harbour insect populations. The results produced by this program have provided a valuable source of information concerning insect population fluctuations that might be related to climatic and biotic conditions (weather, soil conditions, geography etc.). Hence, after appropriate and exhaustive analysis, these data provide an unparalleled opportunity to study the outbreak dynamics and effects of potential pest management strategies of one of the most important insect pests in Europe.

In this paper, we present a spatio-temporal geostatistical analysis of the catches performed in two contiguous Romanian forest districts, Rastolita and Lunca Bradului,

between 1987 and 1994. Our aims are to analyse the spatio-temporal variations of these catches (i.e. to see how catches vary spatially during each year, and how they vary from year to year at a given place), and to build estimates of the catches for places and years where no measure is available.

It is well known that damage due to semi-aggressive bark beetles are dependant on their population density. In particular, colonisation of a tree will be successful only if the number of beetles able to aggregate on that tree is high enough to overcome its defence reactions (i.e., Lieutier 1990). Assuming that trap efficiency does not vary too much from place to place or year to year, it seems logical to think to the number of insects caught in a trap is an indicator of the number of beetles crossing the trap neighbourhood and able to respond to their aggregative pheromone, e.g. able to aggregate on a host tree.

Building predictions of the catches for locations where no traps were set up might be useful to foresters, as it would give them a tool to know where they need to focus on and prepare for possible attacks and help them to locate colonised trees to destroy beetles. Forecasting the catches would be useful as well, as this might provide a tool to decide when and where preventive control methods might be usefully set up.

Data

Insect trapping data were produced by monitoring 300 permanent traps in the two Romanian forest districts of Rastolita and Lunca Bradului. This area covers a total of about 90,000 ha. Traps were black PVC drainpipe tubes 8 cm in diameter with numerous small holes and a Typolur (Cluj, Romania) pheromone dispenser hung inside the tube. Dispensers were set up at the beginning of the flight period and not renewed before next year. Attracted beetles land on the tube, enter one of the holes and fall into a collector (usually a glass jar half-filled with water). These traps have been visited roughly on a weekly basis, depending on accessibility of the location where the trap was set up, by Romanian forest employees.

Catches were combined for time each year to suppress temporal discontinuity inherent to insect catches made at short intervals (each catch is one discrete event). Summarizing data on a yearly basis also avoids problems that arise when comparing catches performed at different periods of the year, due to a decrease of pheromone-trap efficiency as the dispenser dries out (Raty et al. 1995).

Romanian forest are divided in planning units that are defined as homogenous in regard to slope, orientation, soil characteristics, type of station and type of forest. This results in a fairly large variation in the unit area, ranging from approximately 0.5 to 80 ha.

Our data initially associated traps to the planning units where they were set up. To convert these data into geographical co-ordinates, a Geographical Information System (GIS), Arc/Info, was used to digitise 1:20 000-scaled maps of the forest districts. Planning-unit boundaries were encoded in vectorial format, location of the centroids of the polygons delimited by these boundaries were computed, and each trap was associated to its planning-unit centroid. These results were used to produce an ASCII file associating aggregated yearly catches to trap location and the year considered.

Data analyses

We mostly used classical geostatistical tools, from which we will assume an elementary knowledge. Interested readers may find more complete and precise description of these tools in Isaaks and Srivastava (1989) and in Cressie (1993). We generally used the same notations as Cressie (1993). We think to our data as a partial realisation of a random process, noted $\{Z(\mathbf{s}) : \mathbf{s} \in D\}$ where \mathbf{s} , the data location, varies continuously over D , which is a subset of the d -dimensional space \mathcal{R}^d ($d = 2$ when only space is considered and 3 when time is taken into account). Data are noted $\{Z(\mathbf{s}_1), \dots, Z(\mathbf{s}_n)\}$. All analyses were performed on the basis of the ASCII file described above, using FORTRAN 77 routines that were, in most cases, written especially for this purpose.

Exploratory analyses

Exploratory Data Analysis (EDA) was introduced in spatial statistical analyses by Tukey (1977), and has since become a classical precursory stage to geostatistical studies (Cressie 1993, Rossi et al. 1992). Its main goals are visualising data set, analysing data distribution, investigating their stationarity and spatial (or spatio-temporal) continuity, and detecting possible outlying data. EDA mostly uses simple statistical methods, such as computing means, medians and histograms. According to Cressie (1993), EDA may be usefully completed by more spatial analysis techniques, including computation of directional variograms, computation of pocket plots and median polishing.

Data skewness - Our data exhibited a strongly left skewed distribution. Furthermore, when calculated over each year, catch mean was linearly correlated to catch standard deviation ($r = 0.77$; $p = 0.02$). These effects were corrected, as prescribed by Tukey (1977), with application of a logarithmic transformation ($Z = \ln Z$).

Variograms and global non-stationarity - Observed directional spatial variograms were estimated for each year separately, following 4 directions (N-S, NE-SW, E-W and NW-SE), using the classical estimator (Matheron 1962) :

$$2\hat{\gamma}(\mathbf{h}) = \frac{1}{|N(\mathbf{h})|} \sum_{(\mathbf{s})} (Z(\mathbf{s}_i) - Z(\mathbf{s}_j))^2$$

A global pattern emerged from these computations. Variograms were fairly well shaped, exhibiting very small nugget-effects (close to 0), apparent sills ranging between 0.8 to 2 and apparent ranges between 4,000 and 8,000 m. At first glance, the data seem spatially continuous, and do not show evidence of strong measurement errors. However, zonal anisotropy was always clearly present. The E-W and SE-NW directions showed consistently higher sills than the two other directions. Furthermore, in these two directions, semi-variogram sills were typically larger than data variance. Combination of these two observations may be thought as evidence of global non-stationarity, and would indicate presence of a spatial trend in the data. Furthermore, this trend might have a permanent component, as patterns are comparable from year to year.

An observed temporal variogram was also estimated, with the whole data set. This variogram exhibited an apparent nugget effect of close to 0.4. This is much larger than spatial variograms, and may be due to significant variation in population density from year to year. After this abrupt vertical jump, the variogram increased slowly. At the scale of our

study, it remained always smaller than twice the data variance (variance was 0.747: largest computed semi-variogram value, for a 4-years lag, was 0.408). This could be explained if we hypothesise a permanent spatial mean structure: in a purely temporal variogram, suppressed only data from the same spatial location are compared. Variation within these data, even when separated by large temporal lags, would be smaller than global variation.

Data detrending - From the above discussion, we will introduce the following model developed by Cressie (1993): assuming our data are partial realisation of a process that satisfies the following decomposition :

$$Z(\mathbf{s}) = \mu(\mathbf{s}) + R(\mathbf{s})$$

where $\mu(\mathbf{s})$ is a deterministic mean structure, called large-scale variation or trend and $R(\mathbf{s})$ is a stationary process, called small-scale variation. This kind of decomposition applied to a data set is called *detrending*. *Median polish* (Tukey 1977) is an EDA technique designed to identify large-scale and small-scale variation for gridded data, by analysing them as a 2- (or higher-) way table, and using the following additive model :

$$\text{data} = \text{global effect} + \text{row effect} + \text{column effect} + \text{residual}.$$

Decomposition follows an algorithm that alternatively sweeps medians out of rows and columns, and accumulates them in «row», «column», and «global» registers. A table of residuals results as well as preservation of additive decomposition relation at each step. If data are non-gridded, a low-resolution grid may be overlaid onto the data map. Each data point may be assigned to the nearest grid node (Cressie 1993), and median polish performed on this grid. A complete trend surface can be built by planar interpolation between the grid nodes.

A 2 km x 2 km grid was overlaid onto the data map. Each trap was assigned to the closest grid node and a spatial median polish was performed on this grid. To account for the apparently permanent character of the trend, we applied the algorithm only once, taking into account catches performed during the 8 years simultaneously. This produced a median-polish trend surface, showing obvious large-scale variation in both E-W and N-S directions.

Observed directional spatial variograms were estimated for each year, on the basis of the median-polish residuals. Most of the spatial anisotropy was captured by the median polish. Next steps of our analyses will be performed on the median-polish residuals, assuming they behave isotropically in space.

The temporal variogram remained clearly unchanged by the spatial median polish. However, as global variance of the median-polish residuals (0.437) was lower than variance of the original set of catch logarithms (0.747). The variogram values of the largest temporal lags were now much closer to twice the sample variance.

Local non-stationarity - The pocket plot technique (Cressie 1993) was used to detect pockets of local non-stationarity in median-polish residuals reassigned to the 2km² grid nodes that were used for the median polish. These analyses were performed separately for each year, and showed the presence of pockets of non-stationarity in each year.

Spatial geostatistical analyses

All analyses were performed on the basis of median-polish residuals, treated as a spatially isotropic data set. However, since we detected the presence of local pockets of non-

stationarity in the last step of the exploratory analyses, we treat our data as a realisation of a Gaussian stationary process.

As with Hawkins and Cressie (1984), we will consider $R(\mathbf{s})$ as a mixture of a stationary Gaussian sub-process and some other sub-process with heavy-tailed distribution. This last sub-process will act only on measurement errors and micro-scale variations, for a small proportion of the global process (non-Gaussian contamination).

Robust estimation of the variogram - Because the classical variogram estimator presented above is very sensitive to outlying data. We used the robust estimator proposed by Cressie and Hawkins (1980) :

$$2\hat{\gamma}(\mathbf{h}) = \frac{\left\{ \frac{1}{|N(\mathbf{h})|} \sum_{\mathbf{s}_i \in \mathbf{h}} |Z(\mathbf{s}_i) - Z(\mathbf{s}_j)|^2 \right\}^{\frac{1}{2}}}{0.457 + 0.494 \cdot |N(\mathbf{h})|}$$

Robust omni-directional spatial variogram estimators were computed on median-polish residuals for each year.

Variogram model fitting - Choice of a model to be fitted to the observed variograms was made by eye, by comparison between observed-variogram shape of and model shape. We selected the spherical model :

$$2\gamma(\mathbf{h}) = \begin{cases} 0 & \mathbf{h} = \mathbf{0} \\ c_0 + c_1 \left\{ \frac{3}{2} \frac{\|\mathbf{h}\|}{a_1} - \frac{1}{2} \left(\frac{\|\mathbf{h}\|}{a_1} \right)^3 \right\} & 0 < \|\mathbf{h}\| < a_1 \\ c_0 + c_1 & \|\mathbf{h}\| > a_1 \end{cases}$$

A model was fitted to the observed robust variogram of each year, through the weighted-least-square method (Cressie 1993).

Robust Kriging - *Kriging* can be understood as optimal linear prediction (Cressie 1993). This leads to the classical kriging predictor :

$$\hat{\rho}(Z; \mathbf{s}_0) = \sum_i \lambda_i Z(\mathbf{s}_i)$$

where the λ_i 's are weights given to data values that minimise the mean-squared prediction error. However, optimality of *linear* spatial prediction relies on assumption that the expectation of $Z(\mathbf{s}_0)$ at a location \mathbf{s}_0 is linear in the data $Z(\mathbf{s}_i)$, which is the case when the random process Z is Gaussian.

Outliers due to non-Gaussian distribution can have a substantial effect on linear predictors. However, these data often support information and deleting them incorrect would be a loss of this information. It would be better to find some way to downweight them. This leads to *robust kriging* techniques, summarised by Cressie (1993). Turn back to our description of the process distribution, we now build a predictor :

$$\hat{\rho}(Z; \mathbf{s}_0) = \sum_i \lambda_i Z(\mathbf{s}_i) w(Z(\mathbf{s}_i))$$

where $w(Z(\mathbf{s}_i))$ is a weight function, ranging from 0 to 1, which is close to 1 if datum $Z(\mathbf{s}_i)$ appears clean, but decreases to the extent that $Z(\mathbf{s}_i)$ appears to come from the contaminating distribution. Another way of writing this equation is :

$$\hat{\rho}(Z; \mathbf{s}_0) = \sum_i \lambda_i Z^{(e)}(\mathbf{s}_i)$$

where $Z^{(e)}(\mathbf{s}_i)$ is an *edited* modification of $Z(\mathbf{s})$ that behaves as if there was no contamination.

method we used is a geostatistical version of Huber's procedure for robust time-series analysis (1979, in Cressie 1993), but was performed with the robust variogram estimator proposed by Hawkins and Cressie (1984). Models fitted to robust variogram estimators were used to compute kriging weights for each $R(s_j)$ from all the remaining $R(s_i)$. A prediction:

$$\hat{R}_j(s_j) = \sum_{i \neq j} \lambda_i Z(s_i)$$

was built on basis of these weights and the associated error was computed. Using these weights, the $R(s_j)$ were Winsorized. That is, they were replaced by an edited version such as:

$$R^{(w)}(s_j) = \begin{cases} \hat{R}_j(s_j) + c\sigma_j(s_j) & \text{if } R(s_j) - \hat{R}_j(s_j) > c\sigma_j(s_j) \\ R(s_j) & \text{if } |R(s_j) - \hat{R}_j(s_j)| \leq c\sigma_j(s_j) \\ \hat{R}_j(s_j) - c\sigma_j(s_j) & \text{if } R(s_j) - \hat{R}_j(s_j) < -c\sigma_j(s_j) \end{cases}$$

edited values were then used to compute a new robust observed variogram, to which a new model was fitted. This variogram served to perform a new Winsorization, and this procedure was repeated until convergence of the edited values.

Depending on the year, 5 to 8% of the data were edited. Edited data may be separated into two categories: real outliers (data with especially high or low values), and pairs of data points that are spatially very close together, but with differing values. Part of these last data were probably really outlying. Their outlying appearance may have been due to imprecision in the location associated to the data (the planning-unit centroids).

Winsorized data were used to build predictions and to estimate kriging error over the whole study area, on a 500m² grid. Summing these predictions to the median-polish trend surface, we obtained prediction maps for the catch logarithms. It has been showed by Cressie (1993), that error associated to these predictions is the kriging error associated to the usual kriging predictions. Within the area where traps were set up, the prediction relative error (estimated by the ratio of half 95%-confidence interval to the prediction) rarely exceeded 10%. Maps of the predictions and the associated standard deviation for the years 1982 to 1993 are presented in Figure 1.

