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The effect of spruce cone insects on seed production in Switzerland

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Abstract: In 1989 and 1990, spruce cones were harvested at 29 sites distributed over the five main geographic regions of Switzerland, i.e. Jura, Central Plateau, North, Central and South Alps. The presence of insects and the species-specific consumption of seeds was determined for each cone by examination of the median longitudinal section. Seven seed-feeding species (*Assara terebrella*, *Cydia strobilella*, *Dioryctria abietella*, *Eupithecia abietaria*, *Megastigmus strobilobius*, *Plemeliella abietina*, *Strobilomyia anthracina*) and the spruce cone gall midge *Kaltenbachiola strobi* were found in the samples. The proportions of infested cones ranged from 36 to 100%. The regions did not show significant differences in terms of infestation rates, whereas differences between sites within the regions were highly significant. Seed loss ranged from 2 to 100%, its geographical distribution exhibiting a similar pattern to the infestation rates. Considering the number of infested cones, *C. strobilella* was the most abundant species, followed by *K. strobi* and *P. abietina*. Cones infested by conospermatophagous species (*C. strobilella*, *D. abietella*, *E. abietaria*) showed higher seed losses than those infested by spermatophages (*M. strobilobius*, *P. abietina*). Due to the ubiquitous occurrence of *C. strobilella*, its high infestation rates and the resulting seed losses caused by its offspring, this species has to be considered as the most important insect seed predator in Switzerland. A multiple linear regression analysis was carried out for each region to simultaneously explore the impact of site and tree variables as well as the effect of insect attack on the yield of viable seeds. The results indicate that site and tree conditions contributed more to the variability of seed yield than insect presence in a cone. The model predicted significant effects of insect attack mainly for cones with total seed numbers that were higher than the average.

1 Introduction

Cones and seeds of Norway spruce (*Picea abies* (L.) Karst.) present a substrate with a nutritive quality that is much higher than that of most other parts of the tree (Fenner, 1985). Therefore, it is not surprising to find that a substantial proportion of seeds may be lost to predators before maturation and dispersal. Among the predators phytophagous insects are considered an important mortality factor in the reproductive process (Fenner, 1985). The guild of insect seed predators may destroy up to 85% of the seed production in a spruce stand (Kangas, 1940) and a single larva of *Assara terebrella* (Lep., Pyralidae) may consume up to 100% of the seeds in a cone (Roques, 1988).

Apart from the impact of insects and other animal seed feeders the number of viable seeds finally released by a spruce cone is largely influenced by factors such as the availability of pollen, the degree of self-pollination, the nutritional state of the tree, weather, etc. (Fenner, 1985; Schmidt-Vogt, 1986). Earlier studies which tried to estimate the impact of insects on spruce seed yield usually focused on all or single members of the guild of phytophagous species (Kangas, 1940; Lovászy, 1942; Kangas and Leskinen, 1943; Roques, 1988), whereas other influences received little attention. For red pine (*Pinus resinosa* Ait.), a life table analysis during cone development showed, however, that conelet abortion and empty seeds which could not be related to insects were the major causes for seed loss (Katovich et al., 1989). In red pine the larvae of the pyralid moth *Cydia toreuta* only ranked third behind other mortality factors for seeds.

In the present study, the first aim was to quantify the seed loss due to different insects feeding on seeds of Norway spruce in Switzerland. In a second step a multiple regression analysis was applied to simultaneously explore the impact of site and tree variables as well as the effect of insect presence on seed yield and to evaluate the significance of seed-feeding insects in comparison with the other factors.

2 Material and methods

2.1 Sampling procedure

Spruce cones were harvested in 1989 and 1990 at a total of 29 sites in the five main regions of Switzerland (Jura, Central Plateau, North Alps, Central Alps, South Alps). The sites were selected among pure, fructificating spruce stands of good vitality. In 1989 five to six trees were chosen randomly at each site and 10 cones per tree were harvested.