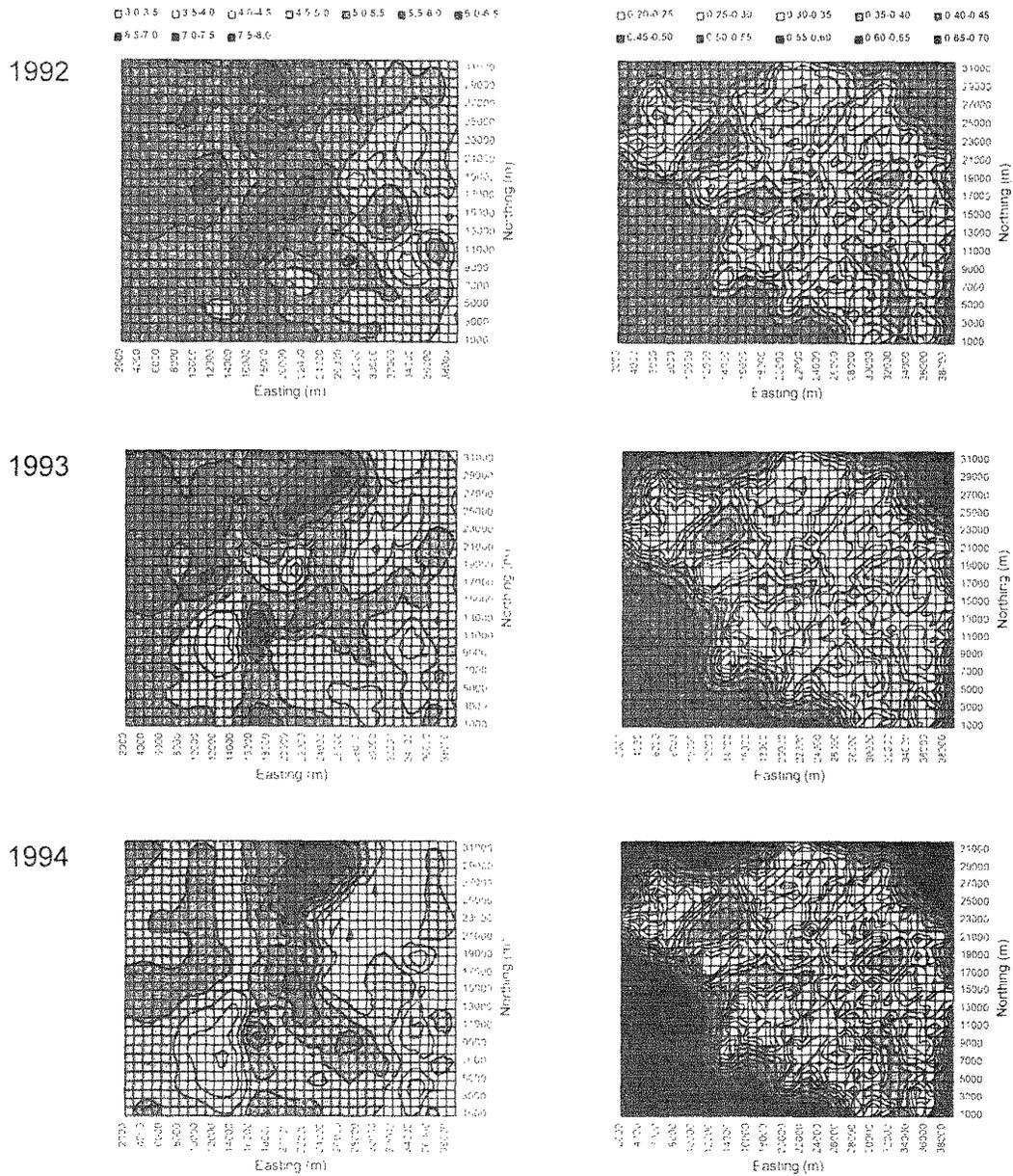


Figure 1. Predictions of the catch logarithms (left), and associated standard deviation (right), computed by spatial robust kriging on median-polish residuals.

Spatio-temporal analyses

Introduction of the time dimension was simply made by letting the location index s vary over an additional dimension. Spatio-temporal analyses were performed on the basis of the Winsorized median-polish residuals, produced by the robust spatial krigings.

Estimation of the spatio-temporal variogram - The robust variogram estimator developed by Cressie and Hawkins (1980) was used to compute an observed spatio-temporal variogram, for spatial lags from 0 to 10,000 m and temporal lags from 0 to 5 years (Figure 2a). In the spatial domain, variogram appeared very « clean », with nugget effect close to zero, and values growing slowly with the lag. An apparent sill was reached around 6,000 m, with a value between 0.7 and 0.8, slightly lower than twice the sample variance (0.437). In the temporal domain, nugget effect was clearly higher, and range was probably not reached within the temporal scale of our study. Given that, in the space-time domain, the variogram reached values that are higher than the apparent spatial sill, temporal sill was probably higher than this spatial sill.

Fitting of a spatio-temporal variogram model - Geometrical anisotropy is clearly inherent to any spatio-temporal variogram, as units are not the same along the space and time axes. Our data, however, showed clearly more complex behaviour than simple geometrical anisotropy : not only ranges differed between the axes, but also nugget effects and sills differed. For anisotropy, the usual way is to search for a linear transformation of the coordinate system that would produce a reduced isotropic variogram (Isaaks and Srivastava 1989, Cressie 1993).

To describe the spatio-temporal variogram of our data, we used a model with four additive structures : one pure nugget effect ($2\gamma_0$), one structure accounting for the anisotropy in the nugget effects ($2\gamma_1(\mathbf{h}_1)$), one accounting for geometrical anisotropy ($2\gamma_2(\mathbf{h}_2)$), and the last one accounting for zonal anisotropy ($2\gamma_3(\mathbf{h}_3)$). These structures were all described by spherical variogram models :

$$2\gamma(\mathbf{h}) = 2\gamma_0 + 2\gamma_1(\mathbf{h}_1) + 2\gamma_2(\mathbf{h}_2) + 2\gamma_3(\mathbf{h}_3),$$

where :

$$2\gamma_i(\mathbf{h}_i) = \begin{cases} 0 & \mathbf{h}_i = \mathbf{0} \\ w_i \left\{ \frac{3}{2} \|\mathbf{h}_i\| - \frac{1}{2} (\|\mathbf{h}_i\|)^3 \right\} & 0 < \|\mathbf{h}_i\| < 1 \\ w_i & \|\mathbf{h}_i\| > 1 \end{cases}$$

$$\mathbf{h}_i = \begin{bmatrix} h_{i,s} \\ h_{i,t} \end{bmatrix} = \mathbf{T}_i \mathbf{h} = \begin{bmatrix} \gamma_{s,s} & 0 \\ 0 & \gamma_{t,t} \end{bmatrix} \begin{bmatrix} h_s \\ h_t \end{bmatrix}$$

This model has 9 parameters, namely $w_0, w_1, w_2, w_3, a_{x,1}, a_{t,1}, a_{x,2}, a_{t,2}$, and $a_{t,3}$ ($a_{x,3}$ is infinite, $a_{x,0}$ and $a_{t,0}$ are zero).

However, to simplify fitting, we assumed some relations between them. $\gamma_1(\mathbf{h}_1)$ accounted for additional nugget effect observed in the time domain. Nugget effect may be viewed as result of measurement error plus result of variations at smaller scale than smallest lag : as measurement errors occurred both in the spatial and temporal domain, additional nugget effect in the time domain had to be due to the other source. Within time domain, $\gamma_1(\mathbf{h}_1)$ needed therefore to have reached its range after one year, which was the shortest temporal lag that we considered. To account for that, $a_{t,1}$ was set to 1 year. Both the purely spatial and purely temporal variograms were well described by single spherical models (two additive models with different ranges did not improve significantly the fitting). Therefore, we set : $a_{x,1} = a_{x,2} = a_x$ and $a_{t,2} = a_{t,3} = a_t$. This left us with 6 parameters, that were estimated through weighted-least-square fitting. A three-dimensional plot of the fitted model is shown in Figure 2b.

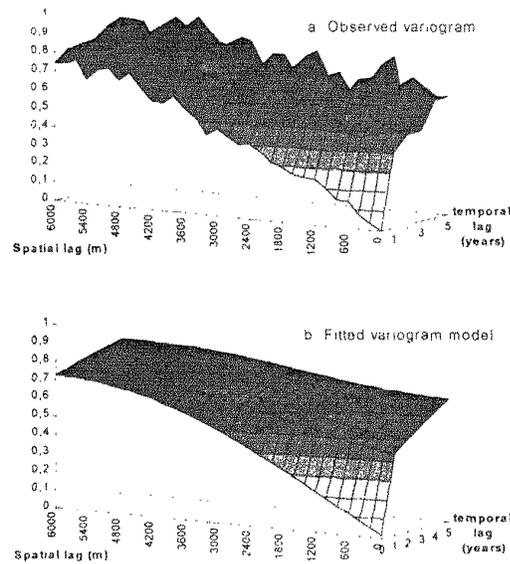


Figure 2. Spatio-temporal observed robust variogram computed on Winsorized median-polish residuals (a), and model fitted to this variogram (b).

Spatio-temporal kriging - Two practical situations may justify the use of spatio-temporal kriging, rather than (much more simple) spatial kriging : (1) to build *interpolation* predictions of the variable during one year where we have data, *if it can improve the prevision precision*, and (2) to *forecast* the variable for one year where no data are (yet) available. We will now take a look at these two situations.

Data values are not necessary to compute kriging weights and kriging error for the variogram if we assume a design with given data location. Let us assume a trapping design where permanent traps are located on a regular square grid. Within this design, locations where kriging error is largest are the square centres. Therefore, we will pay attention to these points. Kriging weights and error are functions of the location of the traps used to build the estimate that can let vary by changing the size of the grid squares. In this case, we vary the *trapping effort*. Furthermore, they are functions of the kriging neighbourhood, that may be expressed in terms of the number of traps used to build the estimate (spatial kriging neighbourhood), and of the number of years over which data are taken into account (temporal kriging neighbourhood). In this case, we vary the *computation effort*.

Taking only the symmetric spatial neighbourhoods into account, and restricting them to a reasonable number of data, a limited set of possibilities exists. The five smallest symmetric spatial neighbourhoods of our case study are illustrated in Figure 6. They respectively account of 4, 12, 16, 24 and 32 traps.

Spatio-temporal kriging used for interpolation - For the trapping device described above, kriging weights and error were computed, for distances between neighbouring traps varying from 500 m to 5,000 m, by steps of 500 m, and taking account of data from the 5 smallest

symmetric spatial kriging neighbourhoods, first over the current year only, then over current and one previous year and, lastly, over current and two previous years.

Results showed that kriging error depended only on distance between traps, and increased, nearly linearly, with this parameter. On the other hand, increasing spatial or temporal kriging neighbourhood did not have any significant effect. When looking at the kriging weights, any data added to the 16-data neighbourhood of the current year was given a negligible weight. Trapping-prediction precision would therefore rely nearly entirely on the trapping effort. This was mainly due to the fast decrease of the spatial correlation between data when the distance separating them increased (this is sometimes referred as screen effect (Cressie 1993)), and to a much lower correlation between data from different years than between data from the same year.

Adding results from previous years has a high computational cost and did not increase the precision : it seemed useless to complicate kriging by adding the time dimension when the goal is only to make an interpolation for a year where data were available. Spatial kriging is much easier to apply and probably more correct as it does not requires hypotheses about temporal stationarity.

Spatio-temporal kriging used for forecasting - For the trapping device described above, kriging weights and error were also computed, for distances between neighbouring traps varying from 500 m to 5,000 m, by steps of 500 m, and taking into account data from the 5 smallest symmetric spatial kriging neighbourhoods, first over one previous year, then over two and, lastly, over three.

Results were obviously different from those obtained assuming current-year data were available. The relation between kriging error and distance separating traps was no longer monotone, but exhibited a minimum : there was a distance between traps that, for a given computation effort, was optimal (1,000 to 2,000 m). Also obvious was the fact that expanding the kriging neighbourhood, in space or in time, led now to increased precision. This last result was due to a slower decrease of the correlation between data when spatial lag increased, as soon as temporal lag was larger than zero (weaker screen effect than for interpolation).

The existence of an optimal trapping effort was probably the most anti-intuitive of these results. It was due to the spatial auto-correlation between data from the same previous year which, being higher than spatio-temporal auto-correlation between data from previous year and data from current year, introduced some redundancy in the information carried by spatially close data. A consequence was that it was not always best to use the spatially closest traps to forecast catches when the computation effort was limited.

In an effort to test the forecast method, it is clear that it cannot be done on the basis of the analyses that were performed up to now. the spatio-temporal variogram, as well as the median-polish trend surface, were computed with our whole data set. Instead, we tried to simulate a situation where forecast would be useful : taking only into account the data from a few first years. and trying to predict results from the next year. We selected a spatial kriging neighbourhood of 32 traps. and a temporal neighbourhood of 3 previous years. To compute a

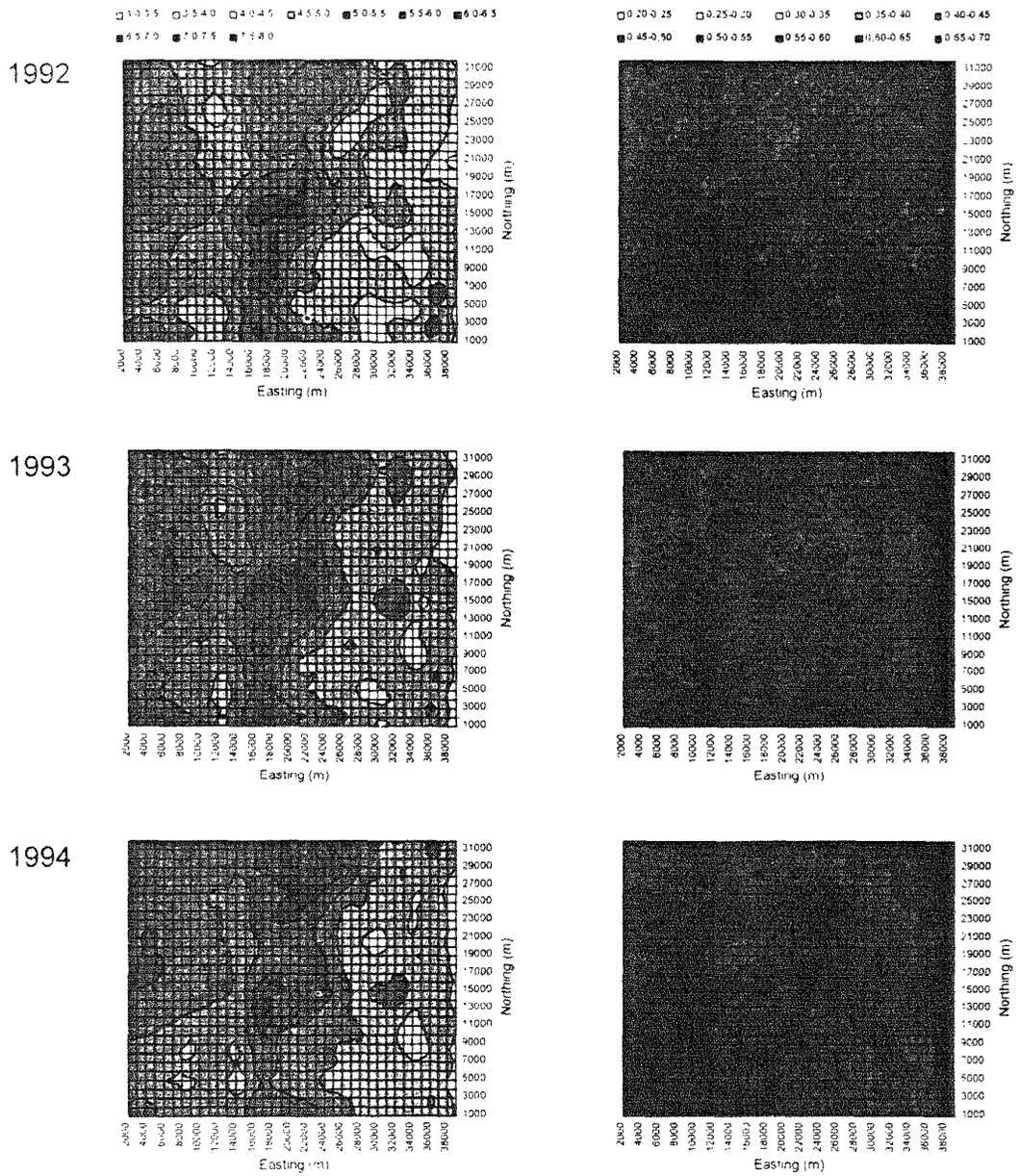


Figure 3. Predictions of the catch logarithms (left), and associated standard deviation (right), forecasted by a spatio-temporal robust kriging performed on median-polish residuals, using only data from previous years.

variogram with temporal lags up to 3 years, data from 5 years were a minimum. Forecasts were therefore computed only for years 1992 to 1994. For each of these three years, 5-previous-years data were used to compute a median-polish trend surface. Residuals of this median polish were Winsorized through robust spatial kriging. Winsorized residuals were then used to compute a spatio-temporal variogram to which a model was fitted. At last, this

model was used to compute predictions and prediction errors for the considered year, with data from the 32 nearest traps and the 3 previous years. Results are mapped in Figure 3 and may be compared to results of the robust spatial kriging performed on the data of these years (Figure 1). There was a good correspondence between the forecast prediction and the robust spatial kriging prediction. For 1992, 1993 and 1994, respectively 100%, 95.89% and 93.67% of the spatial robust kriging predictions fell within the 95% confidence interval associated to the forecast prediction.

Conclusions

In conclusion, we think we showed that *Ips typographus*-monitoring trapping does not produce erratic results. On the contrary, results were highly structured, showing an apparently permanent mean structure and spatial as well as temporal continuity. Our analyses allowed us to build predictions of the logarithmic catch with an acceptable precision when using the current-year data, and to forecast this logarithm, with less precision yet still reliably.

It is important to stress that these analyses do not explain in any way the reasons of catch variations, they only describe them with mathematical tools. However, they might be a good beginning point to start other analyses. The median-polish trend surface, which remains constant in time, might be tentatively correlated to permanent ecological factors (such as forest or soil characteristics, elevation, slope orientation, etc...). Departures from forecast models might be correlated with more sudden events (such as windfall and snowbreak occurrences).

It must also be stressed that these whole analyses were performed on basis of results produced in an area where *Ips typographus* populations are endemic. In epidemic situation, results would have been probably much more erratic and less structured. Moreover, the transition between endemic and epidemic situation in a bark-beetle population is probably not a linear phenomenon. This transition might be described as departure from the linear model that we describe here.

Acknowledgements

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Impact of natural enemies on *Tomicus piniperda* offspring production

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ABSTRACT The occurrences of *Thanasimus formicarius* (L.) (Cleridae) and *Rhizophagus depressus* (F.) (Rhizophagidae) in cut Scots pines attacked by *Tomicus piniperda* (L.) (Col.: Scolytidae) were recorded in the field, and interactions between the species were studied in caged pine bolts attacked by *T. piniperda*. The relative population densities of *T. formicarius*, *R. depressus*, and *T. piniperda* in pine stands with or without attacks of *T. piniperda* the previous year were estimated with flight barrier traps.

T. piniperda offspring production per m² was reduced by 41 % when reared with *R. depressus*, by 81 % when reared with *T. formicarius*, and by 89 % when all three species were reared together, compared with *T. piniperda* alone. Both *T. piniperda* and *R. depressus* were caught in higher numbers in stands with attacks of *T. piniperda* the previous year than in stands without bark beetle attacks. In contrast, there was no difference in catch of *T. formicarius* between the two kinds of stand. The main flight period of *T. piniperda* only lasted for a few days. In contrast, the flight periods of the two predators *R. depressus* and *T. formicarius* were much more extended. The flight period of *R. depressus* lasted for about one and a half month until the beginning of June while the flight period of *T. formicarius* still not had ended after three months in the middle of July when the experiment was ended.

KEY WORDS *Tomicus piniperda*, *Rhizophagus depressus*, *Thanasimus formicarius*, bark beetle predators, biological control, dispersal

LARGE NUMBERS OF arthropod species are found in the subcortical environment of trees attacked by bark beetles (Dahlsten 1982, Weslien 1992, Stephen et al. 1993). Many of these may feed on the immature stages of bark beetles. Studies conducted on bark beetles of the genera *Ips*, *Dendroctonus* and *Tomicus* have shown that complexes of associated species may strongly reduce bark beetle productivity (Linit and Stephen 1983, Miller 1986, Weslien 1992, Schroeder and Weslien 1994a). Few studies have determined the impact of single antagonistic species on bark beetle offspring production (Weslien and Regnander 1992, Weslien 1994, Schroeder and Weslien 1994b, Nicolai 1995). The impact of most associated species on bark beetle productivity still remains to be clarified.

Bark beetle attacked trees are often widely scattered as a result of the spatial distribution of suitable breeding material. In accordance with this, several bark beetle species have been demonstrated to have a capacity to migrate long distances (Nilssen 1978, 1984, Forsse and Solbreck 1985, Weslien and Lindelöw 1989). Thus, the impact of natural enemies on bark beetles is not only determined by the interactions under bark but also by the capacity of the enemies to colonize bark beetle attacked trees in new places.

In the present study, interactions between the bark beetle *Tomicus piniperda* (L.), the clerid *Thanasimus formicarius* (L.) and the rhizophagid *Rhizophagus depressus* (F.) were

analysed both at tree level and stand level. In an earlier field experiment larvae of *Thanasimus* and *Rhizophagus* were the most frequent enemies emerging from bolts under natural attack by *T. piniperda* (Schroeder and Weslien 1994a). In Scandinavia *T. piniperda* is largely confined to Scots pine, *Pinus sylvestris* L. The beetles reproduce in logs, stumps and pines that are windbroken, windthrown or otherwise weakened. *T. piniperda* usually attacks areas with rough bark, which are found on the lower parts of the bole of Scots pine. The species is monogamous, and the female initiates the egg gallery. In Scandinavia the flight period occurs in early spring and may be essentially over within a few days if weather conditions are favourable (Eidmann 1965, 1974, Bakke 1968). *T. piniperda* lacks an aggregation pheromone, but is strongly attracted by host volatiles (Byers et al., 1985, Schroeder 1987, 1988, Schroeder and Lindelöw 1989). After emergence the adult bark beetles fly to the crowns of nearby standing pines where they bore into and feed in the shoots. In late autumn the beetles leave the shoots to hibernate in the bark at the base of the trees. At high population levels the shoot feeding can cause a considerable reduction in growth (Långström and Hellqvist, 1990, 1991). In southern China *T. piniperda* has been reported to cause high tree mortality following a long drought (Ye 1991). Recently, the species has also been discovered in the United States and in Canada where most native pine species seem to provide suitable habitat for breeding and maturation feeding (Haack and Lawrence 1995, McCullough and Smitley 1995).

R. depressus is strongly attracted to conifer host volatiles and may be caught in high numbers in flight barrier traps baited with α -pinene and ethanol (Schroeder and Lindelöw 1989). Adults have been found in the gallery systems of *T. piniperda* (Saalas 1923, Nuorteva 1956, Szujecki 1987). *R. depressus* has been reported to prey on bark beetle broods (Hanson 1937, Nuorteva 1956).

T. formicarius is one of the most abundant and voracious predators of bark beetles (Gauss 1954). The species is attracted to bark beetle pheromones and host tree volatiles (Bakke and Kvamme 1981, Schroeder 1988, Schroeder and Lindelöw 1989). The adults prey upon bark beetle adults, mate and lay eggs in bark crevices. The larvae feed on bark beetle brood and probably also on other insects present under the bark. One of the main prey species of *T. formicarius* in Scandinavia is *T. piniperda*. *T. formicarius* adults are often abundant on pine stems newly attacked by *T. piniperda*. *T. formicarius* has earlier been demonstrated to strongly reduce *T. piniperda* offspring production (Schroeder and Weslien 1994a).

The objectives of the present study were to determine: 1) the impact of the predator *R. depressus* alone on *T. piniperda* progeny production, 2) the impact of the two predators *R. depressus* and *T. formicarius* together on *T. piniperda* progeny production, and 3) the relative population densities of *T. piniperda*, *R. depressus* and *T. formicarius* in Scots pine stands with and without bark beetle attacks the previous year.

Materials and Methods

Impact of *R. depressus* and *T. formicarius* on *T. piniperda* offspring production

The experiment was conducted in the province of Uppland in central Sweden in 1994. Scots pines were felled in late March, and three to four bolts (diam. 12-16 cm, length 35 cm and mean surface area under bark 0.15 m²) were taken from the basal part (with rough bark) of each tree. The bolts were placed under 1-mm screen mesh and held outdoors.

On 11 and 12 April, adult *T. piniperda* were collected in baited flight barrier traps (see Schroeder and Lindelöw 1989) placed in two Scots pine stands thinned one year earlier. *R. depressus* was collected in the flight barrier traps on 23 and 24 April. Copulating pairs of *T. formicarius* were collected on cut pine stems on 25 and 27 April. Collected insects were kept at +5° C in the laboratory until their release in the experimental cages.

The experiment had a randomized design with four treatments. It was conducted outdoors, at a distance of 300 m from the nearest forest in order to decrease the risk of uncontrolled insect colonization of the experimental bolts. Four bolts that had more than 500 egg galleries per m², which is exceptionally high (Nuorteva 1964, Saarenmaa 1983, Långström 1984), were excluded from the analysis. The treatments were:

T = *T. piniperda* alone, seven replicates (three bolts excluded).

TR = *T. piniperda* together with 30 *R. depressus* per caged bolt, ten replicates.

TF = *T. piniperda* together with two pairs of *T. formicarius* per caged bolt, eight replicates.

TRF = *T. piniperda* together with 30 *R. depressus* and two pairs of *T. formicarius* per caged bolt, seven replicates (one bolt excluded).

On 17 April, *T. piniperda* adults were released in each of two large cages containing all the bolts. Due to cold weather the release was conducted in the laboratory (+15° C). Two days later each bolt was placed separately in a cage (40 x 40 x 35 cm) with 0.5-mm screen mesh and held outdoors. On the same occasion the ends of all bolts were sealed with paraffin to prevent severe desiccation.

In a sample of 157 *R. depressus* beetles that were sexed alive, the proportion of males was 43 %. Sex determinations were made by examining the metasternum of *R. depressus*. Adult *R. depressus* were released in the cages on 27 April. *T. formicarius* adults may feed on *R. depressus* adults. Thus, the release of the *T. formicarius* adults was delayed for one week to give the *R. depressus* adults some time to settle in the bark beetle egg galleries. Every second week cages with *T. formicarius* were supplied with live-frozen *Ips* adults as food for the clerids. On days with hot weather the bolts were sprinkled with water.

The bolts were kept in the cages until 20 June, whereupon they were taken out and hung in emergence traps outdoors. Each emergence trap consisted of a white cotton bag (diam. 40 cm, length 110 cm) with a collecting funnel forming the bottom. The emergence bags were emptied about every third day until the emergence of *R. depressus* and *T. formicarius* larvae ended in October. The new generation adults of *T. piniperda* were easily recognized by their light brown colour. During the winter each bolt was debarked and the numbers and the lengths of *T. piniperda* egg galleries were recorded.

To study the developmental times, 87 larvae of *R. depressus* and 14 larvae of *T. formicarius* were sampled alive from the emergence traps on 8 July and put in 100-ml vials with moist sand and pieces of Scots pine outer bark on top of the sand. The vials were stored outdoors in the shade. Two of the sampled *T. formicarius* larvae were 14 mm long, while the rest were 6-12 mm long. The *R. depressus* larvae were distributed among seven vials while each *T. formicarius* larva was placed separately in a vial. The vials were inspected on 19 August.

Large scale spatial distribution of *T. piniperda*, *R. depressus* and *T. formicarius*

The experiment was conducted in the province of Uppland in central Sweden in 1995. The relative population densities *T. piniperda*, *R. depressus* and *T. formicarius* were compared in two kinds of Scots pine stands: A-stands which had been thinned during the winter of 93/94 and B-stands in which no logging operations had been conducted during the last five years. Apart from this difference the stands were similar. Nor had any logging operations been conducted recently in the stands adjoining the B-stands. In the A-stands *T. piniperda* and other insects, including natural enemies, reproduced in the stumps and slash during 1994. Inspections in early spring 1995 revealed large numbers of *T. piniperda*-bored pine shoots on the ground in the A-stands demonstrating the presence of local hibernating populations. No or only a few *T. piniperda*-bored pine shoots were present in the B-stands. In late autumn 1995 inspections of pine stumps in the A-stands revealed the presence of *T. formicarius* pupal chambers. The experiment was pair-wise arranged with one stand of each kind in each of four areas. Within the areas the distances between the stands were 3 to 5 km. The distances between the areas were 20 to 55 km.

Insects were caught in baited flight barrier traps (Schroeder 1988, type b). Under the barrier (a 40 x 40-cm transparent plastic sheet) a funnel ending into a water-filled jar was hung. In each stand five traps were arranged in a circle with a distance of 50 m between the traps.

The chemicals used were (-)- α -pinene (Fluka 97%, $[\alpha]_D^{20} -42 \pm 3^\circ$) and 95% ethanol (5% water). The dispensers (one per trap) consisted of two test tubes, one of which (depth 150 mm, inner diam. 14 mm) was filled with ethanol and one (depth 100 mm, inner diam. 9.5 mm) with α -pinene. Each tube were supplied with a strip of filter paper (Munktell No. 3; ethanol: 145 x 13.5 mm, α -pinene: 96 x 9 mm) reaching from the bottom to about 1 mm from the rim. A plastic 35-mm film canister was fitted over the open ends of the tubes. In a earlier study (Schroeder & Weslien, 1994a) the field release rates were estimated by measuring the amounts of chemicals left before refilling. Based on these results the release rates in the present study should have been approximately 4 mg of α -pinene and 40 mg of ethanol per hour during warm weather. α -Pinene and ethanol were chosen as bait since the combination of these two substances strongly attract *T. piniperda*, *T. formicarius* and *R. depressus* (Schroeder 1988, Schroeder and Lindelöw 1989, Schroeder and Weslien 1994a).

Results

Impact of *R. depressus* and *T. formicarius* on *T. piniperda* offspring production

The new generation of *T. piniperda* beetles started to emerge at the beginning of July, and virtually all beetles had emerged within two weeks. Timing of F_1 emergence was similar for all treatments.

Table 1. *Tomicus piniperda* reproduction in pine bolts of different treatments: Offspring per m², breeding density, productivity and mean length of egg galleries*. T = *T. piniperda* alone, TR = *T. piniperda* + *R. depressus*, TF = *T. piniperda* + *T. formicarius*, TRF = *T. piniperda* + *R. depressus* + *T. formicarius*.