In 1990 the cones were generally collected at the same sites and from the same trees as in the previous year. Due to reduced cone setting, it was impossible to harvest 10 cones per tree at certain sites. Therefore, the number of

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trees sampled per site varied between two and five and the number of the cones per tree between two and 10.

The altitudes of the sampling sites in the Jura, Central Plateau, North, Central and South Alps ranged from 600–1600, 370–740, 1190–1800, 1600–2000 and 1560–1900 m a.s.l., respectively.

The age of the individual trees was determined by wood core samples. Tree age varied between 48 and 335 years. For both years under study, the harvest index (i.e. the estimated relative cone production according to ROHMEDER, 1972; p. 64) of the trees was also calculated. A detailed list of the site and tree characteristics may be found in WERMELINGER et al. (1995).

2.2 Quantification of insect incidence and seed damage

The presence of insects and the occurrence of species-specific damage was determined for each cone by examination of the median longitudinal section. All visible seeds on one face of the section were counted and classified as viable, empty or insect-damaged seeds.

Data on insect incidence, damaged seeds per cone and total seed number per cone were subjected to a nested analysis of variance to detect the factors (year, region, site) contributing significantly to the observed variance. The models also included interactions between year and region as well as between year and site.

2.3 Multiple regression model

A multiple regression model was selected to explain the yield of viable seeds per cone in the 2 years under study.

Three categories of variables were included in the model: site conditions, tree conditions and insects (table 1). The qualitative variables used in the model were coded as dummy variables.

According to AIKEN and WEST (1991), the quantitative predictor variables were centred prior to regression analysis (i.e. put in deviation score form so that their means are zero). Hence, the simple slope of a predictor variable is estimated at the mean values of the other variables. Furthermore, centering variables will often help minimize multicollinearity, which can lead to technical problems in estimating regression coefficients (AIKEN and WEST, 1991).

Initial inspection of the data showed that the categories of the site variable 'phytosociological' alliance were not evenly represented in the five production regions. In addition, the alliances were highly correlated with altitude. Due to the topographic characteristics of the five main regions of Switzerland, the range of altitudes of the sampling sites differed considerably among the regions (see Section 2.1). Thus, the parameters of the regression model were estimated separately for each region in order to avoid incorrect extrapolation beyond the extent of the elevation range of a region. Missing information on tree age and aspect led to the exclusion of the Central Plateau from this analysis.

The aspects of the sample sites were recorded in 22.5° intervals (i.e. N, NNE, NE, etc.). For the regression analysis two groups of site exposures were formed: a northern aspect grouping the sections from WNW to E and a southern aspect grouping the sections from ESE to W. Based on the rationale that aspect is mainly a proxy variable for the irradiation and humidity regime at a given site, this separation leads to the comparison of seed yield of potentially cooler and more humid sites with the yield of potentially warmer and drier sites.

In general, production functions are not presumed to be linear (BAUMGÄRTNER et al., 1990). However, the data of BISSALDI et al. (1970) and STIAVELLI and TOGNOTTI (1987) indicate that the correlation between spruce cone traits and altitude is quite well represented by a linear model. Since few other literature data were available on the form of the relationship between seed production and site and tree variables, several forms of quadratic and other terms in the model were evaluated. Preliminary tests indicated, however, that these terms were statistically less significant than the linear combinations.

To account for the effect of seed-feeding insects on yield, presence/absence scores per cone were used, representing attacked and not attacked cones. For the sake of simplicity of the model, the attack rates of individual species were combined into one predictor variable. As will be shown in

Table 1. *Variables related to sampling sites and individual cones. Seed number/cone and seed consumption of insects refer to one surface of the longitudinal section of each spruce cone*