	T	TR	TF	TRF
Offspring per m ²	2867a ¹ ± 535	1685b ± 1164	531c ± 296	312c ± 125
Egg galleries per m ²	285a ± 150	209a ± 122	149a ± 51	194a ± 39
Offspring per egg gallery	13.6a ± 8.6	11.1ab ± 9.7	4.6ab ± 4.5	1.7b ± 0.9
Mean egg gallery length (mm)	67.0ab ± 8.9	67.9a ± 9.7	80.5b ± 10.9	69.2ab ± 5.3

* Values are means of 5 replicates (bolts) in T, 8 replicates in TR and TF, and 7 replicates in TRF ± standard deviations.

(¹) Means followed by the same letter within rows are not significantly different at p = 0.05 level (ANOVA, Tukey multiple comparison test).

T. formicarius and *R. depressus* strongly reduced the number of *T. piniperda* offspring produced per m² (table 1). The two species together caused the greatest reduction (89 %), followed by *T. formicarius* alone (81 %) and *R. depressus* alone (41 %). All differences in *T. piniperda* offspring production per m² were statistically significant except for the difference between the treatments *T. formicarius* alone (TF) and *R. depressus* together with *T. formicarius* (TRF). Differences between treatments in the number of *T. piniperda* offspring produced per female showed the same pattern as the production per m² but they were much less pronounced. Only the difference between the treatments *T. piniperda* alone (T) and *T. piniperda* together with *R. depressus* and *T. formicarius* (TRF) was significant.

R. depressus and *T. formicarius* readily reproduced in all bolts offered to them. All *R. depressus* and *T. formicarius* offspring emerged from the bolts as larvae. The emergence of larvae of both species started at the end of June and continued for about two months.

Of the 87 larvae of *R. depressus* that were sampled alive from the emergence traps on 8 July, 57 were recovered as light brown teneral adults in the sand, at the inspection on 19 August. Of the 14 larvae of *T. formicarius* only the two fully grown individuals (14 mm long) had survived, one as a larva and the other as an adult. Both these individuals had hollowed out ovoid cells in pieces of bark. No cells had been formed by the other 12 *T. formicarius* larvae.

Large scale spatial distribution of *T. piniperda*, *R. depressus* and *T. formicarius*

T. piniperda, *R. depressus* and *T. formicarius* initiated flight on 13 April. 71 % (1981 of 2782) of all captured *T. piniperda* were collected during 13-19 April (Fig.1). In contrast, only about 5 % (108 of 2113) of all captured *R. depressus* and <1 % (3 of 531) of all captured *T. formicarius* were collected during the same period of time. Only a few *R. depressus* were

collected after 6 June while *T. formicarius* continued to be captured until the end of the experiment on 12 July.

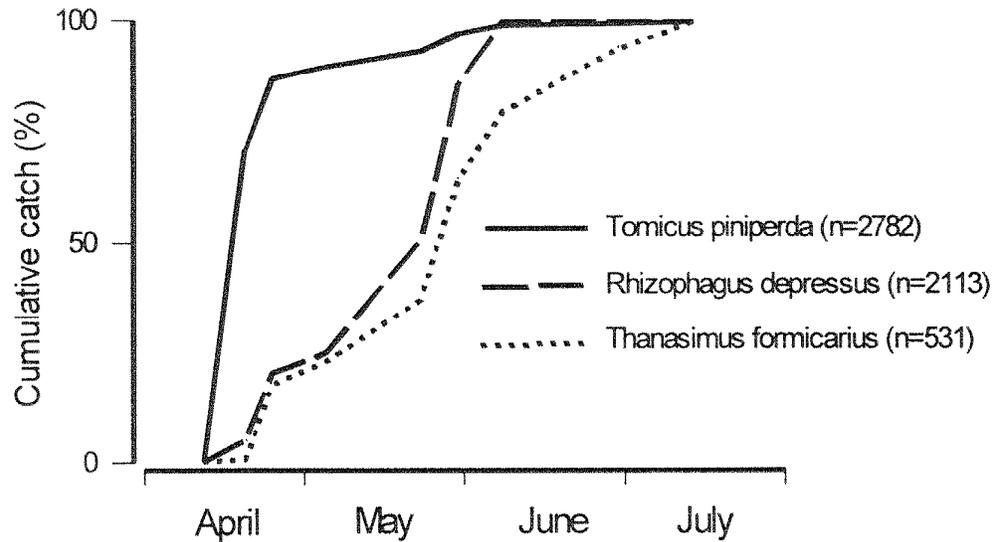


Fig. 1. Cumulative percent collections of *T. piniperda*, *R. depressus* and *T. formicarius* during April-July 1995 in baited traps.

The total catches of *T. piniperda* and *R. depressus* were 4-5 times higher in stands with attacks of *T. piniperda* the previous year (A-stands) than in stands without bark beetle attacks (B-stands) (Fig. 2). In contrast, there was no difference in total catch of *T. formicarius* between the two kinds of stands. The proportions of beetles caught in the two kinds of stands over time differed between the three species. The proportion of *T. piniperda* caught in A-stands was 91 % (N = 1981) during the early part of the flight period (13-19 April) and 55 % (N = 801) in the later part of the flight period (19 April to 12 July). This difference was statistically significant (chisquare test, $P < 0.05$). The proportion of *R. depressus* caught in A-stands was about the same in the early part of the flight period (83 %, N = 1071, 13 April to 22 May) as in the later part of the flight period (81%, N = 1042, 22 May to 28 June). The proportions of *T. formicarius* caught in the A-stands fluctuated strongly (33-88 %) between the different trapping periods and there was no trend over time.

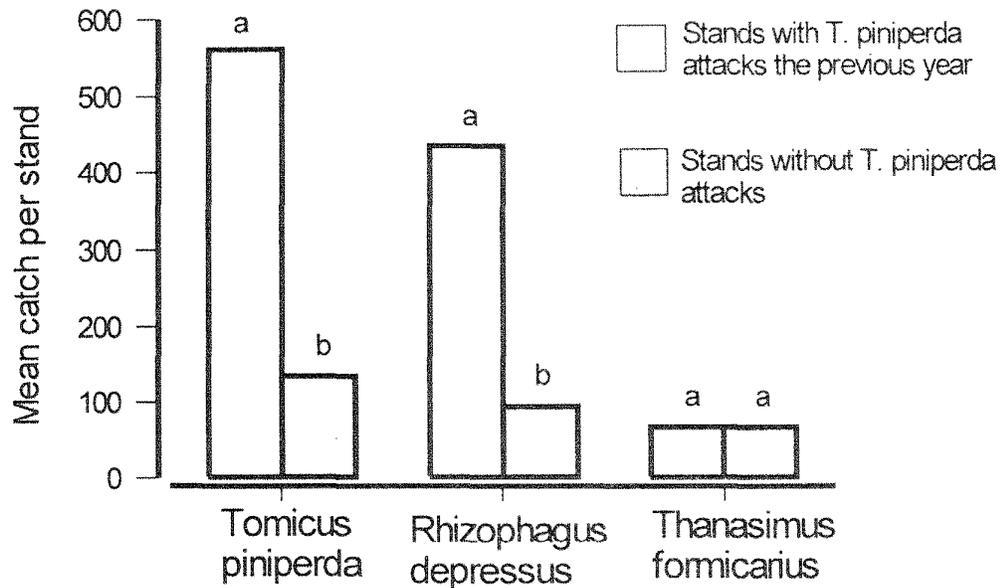


Fig. 2. Mean catches of *T. piniperda*, *R. depressus* and *T. formicarius* in Scots pine stands with and without previous attacks of *T. piniperda*. Five baited traps per stand. Columns with the same letter within the same species are not significantly different at $p = 0.05$ level. One-tailed paired-sample t-test.

Discussion

R. depressus and *T. formicarius* together reduced *T. piniperda* offspring production by 89 %. In a previous field experiment *T. piniperda* offspring production was reduced by natural enemies (including *R. depressus* and *T. formicarius*) by 90 % compared with the production in bolts protected from enemies by cages (Schroeder and Weslien 1994a). Thus, the result of the present study demonstrate that *R. depressus* and *T. formicarius* together are able to cause a reduction in *T. piniperda* progeny production of the same magnitude as that caused by the whole complex of associated species in the previous study.

The reduction in the production of *T. piniperda* offspring per m^2 , caused by the release of 30 *R. depressus* per cage, was not as strong as that caused by the release of two pairs of *T. formicarius* per cage. The clerid larvae reduced *T. piniperda* offspring production by 81 %. In an earlier, similar study (four *T. formicarius* pairs released per cage) *T. piniperda* offspring production was reduced by 92 % (Schroeder and Weslien 1994b).

The percentage reduction caused by the predators was much lower in terms of bark beetle offspring produced per female than in terms of bark beetle offspring produced per m^2 . This was a result of the attack densities being higher on the bolts of the T-treatment than on

the bolts of the TR- and TF-treatments. Earlier studies have demonstrated that when reared alone in cages *T. piniperda* offspring production per m² is fairly constant at attack densities between 150 and 400 egg galleries per m² (Eidmann and Nuorteva 1968, Saarenmaa 1983). In contrast, the number of offspring produced per female decreases strongly with increasing attack density as a result of intraspecific competition. Thus, the reduction in *T. piniperda* offspring production per female, caused by the predators, was underestimated in the present study.

Both adults and larvae of *R. depressus* could have contributed to the reduction of *T. piniperda* offspring production. Nuorteva (1956) observed feeding by *R. depressus* larvae on bark beetle pupae. Adults of the rhizophagid *Rhizophagus grandis* Gyll. have been demonstrated to feed on both eggs and larvae of the bark beetle *Dendroctonus micans* (Kug.) (King et al. 1991).

The reduction in the production of *T. piniperda* offspring per m² caused by *T. formicarius* and *R. depressus* together was of similar magnitude to that caused by the former species alone. Thus, the absence of one predator species does not necessarily mean that bark beetle progeny production will increase.

T. piniperda, *R. depressus* and *T. formicarius* were all able to disperse to the B-stands (without bark beetle attacks the previous year) as demonstrated by the trap catches. But the proportions of beetles caught in the A- and B-stands differed between the three species. *T. piniperda* and *R. depressus* were both caught in much higher numbers in the A-stands (with bark beetle attacks the previous year) than in the B-stands while there was no difference in catch of *T. formicarius* between the two kinds of stands. Thus, despite the fact that *T. formicarius* reproduced in the A-stands the previous year (as demonstrated by the occurrence of pupal chambers in the stumps), the most important source for this species during the flight period in 1995 seem not to have been the stands themselves but the surroundings. The present study demonstrated that the new generation of *T. formicarius* can hibernate both as adults and fully grown larvae. Thus, one explanation for the lack of difference in catch between the A- and B-stands could be that the new adults disperse already in late summer of the first year and/or that the hibernating larvae do not develop into new adults until late in the second summer.

Obviously high numbers of *R. depressus* were produced in the A-stands in 1994 as demonstrated by the high numbers caught in 1995. The cage experiment demonstrated that the *R. depressus* larvae emerging from trees develop into new adults the same summer. But as late as 19 August the beetles were still callow and burrowed in the sand. This suggests that they do not leave the ground until the next summer which is in accordance with the high catches in the A-stands during 1995. The fact that the catches of *R. depressus* were continuously higher in the A- than in the B-stands could have been a result of (1) a low dispersal rate from the A-stands, and/or (2) the new generation adults leaving the ground during an extended period of time.

In the first days of *T. piniperda* flight almost all collected beetles were caught in the A-stands. The difference in flight activity of *T. piniperda* between the A- and B-stands levelled out at the end of the flight period as a result of beetle dispersal. But since the main flight period of *T. piniperda* only lasts for a few days most of the flight activity will take place in stands with hibernating populations.

The results of the present study demonstrate that the risk for attacks of the bark beetle

T. piniperda, estimated as density of flying population, is considerably higher in stands which experienced attacks the previous year, resulting in hibernating populations, than in stands without local populations. *T. piniperda* reproducing in stands with previous attacks of this bark beetle species will be exposed to higher population levels of the predator *R. depressus* than bark beetles reproducing in stands without previous bark beetle attacks.

The main flight period of *T. piniperda* only lasted for a few days which is in accordance with earlier studies (Eidmann 1965, 1974, Bakke 1968, Haack and Lawrence 1995). In contrast, the flight periods of the two predators *R. depressus* and *T. formicarius* were much more extended. A few individuals of the two predator species were caught during the main flight of *T. piniperda* but the main flight periods of the two predators took place subsequently to the main flight of *T. piniperda*. The flight period of *R. depressus* lasted for about one and a half month until the beginning of June while the flight period of *T. formicarius* still not had ended in the middle of July when the experiment was finished.

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Phenolic Compounds As Predictors Of Norway Spruce Resistance To Bark Beetles

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THE PHENOLIC COMPOSITION of Norway spruce phloem varies considerably after wounding, and several compounds have been suggested to play an important role in a tree's induced reaction to impede the development of *Ophiostoma polonicum*, a fungus associated with *Ips typographus* (Brignolas et al. 1995abc). This paper summarizes current research designed to identify phenolic predictors of Norway spruce resistance to bark beetles.

In 1993, the phenolic content of both the unwounded phloem and the phloem reaction zone induced by artificial wounding was compared in 2 clones previously defined as resistant or susceptible. It was suggested that resistance could correspond to a higher ability of the tree to stimulate the flavonoid pathway (Brignolas et al. 1995a). Based on that hypothesis, predictions were made in 1994 regarding resistance of 20 clones from 2 origins (Germany and Norway), according to their phenolic composition in the unwounded and the wounded phloem (Berryman and Christiansen 1995). These predictions were made for all compounds with multivariate analysis (principal component analysis) which defined a resistance axis (based upon the above hypothesis), as well as with some compounds highly correlated with that axis and considered individually. Resistance was evaluated in 1995 from mass inoculations of *O. polonicum* to those clones. High negative correlations were obtained between resistance prediction rankings and extension of sapwood blue stain after mass inoculation rankings. In 1996, 50 other clones belonging to 5 provenances and originating from the three natural geographic areas of Norway spruce in Eurasia (Baltic, Hercynian-Carpathic and alpine) were included in the study. The results confirmed those of the previous experiment. In addition, they clearly separated the Baltic provenances from the Hercynian-Carpathic and alpine ones. The clones from the first area were less resistant than those from the two other areas. Finally, an experiment taking into account 50 clones belonging to the same provenance gave the same separation between clones based upon phenolic content (multivariate analysis).

It is concluded that clone resistance is effectively related to the ability of that clone to favour the flavonoid pathway rather than the stilbene pathway. It is also concluded that phloem phenolic compounds in adult trees can effectively be used as predictors of resistance to bark beetle attacks. The best predictors are: 1) axis 1 from a multivariate analysis based upon all compounds in unwounded and wounded phloem; 2) a high concentration of (+)-catechin in the reaction zone 6 days after wounding; 3) a low concentration of isorhapontin in

unwounded phloem. It is hypothesized that these conclusions are valid at the clone level, independently of origin, and for the whole Norway spruce species.

KEY WORDS *Picea abies*, *Ips typographus*, *Ceratocystis polonica*, Eurasia, phenolics, resistance predictors, induced reaction

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Cryphalus piceae and silver fir decline in Vallombrosa forest

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ABSTRACT Xylophagous insects play an important role amongst the numerous biotic and abiotic factors which have resulted in the serious decline of many silver fir, *Abies alba*, coenosis in Italy. Amongst these insects, *Cryphalus piceae* is the most damaging species in the fir-woods of Vallombrosa, as it attacks silver fir trees of all ages, including trees which had not previously been damaged by other adverse factors. *Cryphalus* infestations have always been damaging in this kind of biocoenosis, but they have reached record levels during the last few years. This is an event which has also coincided with the serious damage that this conifer has suffered as a result of the unusual climatic conditions during this period.

Observations have been carried out since 1992 on the biology and the behaviour of *Cryphalus piceae* in the Vallombrosa forest. The results show that this beetle always develops a first generation, with adults emerging in the middle of the summer; the second generation begins in August and September and is completed in the late autumn. However, in the second generation adults are often immature when they emerge. Moreover, during this period mature larvae and pupae can often be found under the bark of the host trees. Sometimes a sister generation can also be observed developing in parallel to the first. This is due to some of the females interrupting oviposition to feed themselves and then completing oviposition some days later. This phenomenon can sometimes become conspicuous, especially during the culminating phase of an infestation. The attack of *Cryphalus* begins on the most apical part of stressed but still standing trees, and then proceeds towards the base. The behaviour of *Cryphalus piceae* is different when it colonises trees or part of trees that are laying on the ground, for then the attack is massive and involves the whole trunk, resulting in a significant number of family units for every metre of length.

KEY WORDS *Cryphalus piceae*, biology, damage, Tuscany, Italy.

CRYPHALUS PICEAE (RATZ.), Coleoptera Scolytidae, is one of the most important bark beetles on silver fir, *Abies alba*. The activity of this insect in fir stands can become critical when trees are subject to recurrent physiological stresses from a variety of biotic and abiotic factors, as is the case of Vallombrosa Forest in Tuscany.

This bark beetle is found in many parts of Europe. In Italy it has long been known in silver-fir populations of the Alps belt and the Northern Apennines. Reports of *C. piceae* occurring on natural and artificial fir stands in the central and southern Apennine range are of more recent date (Pennacchio 1993).

C. piceae occurs not only on silver fir but also on *Abies pinsapo*, *Abies cephalonica* and *Abies nordmanniana*. In the forest of Vallombrosa there are also sporadic occurrences on Norway spruce and Douglas fir (Roversi *et al.* 1993; Battaglini unpublished data).

In areas where silver fir competes with other vegetation in mixed stands (these are more stable from an ecological point of view), beetle populations generally do not reach high densities, and damage is negligible. However, when conditions are favourable to *C. piceae*

development, population levels remain high and cause serious damage to silver fir which has serious repercussions for the rest of the biocoenosis.

Materials and Methods

In the spring of 1992, after many fir trees in Vallombrosa had been broken and uprooted by an exceptionally heavy snowfall in March of that year, observations were initiated to identify the most favourable conditions for increases in *C. piceae* populations.

In April, efforts were initiated to identify the areas most strongly affected by the adverse climatic conditions, and the biology and behaviour of the bark beetle could be better observed.

Observations were continued over the next years in order to determine whether trees that were not originally infested would later become infested. Various stations at altitudes ranging from 800-1200 m were established during the winter to examine the reproductive cycle of the insect. Bolts of about 1-1.5m in length were cut from infested trees and observed in the field, while other pieces were studied in the laboratory. Stem and branch sections of various diameters were also removed from trees that had been uprooted, broken, or felled during thinnings. All tree sections were placed in the forest in late winter/early spring each year, in shaded or open sites, in order to determine the time and intensity of bark beetle infestations at the onset of reproductive activity.

Results

The results showed that adults of *C. piceae* leave their overwintering sites between the end of winter (mid-March) and the beginning of spring, depending on climatic patterns and the location of the stands. During the last period, it was noted that overwintering adults initiated reproductive activity some two weeks earlier at lower altitudes, where climatic variations (temperature, precipitation) were less pronounced.

In Vallombrosa the bark beetle develops two generations per year, with an occasional sister generation produced by overwintering individuals emerging from the trees after an earlier infestation.

During the first phase of an infestation the most vulnerable trees are those which have been uprooted or broken, or which exhibit signs of stress due to adverse site conditions, or which have been weakened by low winter temperatures. Trees that did not receive enough water during the preceding autumn/winter period were also susceptible. Later, particularly with the arrival of the second generation of beetles, trees that became infested exhibited no sign of stress at the start of the insect growth cycle, even though they had certainly been previously affected by a predisposing cause of some kind.

On silver fir trees colonized by the first generation of bark beetles, up to 35 colonizations per 100 cm² bark area were observed, with the fecundity of the females ranging from 8-26 eggs per colonization. As regards the sister generation, fecundity ranged from three to 18 eggs, whereas in the second generation it ranged from 6 to 20 eggs per female.

Conclusions

Observations since spring 1992 on the biology and the behaviour of *C. piceae* at Vallombrosa confirmed the conclusion that the bark beetle is able to complete two generations per year, with the possibility of a sister generation produced by overwintering beetles.

Thus the Vallombrosa population was not limited to only one generation during the season, with in addition a possible sister generation, as reported by previous research (Pennacchio 1993).

The presence of overwintering populations on the branches of vigorous growing fir can seriously damage the trees, and this will predispose them for colonisation by the bark beetle during the successive reproductive phase.

Overwintering mainly occurs in the adult stage, but *C. piceae* also occasionally overwinters as mature larva or pupa under the bark; however, this mainly occurs in fir stands at higher altitudes.

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Japanese Phoretic Mites and Their Hyperphoretic Fungi Associated with Flying Adults of the Spruce Beetle (*Ips typographus japonicus* Nijima) (Col., Scolytidae).

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THE SPRUCE BEETLE (SBB), *Ips typographus japonicus* (Nijima) is a transpalearctic species occurring mainly in spruce forests but rarely in pine, fir, and larch (Wood and Bright, 1992). In Hokkaido, Japan, it is the most destructive pest of *Picea jezoensis* (Siebold and Zucc.) Carriere and *P. glehnii* (F. Schmidt) Masters. This insect is usually endemic, normally killing only over-matured or physiologically weakened trees. But when trees are harvested, SBB builds up in the slash and kills neighboring trees for about 3 years thereafter (Koizumi, 1977); yet their overall population level does not seem to increase greatly. Heavy winds usually precede SBB outbreaks, the largest of which was seen between 1956 and 1959 after a strong typhoon in 1954 (Yamaguchi, 1963; Yamaguchi et al., 1963).

Flying *Ips typographus japonicus* from Hokkaido (Japan) carried twelve species of phoretic mites, three of which were not previously recorded from Europe. The mite biologies were diverse, including specialists feeding on microorganisms, beetle eggs, and nematodes which were common under beetle elytra. Seven distinct species of fungal spores were found on these mites. In addition, an undetermined number were identifiable only as conidia. The spores stuck anywhere on the mite bodies with no special carrying structures evident. *Ophiostoma bicolor* was the most common species, with the pathogenic *Ceratocystis polonicum* present in small numbers.

This study illustrates that a great deal of information can result from the survey of relatively few bark beetles when time and labor are important constraints to research. Twelve species of mites and at least 4 species of fungi are recorded here for the first time for Japan. The latter includes the virulent tree disease *Ceratocystis polonicum*, at least, which is apparently capable of being transmitted by SBB mites. Future studies should determine if a caucity of mite species really exists in Japan (compared to that of Europe), or if more sampling is needed. Emphasis here should be placed on two important European mite parasitoids, *Pyemotes dryas* (Vitzthum) and *Paracarophaenax ipidarius* (Redikortsev). If they are not native to Japan, then consideration should be given to introducing them as classic biocontrol agents for SBB. *P. dryas*, has been located as far east as Gansu Province, China, phoretic on *Polygraphus poligraphus* ex. *Picea asperata* (Moser, unpublished). At least one mite, *Pleuronectocelaeno japonica*, may have evolved in Japan; another, *Trichouropoda hirsuta*, is a North American species not yet recorded for the rest of Eurasia.

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Current research on genetic resistance to white pine weevil in British Columbia

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THE WHITE PINE weevil, *Pissodes strobi* Peck (Coleoptera: Curculionidae) is the most serious native pest of spruce regeneration in British Columbia, attacking primarily Sitka (*Picea sitchensis* (Bong.) Carr), white (*P. glauca* (Moench) Voss), and Engelmann spruce (*P. engelmanni* Parry). The weevil has one generation a year. The eggs are laid from late April to June in punctures made by the female in the bark just below the buds of the terminal (year-old) shoot. The larvae burrow downward in the terminal beneath the bark, feeding on the phloem, which eventually kills the terminal. In many cases, the larvae mine past the year-old leader into the two- (and occasionally the three-) year-old shoot, causing even more dieback. By midsummer, they construct oval pupal cells in the wood and pitch, and pupation occurs within a "cocoon" of wood fibers. Depending on local climate, a portion of the larvae may remain to overwinter in the attacked leader. Most adults emerge from the leaders in late August and September; the newly emerged adults feed on terminals and branches and overwinter primarily in the duff. The following April or May, the adults move to young spruce terminals and resume feeding. They mate and lay eggs soon afterward. Occasionally, and specially in the interior, adults will re-attack below the previously attacked leader. Adults may live for up to four years (Alfaro 1994).

Current research results

Interior spruce family trials in British Columbia were surveyed for weevil resistance using an index which measured intensity of attack (number of attacks per tree), severity of each attack (how many internodes were destroyed) and tree tolerance to attack (i.e., if tree develops good form after an attack) (Alfaro *et al.* 1996a). The study demonstrated significant family variation in the attack index. Variation in resistance was related to ecoclimatic conditions of the place of origin of the parent trees. Analysis showed that parents from locations with high weevil hazard or high weevil populations yielded higher proportion of resistant trees. These sites are primarily low elevation, low latitude sites, especially on Moist-Warm habitats of the Sub-Boreal-Spruce (SBS) biogeoclimatic zone. Ying (1991) postulated that high selection pressures in high weevil hazard zones increased the proportion of resistant trees in stands located in these areas.

A study of the resin canal distribution on resistant and susceptible families at the Clearwater family trial extended the results obtained for Sitka spruce by Tomlin and Borden (1994): white spruce resistant families at Clearwater had significantly denser

resin canal system in the bark than susceptible families (Alfaro *et al.* 1997). The study demonstrated significant family variation and potential for selection.

Another resistance mechanism was discovered. Dissection of interior and Sitka spruce leaders in which weevil attack had failed (eggs had been laid but no adult emergence occurred) demonstrated the existence of an induced defense reaction (Alfaro 1995). The response was initiated shortly after feeding and oviposition in the attacked shoot and consisted of the cambium switching from producing normal tracheids and parenchyma ray cells to the production of epithelium which differentiated into traumatic resin canals, arranged in a ring fashion in the developing xylem. In sectioned leaders, these traumatic resin canals could be seen emptying their contents into feeding and oviposition cavities dug by the adults, and into the larval galleries. This defense reaction killed eggs and larvae. When the leader survived the attack, the cambium reverted to producing normal xylem tissue leaving one or more rings of traumatic resin canals embedded in the xylem annual ring. Artificial wounding experiments have demonstrated that resistant trees are capable of a faster response and they are capable of repeated response whereas susceptible trees responded more slowly and generally produced a single ring of traumatic resin canals (Alfaro *et al.* 1996b).

Sahota *et al.* (1994) are investigating the existence of chemicals in the bark of resistant spruce which may have negative effects on the weevil reproductive physiology. The weevils utilize several strategies for overcoming the tree defenses. Hulme (1995) found that even the most resistant Sitka spruce clones could be successfully colonized if the attack occurred early in the season. Thus, it appears that the physiological processes that underlay the tree defenses may not be active the entire year, but they may be gradually activated in the spring.

Work in collaboration with University of British Columbia at Kalamalka Forestry Centre, in the interior of BC (McIntosh *et al.* 1996) is determining details of the weevil attack and dispersal behaviour on resistant and susceptible trees and will determine the occurrence of the induced defense mechanism in relation to insect behaviour.

We hope to integrate resistance as a component of an Integrated Pest Management System (Alfaro 1996a). An important consideration when utilizing resistant genotypes in reforestation programs is its deployment in mixtures with susceptible stock. Using cage experiments, Alfaro (1996b) found that, when confined to resistant trees, gravid females oviposited lower in the stem, below the leader, where resin canal density was reduced by the increase in stem diameter (a dilution effect). Therefore, there is a risk that, if large plantations of purely resistant genotypes are created, the weevil could adapt to attack older internodes, where resin canal density is lower. Therefore, deployment of these genotypes should, at all times, take into consideration the need for avoiding the risk of insect selection leading to biotypes capable of overcoming the resistance mechanisms.

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Mass Attack by *Tomicu piniperda* L. (Col., Scolytidae) on *Pinus yunnanensis* Tree in the Kunming Region, Southwestern China

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ABSTRACT Patterns of attack by the pine shoot beetle, *Tomicus piniperda*, on Yunnan pine, *Pinus yunnanensis*, in the Kunming region of southwestern China are described. In some attacks, colonization is initiated by direct attacks on the upper or middle trunk. In other situations, attacks begin by beetles aggregating and boring on shoots. The latter pattern is thought to weaken the tree sufficiently and beetle attacks spread down the trunk. Attacks by *T. piniperda* are often associated with simultaneous colonization by *T. minor*.

MASS ATTACK IS an important phase of the life cycle of the pine shoot beetle, *Tomicus piniperda* (L.); beetles aggregate in and colonize host material for breeding (Bakke 1968; Ye 1991). In the Kunming region of southwestern China, mass attack occurs on the trunk of living pines and causes considerable damage to the local forest (Ye 1991, 1992). Over the past 15 years, more than 1.5 million ha of Yunnan pine (*Pinus yunnanensis*) forests have been destroyed there (Ye 1992). The paper compiled here is an introduction of information about these beetle attacks in southwestern China.

Attack Initiation

Two basic attack patterns were proposed for trunk attack on the living Yunnan pine tree Kunming.

- 1) **Attack is initialed by 2 - 4 pairs of beetles.** These beetles are regarded as pioneer beetles (Ye 1995). The primary invader detects and locates the suitable host first; it is followed immediately by other beetles landing the same tree. The attack proceeds until most of the trunk surface is occupied. The location of the pioneer beetle on the host tree trunk is not fixed but it usually attacks the upper trunk, middle trunk, or the middle and upper trunk. The secondary beetles always land near to the pioneer beetles. The attacking population progressively disperses over the trunk surface as the attack population increases (Ye 1995). Under this attack pattern, attacks do not always occur on the trunk inside the crown, and most shoots are not damaged as in attack pattern two.
- 2) **Attack commences from the attack of shoots.** In early spring or late winter just before trunk attack, many beetles fly to the crown and form shoot aggregations. On trees with shoot aggregations, more than 60% of the shoots are bored but only a few shoots are bored in nearby trees (Ye and Lieutier, unpublished manuscript). Shoot aggregation greatly weakens trees and causes subsequent trunk attacks.

Shoot attack is regarded as one of the critical phases of trunk attack, or the first step of mass attack. In attack pattern two, the attack is frequently started from the upper trunk, even from the trunk inside the crown. The attacking population disperses from the upper trunk down to the middle and base trunk.