Variable	Remarks	Range
Yield		
Viable seeds (seeds/cone)	dependent variable	0; 56
Site conditions		
Altitude (m a.s.l.)	continuous variable	370; 2000
Slope (N, NNE, NE, etc.)	categorical variable	1; 4
Tree conditions		
Tree age (years)	continuous variable	67; 335
Harvest index	continuous variable	10; 100
Cone traits		
Total number of seeds (seeds/cone)		8; 76
seed and cone insects		
Assara terebrella (seeds/cone)		0; 18
Cydia strobilella (seeds/cone)		0; 58
Dioryctria abietella (seeds/cone)		0; 36
Eupithecia abietaria (seeds/cone)		0; 42
Kaltenbachiola strobi (individuals/cone)		0; 34
Megastigmus strobilobius (seeds/cone)		0; 4
Plemeliella abietina (seeds/cone)		0; 22
Strobilomyia anthracina (seeds/cone)		0; 70

the results from seed-loss analysis, insects react differently to larger cones (i.e. to cones with higher numbers of seeds) than to smaller ones. Hence, an additional dummy variable was created for cones with total seed number higher than average. Its interaction with the insect presence/absence variable allowed for testing the significance of the effect of cone size on insects.

Consequently, the following linear model was adopted

$$y_i = a + \sum_{j=1}^{5} b_j x_{ij} + \sum_{j=1}^{4} \sum_{n=j+1}^{4} c_{jn} x_{ij} x_{in} + \sum_{j=1}^{3} d x_{ij} x_{i5} + e x_{i3} z_i + f x_{i5} z_i + \varepsilon_i \qquad (1)$$

for $i = 1, \ldots n$, where: y_i = yield in number of viable seeds per cone in cone i; a = intercept; b_j = regression coefficient for variable j; x_{ij} = the observed value of variable j for cone i; c = regression coefficient for the interaction between the variable j and n for stand and tree characteristics; x_{i5} = dummy variable for insect presence ($x_{i5} = 1$ = attacked cone; $x_{i5} = 0$ = unattacked cone); z_i = dummy variable for total seed level ($z_i = 1$, if total seed number in observation i is higher than the average total seed number; $= 0$, if total seed number is equal or lower than average); d = regression coefficient for the interaction between altitude (x_{i1}), aspect(x_{i2}), harvest index (x_{i3}) and insect presence (x_{i5}); e = regression coefficient for the interaction between harvest index (x_{i4}) and total seed level (z_i); f = regression coefficient for the interaction between insect presence (x_{i5}) and total seed level (z_i); e_i = stochastic disturbance.

If qualitative variables are coded as dummy variables one of the levels of the variable is designated as the comparison group. In the regression analysis the coefficients of the dummy variables denote their deviation from this comparison group (for more details see Aiken and West, 1991). In the present analysis dummy variable coding was set up to produce the following comparison group: aspect = south, insect attack = none and total seed level = low. Consequently, the regression coefficient for aspect contrasts high seed level with low seed level, etc.

To quantify the individual contribution of the predictor variables to the variation in seed yield, the squared semipartial regression coefficient was calculated for each variable and interaction by eqn 2. According to Cohen and Cohen (1983) the coefficient equals the increase in the squared multiple correlation, expressed as proportions of the variance of the dependent variable, that occurs when the corresponding variable is added to the other independent variables.

$$sr_j^2 = \frac{F_j(1 - R^2)}{n - k - 1} \qquad (2)$$

where: sr_j^2 = squared semipartial correlation coefficient for the variable j or interaction; F_j = F-ratio of the variable j or interaction; R^2 = squared multiple correlation coefficient; n = sample size; k = number of independent variables in the model.

The main interest in the present regression analysis was focused on the effect of insect presence on the number of viable seeds per cone. According to the regression model proposed above (eqn 1), insect presence is affected by altitude, aspect, harvest index and total seed number, i.e. the influence of insects varies as a function of these factors. In order to explore the interactions between insects and site and tree characteristics as well as their effect on the number of viable seeds, a simple slope analysis (Aiken and West, 1991) for the variable 'insect presence' (x_{i5}) was carried out. The parameters of the regression model were estimated using different (conditional) values for the variables interacting with x_{i5}. The resulting regression coefficient (simple slope) for x_{i5} represents the (marginal) effect of insect presence at the conditional values, whereas the corresponding F-value allows for testing the significance of the effect. Details on the computing procedure may be found in Aiken and West (1991).

Conditional values for altitude (x_{i1}) were set at one standard deviation below and above the average regional altitude. Furthermore, simple slopes were estimated at north and south exposure (x_{i2}) as well as at high and low total seed number per cone (z_i).

All computations involving analysis of variance and multiple regression techniques were carried out with the Systat® MGLH procedure (Wilkinson et al., 1992).

3 Results

3.1 Insect infestation rates

The following seven seed-feeding insect species or their damage were identified in the cone samples (table 1): *Assara terebrella* Zinck (Lep., Pyralidae), *Cydia strobilella* L. (Lep., Tortricidae), *Eupithecia abietaria* Goeze (Lep., Geometridae), *Dioryctria abietella* (Den. et Schiff.) (Lep., Pyralidae), *Megastigmus strobilobius Ratz.* (Hym., Torymidae), *Plemeliella abietina* Seitn. (Dipt., Cecidomyiidae), and *Strobilomyia anthracina* (Czerni) (Dipt., Anthomyiidae). In addition to the seed-feeding insects, the presence of the spruce cone gall midge, *Kaltenbachiola strobi* Winn. (Dipt., Cecidomyiidae), was recorded. The larvae of this cecidomiid fly do not directly damage seeds. The galls on the scales induced by this species may hinder the opening of the mature cone and thus affect the dissemination of the seeds. Detailed information on the biology and the ecology of the spruce cone insects mentioned above may be found in Barnes (1951), Bakke (1955, 1963) and Roques (1983).

As depicted in fig. 1 the mean proportions of cones attacked by all seven seed-feeding insect species described above reached more than 62% in four of the five main regions of Switzerland and in both years covered by this investigation. In 1989 the entire crop from the sample sites on the Central Plateau was infested by these insects. The northernmost region (Jura) showed lower average infestation levels (36–39%) in 1989 as well as in 1990.

However, analysis of variance did not reveal any significant differences in infestation rates between the five regions and between the 2 years ($P > 0.05$). Significant differences were found among the sampling sites within the regions ($P \leq 0.001$).

Four of the seven seed-feeding species (*C. strobilella*, *D. abietella*, *P. abietina*, *S. anthracina*) were present in all five regions. With the exception of *D. abietella*, these four species were quite abundant in the cone samples, infesting between 9 and 47% of all cones. *Eupitheica abietaria* was found only in samples from spruce stands above 1000 m a.s.l. (Central Plateau, Jura). On the other hand, the presence of *M.*

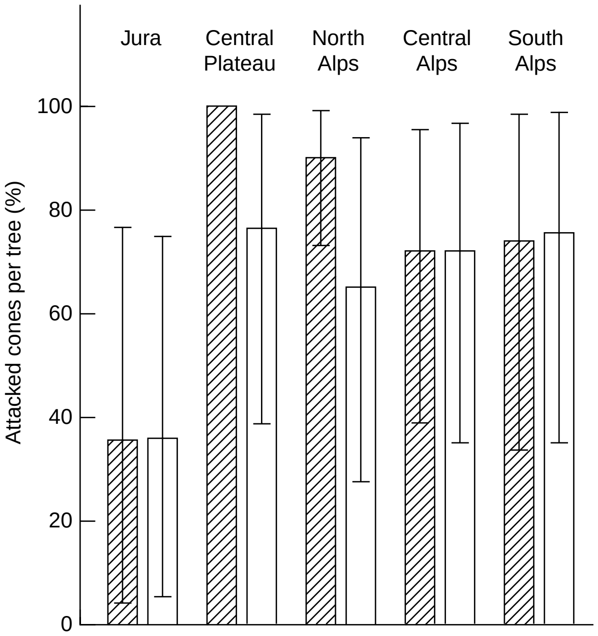

Fig. 1. Average proportions (± SD) of spruce cones attacked by seed-feeding insects in the five main regions of Switzerland in 1989 (hatched bars) and 1990 (white bars)

strobilobius seems to be confined to spruce stands at low elevations (below 1000 m a.s.l.) in the Jura region and to the Central Plateau.