Attack Distribution on Trunk

In Yunnan pine trees of 5-7 m height, the pine shoot beetle is capable of dispersal over the entire surface of the trunk, from the upper to the base. However, in most cases, the beetle is distributed on the trunk surface from the top to the base 1-2 m high above the ground (Ye 1995).

Attack Density

Attack populations rapidly increase in numbers during the primary attack phase. Attack rates reach their maximum about half way through the attack interval and attacks decline progressively (Ye 1995).

The highest attack densities are always concentrated on the middle-upper trunk, which contains more than 40% of the attacking population. Population densities decrease progressively above or below this position. The distribution of the attacking densities on the trunk appears to be normally distribution with a mean position in the upper and middle trunk (Ye and Ding, unpublished manuscript).

Attacks in the Consecutively Two Years

On Yunnan pine greater than 10 m height, trunk attacks are often observed in two consecutive years. In the first year, the attacks mostly occur the upper trunk, weakening the tree but not killing it, particularly in the case of attack pattern one. During the next spring, attacks are launched on the position of the trunk just below the attack from the previous year. The tree will be killed after two-years of attack (Ye 1992).

Attacks in Association with *Tomicus minor* (Hart.)

T. minor was always found to be associated with *T. piniperda* in the attacked tree in Kunming. This beetle is a secondary attacker that occurs in the spring later than *T. piniperda*. *T. minor* is mainly distributed on the middle and base trunk. The attack position of *T. minor* on the trunk is exactly opposite that of *T. piniperda*, and opposite the distribution of *T. minor* in Scandinavia, where *T. minor* colonized on the upper trunk (Langstrom 1986). *T. minor* attacks benefit from *T. piniperda*, and *T. minor* also are helpful for *T. piniperda* colonization. (Ye 1992, Ye and Ding, unpublished manuscript).

Discussion

The attack of *T. piniperda* on Yunnan pine is apparently related to mild winters in Kunming. The beetle initiates mass attack once sexual maturity is complete and does not

require a period of over-wintering as occurs in European countries. The drought season from Oct. to May also often benefits the beetle to overcome tree resistance. Under these conditions the beetles damage not only weakened trees, but also some health trees (Ye 1991).

The attack density and distribution on the trunk is thought to be determined by the attack pattern and the locality of the beetle before attack commencement. When beetles attack the crown, it is likely that the pine shoot beetle will locate at upper and middle trunk.

The two different attack patterns explain why the beetle can attack and directly kill healthy trees. Beetles can weaken the tree through shoot aggregation as the first of attack which is then followed by trunk attack. This attack sequence makes the beetle more effective in overcoming the tree's resistance. This explains why shoot aggregation plays a critical role in tree killing.

Recent studies indicate that when *T. minor* joins attacks by *T. piniperda* this increases the speed by which the two populations overcome tree resistance. The mixed population adjusts their distribution efficiently, which, decreases inter-specific competition. The two pine shoot beetles working together strengthened their aggressions in population establishment in Yunnan pine tree.

There still exist some questions which we can not answer for the moment. For example, why does the beetle appear to have two varying attack patterns? Why does the beetle not colonize the base trunk in most cases? Why has this beetle developed shoot aggregation and is it a necessary phase for the beetle attack? All of these are being studied in current and future research.

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Uncommon Cases Of Damage To Young Coniferous Trees By Several Curculionoidea Species, And Possible Ecological Reasons

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ABSTRACT During the course of field observations and laboratory rearing, data on uncommon supplementary feeding on conifers was obtained for 5 specialized weevil species and for 8 species normally associated with herbaceous vegetation and deciduous trees and shrubs. In the case of specialized group, the uncommon feeding behaviour and change of food were registered on the conifers only, when the preferable food sources were present but sparse. Most unspecialized species demonstrated a change-over from the natural host plants to alternative ones but did not change their feeding manner under the conditions when their preferable food plants were absent. The wide food specialization was not taken as the only reason for uncommon feeding of polyphagous weevils on conifers. Probably, certain of the local conditions could be responsible for the facts described. Practically all the cases of uncommon curculionid damage to conifers were documented under the boundary or similar conditions, and the weevil species discussed were mostly registered on the border or separated trees. It is supposed that the change in insect behaviour and food preferences could be one of the "edge effects". Natural regeneration in openings and borders as well as young forest plantations, hedgerows and shelterbelts may be subject to damage by unspecialized weevils. Due to this, the study of the biology and ecology of phytophagous insects as related to forest borders has become important.

KEY WORDS Coleoptera, Curculionidae, uncommon behaviour, conifers, edge effects

IT IS WELL documented that the fragmentation of woodlands, and different kinds of silvicultural practices can cause changes in the behaviour, bionomical features and economic status of some phytophagous insect species (e.g. Arnoldi 1953, Graham and Knight 1965, Eidmann 1985). These are reflected by the broadening of the host plant ranges, changes in food preferences and level of specialization of species. As a consequence, formerly non-outbreak insect species have become economically important, and the list of potential forest pests increases. This could be illustrated with examples from the different taxonomic groups of dendrophagous insects in some regions: *Boarmia bistortata* Goeze (Lepidoptera: Geometridae), *Cephalcia lariciphila* Wachtl. (Hymenoptera: Pamphiliidae), and *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae) in Siberia, Russia (Prozorov 1934, Pleshanov 1982, Kolomiez 1990); *Zeiraphera diniana* Gn. (Lepidoptera: Tortricidae) in North England (Day 1994). Thus, the observation of "unusual behaviour" in some species could be useful from a preventional viewpoint.

Weevils (Coleoptera: Curculionoidea) constitute a complex insect superfamily, most species of which are phytophagous. Many species are known as dendrophagous although the

majority is associated with herbaceous plants (Arnoldi et al., 1965). Relatively small groups of species (especially from gg. *Hylobius*, *Pissodes*, *Magdalis*) are specialized to develop on conifers. Besides these, there are weevils characterized only by imaginal feeding on needles (gg. *Brachyderes*, *Philopeton*, *Strophosomus*, etc.), and the adults of some species can damage conifers although they prefer to feed on other host plants (e.g. *Otiorhynchus*, *Polydrosus*, *Phyllobius* sp. pl.). This knowledge is not adequate, since it often only refers to the location of damage and coniferous tree species. Moreover, there is little information on the feeding ecology and behaviour of many weevil species. When it is considered that the last more or less comprehensive reviews of the insect pests of Eurasian boreal forests (including weevils) were published before the mid seventies (Pavlovsky and Shtakelberg 1955, Schwenke 1974), even the data on well-known important species deserves further comment.

In this paper, the uncommon cases of damage to young coniferous trees by several specialized and nonspecialized weevil species is described. The supplementary feeding of *Rhynchaenus fagi* L., *Rhinomias forticornis* Boh., *Apion pisi* F. and some *Otiorhynchus* species on shoots and needles are recorded for the first time. A description of the biotope, the type and distribution patterns of damage are provided for every species observed.

Materials and Methods

Field observations were carried out in the forest-steppe, southern and mountain taiga subzones of Central Siberia and adjacent territories (Abansky, Bol'shemurtinsky, Ermakovsky, Nazarovsky, Suhobuzimsky districts of Krasnoyarsk Region, Bratsky and Ust'-Ilimsky districts of Irkutsk Region, Russia) in 1978-88, 1996, and in several mountain forest districts of the Italian Alps (Asiago, Auronzo di Cadore, Bosco del Consiglio (Veneto), Monte Bondone (Trentino), Northern Italy) in 1993-1996.

Data on the accidental imaginal feeding of weevils on conifers was obtained during the course of visual examinations of the crowns of young trees. Most observations were organized along orthogonal transects crossing forest borders from the inner-stand positions to sparse young trees on adjacent openings or grassland. To reveal the structure of curculionid guilds, and the occurrence and distribution patterns of species, the method of branch beating was used along the transects. For this, 3-5 sample trees were chosen randomly per every 5-10 m interval depending on the local situations, and from 3 to 5 randomly chosen branches per sample tree were beaten. Dropped insects were collected with an entomological net with the diameter of 40 cm. The distribution of curculionids crawling on the land surface was observed by pitfall trapping with the use of 200 ml plastic vessels with a neck diameter of 65 mm which were placed at 1 m intervals along the transects.

In order to describe the distribution of damage to needles caused by phyllophagous insects, 40 cm-long apical twigs were collected from 1 to 3 differently exposed branches of the sample trees along the transects mentioned above. The number of sample trees changed from 3 to 5 per every 5 m or 10 m interval as in the beating sampling. During the examination of needles, the deep holes gnawed through the needle body were recognized as the curculionid type of damage among other traces of grazing. The level of damage was measured as the percentage of holed needles from the total number of needles examined per sampling unit.

If some curculionid species were constantly collected on conifers, laboratory rearings were used to verify the possibility of feeding on shoots and needles. For this, single samples or small groups of weevils were reared in plastic cages where 1-year and current year shoots of coniferous trees were provided as food sources. Experiments were not aimed at revealing a food preference of species, that is why the weevils were allowed to feed on the conifers from which they were sampled.

In addition to observational data, appropriate information from the literature was used. Due to this, the paper is prepared partly as a short review especially in relation to curculionids which are not specialized in feeding on conifers. With one exception, the weevil species' names were used according to Abbazzi et al. (1994), and the names of the trees according to Kozłowski et al. (1991) and Vidakovic (1991).

Results

During the course of field observations and laboratory rearing, data on uncommon host associates on conifers was obtained for 5 specialized weevil species and for 8 species normally associated with herbaceous vegetation and deciduous trees and shrubs. Descriptions are given in order of decreasing weevil specialization regarding feeding on conifers.

***Pissodes validirostris* (Sahlberg)**, pine cone weevil. This is a wide-spread species in Scots pine stands, and the only *Pissodes* species adapted to development in cones. Besides *P. sylvestris*, it can colonize the cones of *P. sibirica* Du Tour (Florov 1951), *P. brutia* Ten., *P. contorta* Dougl. ex Loud., *P. halepensis* Mill., *P. nigra* Arnold, *P. pinaster* Ait., *P. pinea* L., and *P. uncinata* Ramond (Roques 1983). According to numerous studies, the supplementary feeding by adults occurs on young green cones.

In early summer (end of May - beginning of June) 1979-1986, we repeatedly observed the uncommon adult feeding of *P. validirostris* on the apical shoots of Scots pines in the forest-steppe pine stands of Central Siberia (Gourov 1987). Apparently, this supplementary feeding occurred during the mating period and before egg-laying, because it had not been documented later in the season. The feeding behavior was similar to that of other *Pissodes* species: round holes were chewed through the bark thereby damaging the phloem. Weevils occupied the upper crown of young pines on the borders of dense clumps in light pine stands, or sparsely growing pines under the canopy of secondary birch forests adjacent to mature pine stands. Perhaps, this feeding behavior could be responsible for the accidental development of *P. validirostris* in the pine leader shoots as mentioned by Bevan (1987).

***Hylobius albosparsus* Motschulsky**, larch root weevil. This is an endemic Siberian species. A short review of its distribution in the Siberian territory was made by Opanasenko (1976). According to published data, the species is polyphagous on conifers. The supplementary feeding of adults has been observed in young stands of Siberian larches, *Larix spp.* (Petrenko 1965, Rozhkov 1970, Galkin 1971), on the Siberian stone pine, *Pinus sibirica* (Zemkova 1963), and Scots pine, *P. sylvestris* L. (Rozhkov 1957). Spruces, *Picea spp.*, are also included in the list of food plants (Arnoldi et al. 1965). However, the latter authors noticed that serious damage by *H. albosparsus* occurred in larch stands, and Rozhkov (1970) proposed that larch is the preferred host tree of this species. All the authors agree that the adults normally feed on young shoots and thin branches where they damage the bark and form feeding areas with roughly grazed borders.

The uncommon adult feeding of the larch root weevil was recorded for the first time during our observations on the Siberian fir, *Abies sibirica* Ledeb. It was noticed in June 1984 under the canopy of a dense, mixed Siberian pine/spruce/fir stand with the addition of *Betula verrucosa* Ehrh. and *Larix sibirica* Ledeb. in the basin of Upper Ket' river (Verkhazanskoe Forestry, Bol'shemurtinsky district of Krasnoyarsk Region, Central Siberia). The feeding occurred on 1-2 m-high firs along the borders of dense understory clumps. Individual weevils fed on apical shoots, grazing not only on soft tissues and green juvenile bark, but also on young short needles. As a consequence, the longitudinal (up to 5-6 cm) shallow depression was usually organized on one side of the shoot. Later in the season, some curved apical shoots having this type of damage were repeatedly observed on young firs. This type of adult feeding, as well as its choice of fir as a host tree, had not previously been described for *H. albosparsus*.

***Hylobitelus (Hylobius) pinastri* (Gyllenhal)**, coniferous root weevil. This is a common but not abundant species widespread in Palearctic boreal forests. Supplementary feeding of adults on Scots pine (Florov 1950, Rozhkov 1957, Opanasenko 1976, Ozols 1985), Siberian larch (Rozhkov 1970) and, probably, on some other conifers (Arnoldi et al. 1965, Eidmann 1974) is known. Usually, adults damage the thin bark of young shoots in the proper "Hylobius manner".

In early July 1996, we collected several samples of *H. pinastri* on sparse young spruces, *Picea obovata* Ledeb., growing on the boundary between a mixed fir/pine stand and a wet meadow in the Buiba locality (Western Sayan mountain system, Ermakovsky district of Krasnoyarsk Region, Central Siberia). The branch-beating procedure along the transect crossing the forest border did not reveal the occurrence of this species under the canopy of the mature stand. It was also not noticed on young regenerations of *P. sibirica* and *A. sibirica*. Under laboratory conditions, the beetles were provided with apical shoots of spruce as host material. During the 1-week rearing, the bark of the shoots was not damaged by weevils, but a preference for the previous year's needles was markedly demonstrated. Deep and rough but "economic" grazing was oriented along the needle edges, and no remains (pieces, cut needles) were found at the bottom of cage. The replacement of shoots by the fragments of thicker branches (also having needles) did not change the weevil feeding behaviour. This type of supplementary feeding is uncommon for the *Hylobius* species, although needle damage by *H. abietis* L. has been previously noticed as very rare and accidental (Schwerdtfeger 1981).

***Magdalis phlegmatica* (Herbst)**, blue inert weevil. This species belongs to a group of poorly studied blue coniferous weevils (some species of the genus develop on deciduous trees and shrubs). The species is widespread but not abundant in the Scots pine stands. Besides *P. sylvestris*, other conifers may also be hosts of *M. phlegmatica* (Arnoldi et al. 1965), especially *Picea spp.*, as was noticed for related *Magdalis* species (Maisner 1974). Usually, the supplementary feeding by adults occurs on the bark and phloem of shoots, thin stems and branches in young coniferous stands and plantations (Rozhkov 1957, 1970, Opanasenko 1976). In other species who use conifers as their primary hosts (e.g. *M. violacea* L.), supplementary feeding on deciduous trees has also been documented (Maisner 1974).