According to the total number of cones infested by each species (see table 4), *C. strobilella* and *P. abietina* were the most abundant seed predators considering the whole area under study. Only the abundance of the gall midge *K. strobi*, which does not feed on seeds, reached comparable numbers. The relative frequencies of the seven seed-feeding species in the five regions are depicted in fig. 2. *Cydia strobilella* and *D. abietella* totalled between 60 and 90% of all infestation events in the different regions, indicating that the dominance of these two species in Switzerland is independent of regional differences in vegetation, topography or climate. *Strobilomyia anthracina* and *D. abietella*, the other two species present in all regions, showed infestation levels between 2 and 24% and between 0.3 and 8%, respectively.

About half of all infested cones were attacked by more than one species, with a maximum of five species occurring in the same cone (table 2). In the majority of the infested cones each species was associated with one or more other species. The two-species association was the most frequent one, except for the relatively rare pyralid *A. terebrella* which attacked only four cones at all. For *M. strobilobius* single-species attacks occurred only in 4% of the infested cones whereas for the other species this rate varied from 15 to 32%. The low rate for *M. strobilobius* reflects the fact that it is the latest species to attack spruce cones and in general colonizes only seeds left undamaged by other insects (Skrzypczyńska and Roques, 1987).

As shown in table 3, the average seed number of cones infested by seed-feeding insects was significantly higher than that of uninfested cones. The cones

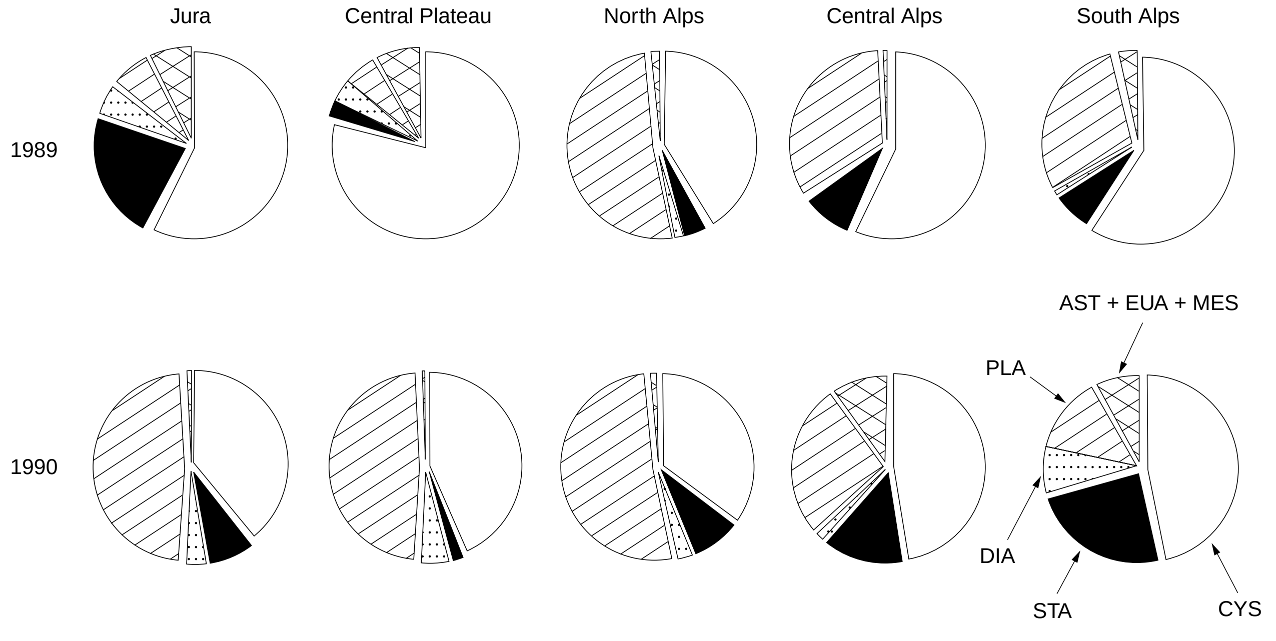

Fig. 2. Relative frequencies of seven seed-feeding insect species attacking spruce cones in the five main regions of Switzerland in 1989 and 1990. Proportions are based on the numbers of cones infested by each species: CYS, Cydia strobilella*; STA,* Strobilomyia anthracina*; DIA,* Dioryctria abietella*; PLA,* Plemeliella abietina*; AST + EUA + MES, sum of* Assara terebrella, Eupithecia abietaria *and* Megastigmus strobilobius