At the end of June 1984, we observed a single episode of uncommon supplementary feeding by an adult *M. phlegmatica* on the needles of a young Siberian spruce, *P. obovata*, under the canopy of a secondary birch stand adjacent to a mixed coniferous forest of dark

taiga type (basin of Kem' river, Talovskoe Forestry, Bol'shemurtinsky district of Krasnoyarsk Region, Central Siberia). The type of damage was similar to the well-known imaginal feeding manner of *Brachonyx pineti* Payk. on the needles of Scots pine: the small hole is followed by a cavern in the needle body (Opanasenko 1976, Bevan 1987). Confirmation of the possible *Magdalis* maturation feeding on needles was obtained in early July 1996 in the Aradan locality (Western Sayan mountain system, Ermakovsky district of Krasnoyarsk Region, Central Siberia). Adults of *Magdalis* sp. were sampled on young spruces along the border of a pure *P. obovata* stand. In the laboratory, beetles were provided with apical shoots with 1-year and current-year needles. During the 1-week rearing, weevils demonstrated a marked feeding preference for young needles instead of shoot stems. The feeding manner was similar to that described above for *M. phlegmatica*.

Besides Siberian spruce, such type of needle damage was documented during our observations on several conifers in Europe: Swiss stone pine, *Pinus cembra* L. (Briançon, French Alps), European silver fir, *Abies alba* Mill. (Auronzo di Cadore, Northern Italy), Norway spruce, *Picea abies* (L.) Karst. (Bosco del Cansiglio, Northern Italy), and European larch, *Larix decidua* Mill. (Monte Bondone, Northern Italy). In the last two localities, the distribution of needles damaged in this manner was examined along the transects crossing forest borders. The results showed that such curculionid supplementary feeding, even if not intensive, occurs in plantations of different ages and in natural forests more or less constantly (Fig. 1). However, the low level of damage made it difficult to reveal any tendency in the distribution via an appropriate statistical treatment.

***Polydrusus (Metallites) pallidus* (Gyllenhal) (= *atomarius* Olivier).** Rather numerous members of the genus *Polydrusus* (*Polydrosus*) Germar, 1817 are mainly known as being polyphagous on deciduous trees and shrubs (Arnoldi et al. 1965). However, the more or less constant host associations with conifers were noticed for more than 10 Palearctic species (Pavlovsky and Shtakelberg 1955, Arnoldi et al. 1965, Rozhkov 1970, Schindler 1974, Joly 1975, Schwerdtfeger 1981). Among these, *P. pallidus* is one of the most important *Polydrusus* weevils to forestry. Adults of this species can damage buds, needles and young shoots of pines, spruces and firs, especially in young plantations (Schindler 1974, Schwerdtfeger 1981). Recently, a serious damage to *P. cembra* conelets by this weevil was observed in the French Alps (Dormont, Roques and Trosset, 1996). According to our knowledge, *Larix* spp. were not included in the list of food trees of *P. pallidus*, although for some related species (*P. impressifrons* Gyll., *P. marginatus* Steph., *P. sericeus* Schaller) associations with *L. decidua* have been noticed (Schindler 1974), and for *P. cervinus* L. the supplementary feeding on *L. sibirica* was documented (Rozhkov 1970).

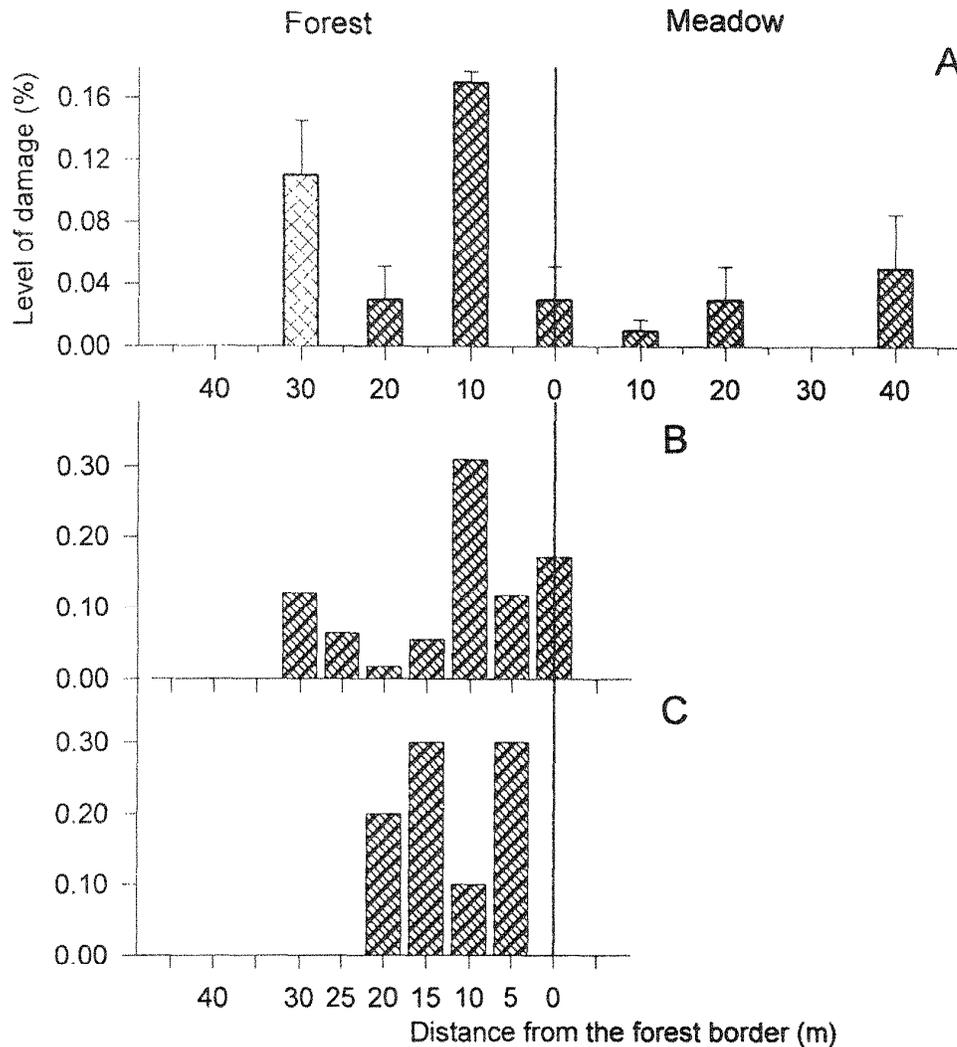


Figure 1. Distribution of needle damage by curculionids (“uncommon *Magdalis* type”) along the transects crossing forest border: A - natural *Larix decidua* stand (August 1994) in Monte Bondone, Northern Italy; B - 50-year old Norway spruce plantation (May 1994, last year needles) and C - 20-year old Norway spruce plantation (July 1994, last year needles) in Bosco del Cansiglio, Northern Italy.

We observed the feeding by adult *P. pallidus* on the needles of *Picea abies* (Bosco del Cansiglio, 19.06.1994; Auronzo di Cadore, 5.06.1996, Veneto, Northern Italy) and *L. decidua* (Auronzo di Cadore, *idem*; Monte Bondone, 7.09.1996, Trentino, Northern Italy). In all localities, the weevils were collected from young trees planted artificially along the

boundaries between woodlands and pastured meadows, using the branch-beating method. According to visual observations, weevils were most abundant in the low branches, just at the level of grass cover. In the mixed spruce/larch clumps, the beetles preferred to stay on spruce trees. For example, in Auronzo di Cadore, 15 spruces and 10 larches growing together were sampled (3-5 branches per tree). The density of weevils on spruce reached 2.96 ± 0.6 ex./sample, whereas only 3 specimens were caught on larch in total. But in the laboratory, weevils did not demonstrate any preference for a host tree: the needles of both tree species were damaged intensively, although on spruce the current year needles were preferred. Larch needles could be grazed along their full length, rather carefully, without numerous remains being lost, whereas some needles were cut just near the base. There were two types of damage to spruce needles: (1) the rough grazing similar to the feeding by *Brachyderes incanus* L. on pine needles (Schindler 1974), and (2) the grazing of small holes similar to those made by *Magdalis phlegmatica* mentioned above, but not so deep. Some examples of *P. pallidus* were reared in the laboratory for three weeks and they also fed on the needles of *Cedrus sp.* and decorative dwarf forms of spruce (the latter were preferred) showing the same type of grazing.

Otiornychus weevils. The genus *Otiornychus* Germar, 1824 is the most rich and complex taxonomic group in the Curculionidae family (Arnoldi et al. 1965). In Italy alone it is composed of 63 subgenera with 252 species and subspecies (Abbazzi et al. 1994). Besides this, a large number of species organize parthenogenetic forms and local ecological races. Most species are polyphagous on plants, and for some of them, feeding by adults on conifers is known (see a short review of Schindler (1974) on 10 Eurasian species). We observed uncommon feeding behaviour in *O. ovatus* L., and found a possibility of host associations with conifers for *O. vestitus* Gyll., *O. armadillo* Rossi, and *O. geniculatus* Germ.

***Otiornychus (Pendragon) ovatus* (Linné),** the strawberry root weevil. This species damages Rosaceae, especially strawberry, and also the seedlings of conifers (e.g., Arnoldi et al. 1965). According to Western authors, it was noticed on young pines and spruces, when introduced in the USA with exotic conifers - on *Picea omorica* (Panc.) Purk., *Thuja occidentalis* L. and *Tsuga spp.* where the bases of needles were damaged during adult feeding (Schindler 1974). For Norway spruce, grazing on needles and buds, and also the debarking of 2-4-year seedlings were documented (Novák et al. 1976).

We repeatedly observed supplementary feeding of *O. ovatus* at the bases of young growing (green) shoots of Scots pine in the light forest-steppe pine stands of Central Siberia (Gourov 1987). Feeding occurred in May - June and continued until the beginning of July when the period of full development of grass cover finished. Weevils preferred to feed on young pines, about 1 m in height growing along the forest roads or on the boundaries of small gaps. Often, the feeding occurred on curved shoots damaged by some other factors.

***Otiornychus (Dodecastichus) geniculatus* (Germar).** Five specimens were sampled on in June, 1996 during a branch-beating procedure on the borders of dense clumps of the Mugo pine, *Pinus mugo* Turra in the locality of Cima Larici (Asiago (VI), Veneto, Northern Italy). Pine clumps formed a patchy transition between the upper boundary of a fir stand and an alpine meadow, and thus, organized a local timberline (at about 2050 m asl). In the laboratory, beetles were provided with pine shoots but demonstrated a marked preference for the previous year's needles. Resulting damage was strong because of inefficient feeding when the needles were grazed roughly and many remains were dropped at the bottom of

cage. According to our knowledge, this is a first report on the possible host association of *O. geniculatus* with conifers in general and particularly with *P. mugo* entomofauna of which has not been well-documented till now.

Otiorhynchus (Elecranus) vestitus Gyllenhal. 27 specimens were sampled by the branch-beating method from the young trees of *Picea abies* (25) and *Abies alba* (2) in the mixed spruce/fir forest of Auronzo di Cadore (BL) (Veneto, Northern Italy) 5.06.1996. The dense (0.7-1.0) mature stand was dominated by the European silver fir and the Norway spruce (the latter was planted artificially) with the addition of *Fagus sylvatica* L. (particularly on slopes), *Acer platanoides* L., and *A. pseudoplatanus* L. in the gaps. In some areas, *Corylus avellana* L. and *Alnus sp.* organized the undergrowth but around the gaps and openings only. The under-canopy regeneration of conifers was intensive but concentrated (as well as the poor-developed grass cover) in lighter microhabitats.

O. vestitus constituted the majority of weevils found on young conifers (Table 1). Most samples were caught on spruce trees growing on the borders of small gaps.

Table 1. Structure of the Curculionidae community, sampled by the branch-beating method, from young coniferous regeneration in *Picea abies/Abies alba* forest 5 June 1996 (Auronzo di Cadore, BL, Veneto, Northern Italy, about 1000 m asl).

Species	Number of specimens caught			Total number caught
	Understory	Borders	Openings	
<i>Otiorhynchus vestitus</i>	2	25	-	27
<i>O. armadillo f. obsitus</i>	1	10	-	11
<i>O. scaber</i>	-	6	-	6
<i>O. pupillatus</i>	2	3	-	5
<i>O. rhododendri</i>	1	3	-	4
<i>O. bisulcatus (n. f. ?)</i>	-	1	-	1
<i>Phyllobius calcaratus</i>	-	3	-	3
Average number/sample*	0.12 ± 0.05	0.51 ± 0.07	0	0.29 ± 0.04

* Mean ± st. error from 50, 100, and 50 trees sampled in understory, border and open conditions correspondingly.

Under laboratory conditions, the weevils fed actively on the 1-year old and current year needles of *P. abies*. Feeding was not economic, and the grazing could start from any part of needle with a lot of remains dropping down as a consequence. There was no marked preference for old or young needles. Apparently, the frequent occurrence of *O. vestitus* in crowns and its active damage of needles presuppose the existence of the host associations of this species with conifers at least during the period of supplementary feeding.

Otiorhynchus armadillo (Rossi) f. obsitus (Gyllenhal). Eleven samples were collected in the same biotope as *O. vestitus* described above. The only specimen was caught in an under-canopy position whereas others were collected on young spruce trees along the borders of gaps (Table 1). The species is polyphagous on different deciduous trees and shrubs, but can probably feed accidentally on conifers (M. Covassi - personal communication).

In the laboratory, weevils were provided with apical portions of the branches of *Picea abies* and showed a marked preference for current year needles and shoots. Beetles began to eat from the needle base and quickly grazed the lower part of the needles, so that numerous remains dropped down. Sometimes, the thin stems of shoots were also grazed or cut. The damaged shoots looked like those of *A. sibirica* grazed by *Hylobius albosparsus* described above, but without the longitudinal depression along the shoot stem.

Other *Otiiorhynchus* species caught were not so abundant as *O. vestitus* and *O. armadillo* (Table 1) and have not been examined in the laboratory. Among these, *O. scaber* L. is a well-known pest of conifers (Arnoldi et al. 1965, Schindler 1974, Schwerdtfeger 1981). As for *O. pupillatus* Gyll. noticed as a pest of *Salix spp.* (Schindler 1974), *O. rhododendri* St. and *O. bisulcatus* F., it is necessary to provide a repeat sampling on conifers following by laboratory examination.

The only member of other Curculionidae genera collected with *Otiiorhynchus spp.* in Auronzo di Cadore was *Phyllobius (Metaphyllobius) calcaratus (Fabricius)*. Species of this genus are mainly connected with deciduous trees and shrubs (Arnoldi et al. 1965), but there are also the accidental pests of conifers: *Ph. arborator* Hbst. on *Picea spp.* (Schindler 1974, Schwerdtfeger 1981), *Ph. argentatus* L. on *Pinus sylvestris* (Arnoldi et al. 1955) and *Picea spp.* (Schindler 1974), *Ph. tournieri* Smirn. on *Larix sibirica* (Rozhkov 1970), *Ph. chloropus* L. (= *viridicollis* F.) on *Pinus spp.* (Schindler 1974, July 1975). As for *Ph. calcaratus*, it was documented that this species mainly damages *Corylus avellana* L. and *Alnus spp.* (Arnoldi et al. 1965) and in our case, all three specimens were caught on young spruces growing near hazel trees. In the laboratory, weevils refused to feed on spruce needles, and died.