Table 2. Species-specific distribution of single and multiple attacks of spruce cone insects in Switzerland

Species per cone (n)	Number of cones (n)	(%)	Relative frequencies of cones attacked by one or more species: *A. terebrella* (%)	*C. strobilella* (%)	*D. abietella* (%)	*E. abietaria* (%)	*K. strobi* (%)	*M. strobilobius* (%)	*P. abietina* (%)	*S. anthracina* (%)
1	898	48.0	0.0	32.0	24.6	15.4	27.3	4.3	29.2	20.9
2	714	38.1	25.0	46.9	47.5	46.2	44.8	69.6	45.4	37.7
3	228	12.2	75.0	18.3	21.3	21.5	24.2	21.7	22.4	28.8
4	30	1.6	0.0	2.6	6.6	13.8	3.5	4.3	2.8	11.6
5	2	0.1	0.0	0.2	0.0	3.1	0.2	0.0	0.3	0.9
Total		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Total no. of cones	1872		4	1161	61	65	824	23	787	215

attacked only by *C. strobilella*, one of the two most abundant species, contained about 14% more seeds per cone. Likewise, if all cones with single and multiple attacks of the different species are pooled, their average seed content exceeds that of uninfested cones by 13%. Contrasting with the results for seminivorous insects, cones infested by the conophagous species *K. strobi* showed significantly fewer seeds per cone (−9%) than cones not infested by insects (note that all results concerning seed numbers are based on one surface of a cone section).

3.2 Seed losses

On average all seed-feeding insects considered in this study consumed 33% of the seeds of a cone, the loss ranging from 2 to 100% per cone. The regional distribution of the seed losses showed a similar pattern to the distribution of the infestation rates, the highest losses occurring on the Central Plateau (49 and 15% in 1989 and 1990, respectively), whereas the lowest losses occurred in the Jura region (15% in 1989; 7% in 1990). Significant differences were found on the site and tree level with significant site × year and tree × year interactions ($P < 0.05$). Year, region and the year × region interaction did not contribute significantly to the variance. Interestingly, differences in total number of seeds per cone were highly significant ($P \leq 0.001$) at all sampling levels (region, site and tree).

The species-specific impact on seed yield varied considerably (table 4). Considering the average number of seeds consumed in cones with only one species present, two groups of species could be distinguished: *C. strobilella* and *E. abietaria* consumed about double the amount of seeds in comparison with *P. abietina* and *S. anthracina*. This is also true when the seed loss is expressed as a fraction of the total number of seeds per cone. One reason for the differences in seed consumption of these species is the divergent manner of larval development. Whereas each larva of *P. abietina* develops inside a single seed, *C. strobilella* and *E. abietaria* tunnel through the cone and feed on the seeds they encounter. *Strobilomyia anthracina* combines the two feeding habits, leaving the seed at the end of the first larval instar.

3.3 Impact of site and tree variables and insect presence on seed yield

Table 5 shows the results of the parameter estimation of the regression model. The correlation coefficient R^2 stands for the proportions of variation in the number of viable seeds explained by the model. The low

Table 3. Average number of seeds in uninfested cones and in cones infested by all seed-feeding species as well as by the most abundant species C. strobilella, P. abietina, K. strobi *(SD: standard deviation). Only cones with the presence of a single species are considered*

Cones	Seeds per cone: mean	SD	Sample size n
Not infested	35.6^{a}	7.7	573
Infested by			
all seed-feeding species	39.9^{b}	10.5	673
Cydia strobilella	41.6^{b}	9.4	372
Plemeliella abietina	38.7^{ab}	9.5	230
Kaltenbachiola strobi	32.7^{c}	7.3	225

Means followed by different letters differ significantly from each other, $P < 0.05\%$, ANOVA, Bonferroni-test.
Note that 'seeds per cone' refers to one surface of the longitudinal section of a cone.

Table 4. *Mean values and standard deviations (SD) of absolute (n) and relative seed losses (%) caused by single insect species in spruce stands in Switzerland. Relative seed loss is the proportion of seeds damaged per number of total seeds per cone*

	Seed loss per cone				
	(*n*)		(%)		
Species	Mean	SD	Mean	SD	Sample size (*n*)
Assara terebrella *	–	–	–	–	0
Cydia strobilella	14.6^{a}	13.25	33.4^{ac}	27.3	372
Dioryctria abietella	12.5^{ab}	9.42	29.4^{ac}	21.3	15
Eupithecia abietaria	17.7^{a}	8.17	51.9^{a}	20.4	10
Megastigmus strobilobius *	1.0	–	2.1	–	1
Plemeliella abietina	6.0^{b}	4.26	16.4^{b}	12.9	230
Strobilomyia anthracina	7.6^{b}	6.34	24.0^{c}	20.6	45

Means with different letters within a column differ significantly from each other, $P < 0.05\%$, ANOVA, Bonferroni-test.
* not tested. Note that 'seeds per cone' refers to one surface of the longitudinal section of a cone.

values (0.34–0.58) indicate that there were other important factors explaining the variation in seed yield, which were not considered in the model. For example, a fluctuation between years in the proportions of cones attacked by insects was observed in the North Alps, whereas in the other regions considered in the analysis the attack rates were almost identical for both years under study (cf. fig. 1). The introduction of a dummy variable for a time component into the model produced a small but significant increase of R^2 of about 6% ($R^2 = 0.403$) for the North Alps, whereas the increase for the other regions ranged from 0.5 to 3% only.

Furthermore, the regression results for the four production regions reveal diverging significance levels of the same predictors and interactions as well as marked differences of the coefficients of determination (R^2). Only two predictor variables (tree age, harvest index) and one interaction term (altitude × aspect) show significant coefficients in all regions considered in the analysis. These findings indicate that a further improvement of the model may be achieved by incorporating region-specific information.

To illustrate the contribution to variability by the predictor 'insect attack' and its interactions as opposed to site and tree characteristics, the respective sums of the squared semipartial regression coefficients sr_j are shown in fig. 3. According to the proposed model the dominating causes for the variation of viable seed numbers in all regions were tree and site conditions. This is also true if the comparison group (see above) is changed to southern aspect and high total seed level. The region North Alps shows the smallest differences between the two groups of predictors, reflecting the considerable change in insect attack rates from 1989 to 1990.

Table 6 summarizes the results of the simple slope analysis for the effect of insect presence at conditional values of altitude, aspect and total seed number per cone. Since insect presence is a qualitative variable with two categories (i.e. presence or absence) the estimated coefficients represent the change in number of viable seeds if a cone is attacked. In correspondence with the results in table 5 the values of the regression coefficient as well as the respective significance levels differed greatly among the four production regions considered in the analysis.

However, three trends were apparent in all regions: firstly, the marginal effect (insect presence) was posi-