Holotrichapion (Apion) pisi (Fabricius). The constituents of the *Apion* curculionid complex are rather numerous and highly diversified (about 500 Palearctic species, according to Arnoldi et al. 1965) to be isolated in the Apionidae family (Abbazzi et al. 1994). These weevils are mainly associated with herbaceous vegetation but also with deciduous trees and shrubs. Examples of damage to conifers are very rare. For example, feeding by adults on the anthers of *Pinus sylvestris* and on young pine needles in nurseries and plantations was noticed for *Aspidapion (A.) aeneum* F., *Malvapion (A.) malvae* F. and *Oxystoma (A.) pomonae* F. (Pavlovsky and Shtakelberg 1955).

We observed serious damage to young developing shoots and needles by *Holotrichapion pisi* on a sapling of *Picea abies* planted in a small town park (Padova, Northern Italy) on 15 May 1996. The poorly developed sapling (0.5 m in height) was planted in a shady location surrounded by *Rosa sp.*, *Spiraea sp.* and *Nerium oleander* L. The nearest spruce trees were located at a distance of 25-30 m. Visual observation showed that 79 out of 82 developing shoots with needles were damaged by numerous "pin-holes" and small light spots originated from the grazing of the epidermis. In the laboratory cage, the weevils were provided with undamaged spruce shoots from the same sapling. All the shoots were damaged in a similar manner during the 1-week rearing. A mass occurrence of *H. pisi* was recorded on 20-23 May, when the specimens were collected both from coniferous (*P. abies*, *Cedrus sp.*) and deciduous trees and shrubs (mainly Rosaceae). The supplementary feeding of weevils on the needles of *Cedrus* was not noticed. Later (5 June), a single sample *H. pisi* was found on the needles of isolated spruce tree growing in the meadow in Auronzo di Cadore (Veneto). At the end of the season, all the damaged shoots of the sapling described above were dead or poorly-

developed. According to our knowledge, this is the first report of feeding by adult *H. pisi* on conifers.

***Rhynchaenus (Euthoron) fagi* (Linné)**, the beech leaf mining weevil. This is a well-known forest pest from a genus of highly specialized mining weevils associated with deciduous trees and shrubs. In many cases, the larvae are monophagous on the host plants mined, whereas adults may conduct supplementary feeding on different tree species (Maisner 1974). Previously, the occurrence of adult feeding on conifers (needles of *P. sylvestris*) was noticed for *R. jota* F. only (Pavlovsky and Shtakelberg 1955). Adults of *R. fagi* feed not only on different deciduous trees but also on herbaceous plants, and this feeding is of great importance in the seasonal activity of beetles (Bale and Luff 1978, Bale 1981).

We recorded uncommon adult feeding of *R. fagi* on the needles of *Larix decidua* in Monte Bondone (Trentino, Northern Italy) in late June 1994. Weevils were found on the low branches of larch trees growing along the boundary between the natural light *L. decidua* forest and an alpine meadow at about 1750 m asl. The density of beetles on trees was not measured numerically but, sometimes, it was possible to observe up to 4 individuals per branch. According to visual observations, the occurrence of weevils decreased sharply as the distance from the border increased: the only individuals were found on sparse larches at about 20 m from the border into the meadow, and none were noticed under the canopy of a mature stand. It was found that *R. fagi* came from the sparse shrubby foliage of *Fagus sylvatica* near the visual border line. All the beech leaves were strongly damaged by mines constructed during the development of larvae, and by phyllophagous grazing. The adults of *Phyllobius chloropus* L. (= *viridicollis* F.) were found together with *R. fagi* on beech leaves, herbaceous plants and the needles of *L. decidua*. It is known that this *Phyllobius* species feeds on deciduous trees and also on pines (Arnoldi et al. 1965, Joly 1975).

In the laboratory, both males and females of *R. fagi* fed actively on larch needles for about 10 days. Weevils formed light spots but not holes on the surface of the needles by grazing on the epidermis. In the field, the beetles disappeared from larch at the beginning of July.

***Rhinomias forticornis* (Boheman)**. This is a rather rare species representing the depauperate genus *Rhinomias* Reitter, 1894 close to *Omius* Germar, 1817. The species is spread throughout Central Europe, Caucasus, and Asia Minor. The biology and ecology of this weevil has not been studied well. Probably, this is a meadow species occurring on low grassy vegetation (Hoffmann 1950).

In June and July 1994 we noticed samples of *R. forticornis* in pitfall traps along the transects crossing the boundary between a 50-year old Norway spruce plantation and a calcareous meadow in Bosco del Cansiglio (Veneto, Northern Italy). The pitfall-trapping did not permit evaluation of the real density of epigeic organisms but the catches at least showed that weevils were distributed both in the meadow and woodland (Fig. 2). Thus, the fact that this species belongs exclusively to the meadow weevil community is doubtful.

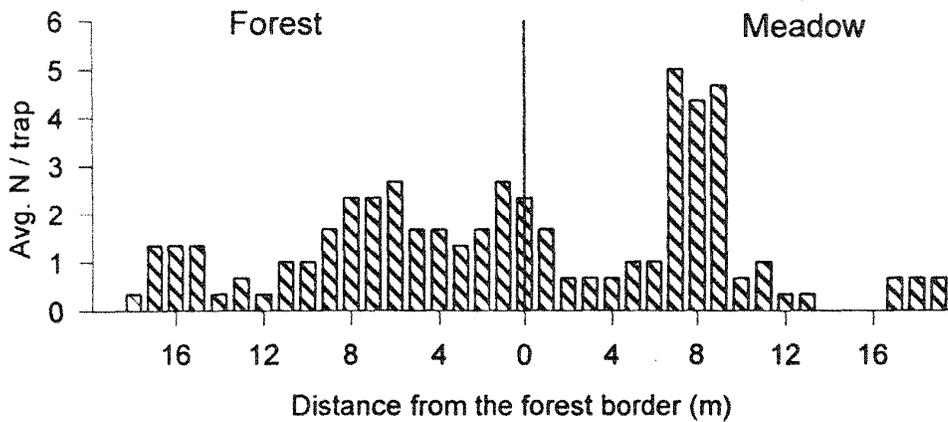


Figure 2. Distribution of *Rhinomias forticornis* across the boundary between a 50-year old Norway spruce plantation and a calcareous meadow (June - July 1994, Bosco del Cansiglio, Northern Italy).

The lower branches of the spruce trees growing along the forest margin were in contact with the ground. Living specimens of *R. forticornis* from the border traps (placed just near that branches) were reared in the laboratory where they fed on shoots and needles. Observations showed that the weevils were very bad climbers and thus fed on the needles at the bottom of cage. Feeding was not "specialized": the beetles gnawed through the needle rib in one place, and the needles were curved as a result. The needles of border spruces probably are only an accidental food source for *R. forticornis* which normally crawls on the ground, especially where a well-developed grass cover is absent under dense conifer plantations.

Discussion

The ability to switch from primary food sources to alternative ones is a well-known feature of phytophagous insects. It is closely related to the degree of dietary specialization of the insect species. Also, local conditions may influence insect feeding behaviour and food choice to a large extent (Fox and Morrow 1981, Futuyma and Moreno 1988, Jaenike 1990). In their review, these authors provided a description of some general sources of variation in food plant selection as affected by local conditions: herbivore behaviour, genetic variation among insects, competition among insects, changes in abundance of plants, changes in plant quality, and others. Probably, the cases of uncommon host associations in the curculionid species described above may be analysed both in the context of weevil specialization and from the viewpoint of the possible effect of local conditions.

First, when more attention was paid to the forestry needs, we examined the weevils from the viewpoint of their possibility to feed on conifers. That is why the species were ranged in decreasing order of this capability. *Pissodes*, *Hylobius* and *Magdalis* species could be combined into a highly specialized group as most of them are characterized by larval and adult feeding on conifers (Arnoldi et al. 1965, Eidmann 1974, Kudela 1974, Maisner 1974). The second group was composed of *Polydrusus*, *Otiorhynchus* and *Phyllobius* species, the larvae of which are probably super-polyphagous on roots. Most adults feed on herbaceous vegetation, deciduous trees and shrubs whereas a number of species are usually associated with conifers in the period of supplementary feeding (Arnoldi et al. 1965, Schindler 1974). The third group was rather mixed, including *Apion*, *Rhynchaenus* and *Rhinomias* species whose host associations with conifers are rare or accidental (Hoffmann 1950, Bale 1981). Of course, it is also possible to recognize the different levels of specialization on conifers within the limits of each group. Taking into account adult supplementary feeding only and basing ourselves on published material, it is necessary to conclude that most species under discussion are polyphagous or widely oligophagous herbivores. It could be one of the reasons why these weevils have demonstrated an uncommon feeding behaviour, change of food objects and host plants. But the individuals of polyphagous *Ph. calcaratus* mentioned above, when collected on spruce together with *Otiorhynchus* spp., refused to feed on spruce needles and died. Thus, wide food specialization is not the only reason for uncommon feeding of some polyphagous weevils on conifers. Probably, some of the local conditions, for example, the relative abundance and distribution patterns of host and nonhost plants, were responsible for the observations.

In the case of a specialized group, uncommon feeding behaviour and change of food objects were observed on conifers only. Thus, the more specialized *P. validirostris* was observed when provided leaders instead of green cones, but it did not change the host plant, *Pinus sylvestris*. Having been polyphagous on conifers, *H. albosparsus*, *H. pinastri* and *M. phlegmatica* demonstrated uncommon adult feeding on needles without leaving the host trees for some other vegetation. Even for *O. ovatus*, which belongs to a less specialized group but is known as a conifer pest, the change of host feeding location but not of the host tree was observed. The analysis of the local conditions showed that in cases of specialized weevils, the preferable food sources were present but sparse and thus, not "convenient energetically from the foraging point of view" (Vladyshvsky 1980) in comparison with other available coniferous food plants. The best example was demonstrated by *P. validirostris* in very light pine forests or in the secondary birch stands where mature pines with cones were distributed rather irregularly. However, under extreme conditions when the usual food trees are absent, the highly specialized coniferous weevils can also feed on absolutely uncommon plants as was noticed for *H. abietis* L. (Schwerdtfeger 1981, Eidmann 1985).

On the contrary, most unspecialized species demonstrated a change-over from their natural host plants (deciduous trees etc.) to alternate ones (conifers) but probably did not change their feeding manner. First of all, this concerned the rough grazing of needles by *Otiorhynchus* spp. For this group of polyphagous weevils, the local conditions were not characterized by irregular distribution but almost by an absence or very scarce growth of the preferred food plants. A dense, mixed coniferous stand in Auronzo di Cadore described above was distinguished by the absence of grass cover, poorly-developed undergrowth and the concentration of spruce/fir regeneration on the borders of the gaps. Apart from sparsely

growing young deciduous trees, only conifers were constantly available for the supplementary feeding of weevils. That is why several unspecialized species were observed simultaneously on the young spruces on the borders of small gaps but not one individual was caught on the regenerating conifers in the opening covered by well-developed shrub and grass vegetation (Table 1).

Besides other reasons for a local food plant selection, Fox and Morrow (1981) noticed the effects of abiotic factors. Probably these could be partly responsible for the feeding of *R. fagi* on larch, and *O. geniculatus* on *Pinus mugo* under the conditions near the upper timberline in Italian Alps. For example, in the biotope observed, there was a well-developed undershrub and herbaceous layer where the adult feeding of *R. fagi* may occur (Bale 1981). The low ground-level temperatures at night could force some weevils to climb up the nearest larch trees.

The importance of changes in plant quality was carefully reviewed and discussed in Thorsteinson (1960), Futuyma and Moreno (1988), Jaenike (1990). It is possible to expect it on different forest borders exactly where the trees are subject to stronger effects of abiotic factors (e.g. Stevens and Fox 1991). The results of observations showed that practically all the cases of uncommon curculionid damage on conifers were documented under boundary or similar conditions, and the weevil species described above were mostly observed on the border or on separate trees. It was previously noticed that young Scots pine trees can be subject to serious damage by specialized weevils when they grow along the borders (Rozhkov 1955). Later, it was assumed that the forest borders and their analogues are preferable habitats for a great number of dendrophagous insects (Gourov 1991). The reasons for this preference could be discussed with the examples of weevil species in the situations described above.

Beetles could be attracted to the borders and its analogues due to: (1) a higher abundance of preferable food trees in comparison with under-canopy habitats (*H. pinastri* in Buiba, *Magdalis sp.* in Aradan, *R. fagi* in Monte Bondone); (2) the availability of alternative food sources when the preferable ones were scarce (*P. validirostris*, *H. albosparsus* in Kel'tom, *Otiorhynchus spp.* in Auronzo di Cadore). The change of food objects and feeding behaviour under border conditions could be explained by: (1) changes of nutritional quality of plants (*H. albosparsus* on *Abies sibirica*, *Apion pisi* on sapling of *Picea abies*); (2) microclimatic effects (*R. fagi*, *O. geniculatus*, *P. pallidus*); (3) accidental availability of the living low branches of border and separate trees for insects in comparison with the core forest habitats where the low branches are dead (*R. forticornis* in Bosco del Cansiglio, *P. pallidus* in Auronzo di Cadore). And of course, an element of chance must be taken into account because the boundary (ecotonal) zones are usually characterized by high biodiversity (Odum 1971), and there is a greater possibility of recording some accidental species (e.g., polyphagous *Otiorhynchus spp.*) feeding on uncommon food plants.

It is necessary to note that for several of the weevil species under study (*H. albosparsus*, *P. validirostris*, *M. phlegmatica*, *P. pallidus*, *O. ovatus*, and *A. pisi*), the uncommon feeding patterns were noticed by direct field observations. For all the rest (*H. pinastri*, *Magdalis sp.*, *R. fagi*, and *Otiorhynchus spp.*), the results of laboratory rearing were obtained. Some artificial conditions could be responsible for *H. pinastri* and *Magdalis sp.* refusing to feed on shoots, and for their uncommon feeding on needles. However, the bionomics and behaviour of many weevils such as *H. pinastri* and *Magdalis sp.pl.* have not been studied carefully yet

(Rozhkov 1970, Opanasenko 1976) because attention has been given to more important pests. That is why it is not unlikely to discover some new facts concerning the biology of groups and species of weevils, as exemplified by the more or less common occurrence of "Magdalis type" damage on the needles of spruce (Fig. 1) and the forest/meadow distribution of *R. forticornis* (Fig. 2). But of course, the capability of some species to damage conifers in the cage had to be confirmed by food-choice experiments because the food plant ranges are known to be wider under laboratory conditions (Bale and Luff 1978, Leather, Ahmed and Hogan 1994). During laboratory examinations we tried to recognize the potential possibility to feed on conifers for the weevils collected in the crowns of young coniferous trees only. The fact that not all the species managed to show such a capability (e.g., *Ph. calcaratus*) will make us take into account the cases of "positive response" as a basis for future investigations.

The main conclusion that uncommon adult feeding of many species is observed on the forest borders, suggests that the change in insect behaviour and food preferences is one of the "edge effects". Numerous borders which have originated during the course of forest fragmentation can be responsible for the spread of these phenomena. As a result, the natural regeneration in openings and borders as well as young forest plantations, hedgerows and shelterbelts may be subject to damage by unspecialized herbivores. Due to this, the study of the biology and ecology of phytophagous insects as related to forest borders has become important.

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