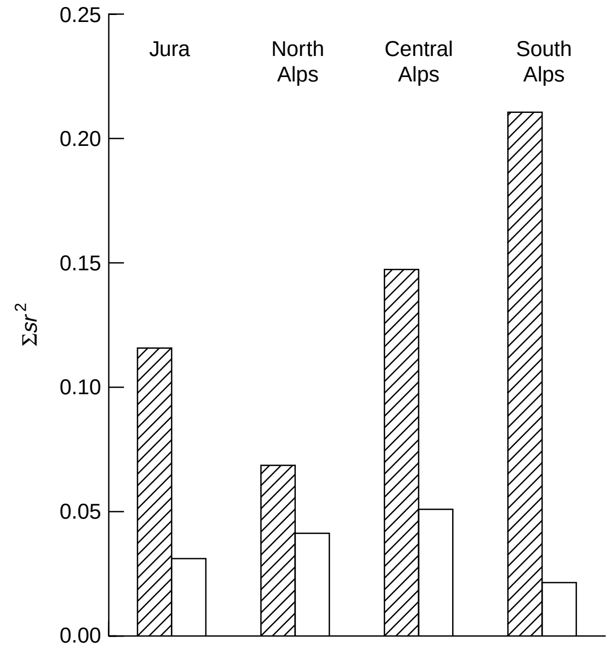

Fig. 3. *Sum of the squared semipartial correlation coefficients (Σsr^2) representing the contribution to the overall variance by the predictor variables 'site' and 'tree characteristics' (hatched bars) and 'insects' (white bars) (cf. table 5). In both categories only variables and interactions with regression coefficients differing significantly from 0 ($P < 0.05$) were summed*

Table 5. *Regression statistics for the seed yield model in four regions of Switzerland*

Predictor variables	Regression coefficients			
	Jura	North Alps	Central Alps	South Alps
Site and tree characteristics				
Altitude	0.0130	0.0163 *	0.0500 **	0.0146 *
Aspect	1.9086	1.0423	4.9226	−1.5060
Altitude × aspect	−0.0307 **	−0.0430 **	−0.0609 **	0.0253 *
Harvest index	0.2337 **	0.2531 *	0.5817 **	0.1519 *
Tree age	−0.0873 *	0.0694 *	0.1868 **	0.0473 **
Altitude × tree age	0.0006 **	−0.0003 *	−0.0003	−0.0007 **
Aspect × tree age	−0.0650 *	−0.0796	−0.2019 **	0.0318
Altitude × harvest index	−0.0002 *	0.0004	0.0004	0.0025 **
Aspect × harvest index	−0.1744 *	−0.0314	−0.4099 **	0.0986
Tree age × harvest index	0.0036 **	0.0002	−0.0004	−0.0062 **
Harvest index × total seed level	−0.1737 *	0.2161 **	0.0024	−0.1914 *
Insects				
Insect attack	−5.0717 *	−3.4356	−3.0774	−3.5464 **
Insect attack × altitude	0.0105 *	0.0171 *	−0.0056	−0.0098
Insect attack × aspect	1.7712	4.3767	−4.3699	0.4151
Insect attack × harvest index	0.2291 **	−0.1592 *	−0.0649	0.1448
Insect attack × total seed level	1.4964	3.0613 **	5.1912 **	2.0470 *
Constant	7.2	4.8	10.6	11.3
R^2	0.483	0.336	0.407	0.583
Number (n)	480	449	509	374
Mean yield (seeds/cone)	12.0	9.0	14.3	8.9
SE of estimate	7.13	6.12	7.28	5.33

* and ** denote regression coefficients differing significantly from 0 with $0.05 \geq P > 0.001$ and $P \leq 0.001$, respectively.
Note that 'seeds per cone' refers to one surface of the longitudinal section of a cone.

tively correlated with levels of total seed number. Secondly, it was correlated with aspect if the seed number level was held constant. For the Jura, North and South Alps, northern aspects showed higher values of the coefficient, whereas the inverse was true for the Central Alps. Thirdly, the marginal effect is correlated with altitude. In the Central and South Alps the coefficient decreased with increasing altitude, whereas in the Jura and the North Alps the inverse was true.

In the three alpine regions only a minority of the preset conditional values were associated with effects differing significantly from zero. In the Central and South Alps only cones with a high total seed number showed significant coefficients. According to the

Table 6. *Simple slopes for the marginal effect 'insect presence' in four regions of Switzerland, estimated at conditional values of the predictor variables altitude, aspect and total seed number per cone. Low and high altitude are set at one standard deviation below or above the average elevation of each region*

Predictor variable			Slope			
Altitude	Aspect	Total seed number/cone	Jura	North Alps	Central Alps	South Alps
Low	north	low	0.8	0.9	−8.3	−4.2
	north	high	2.3	4.6	−3.2 **	−2.2 **
	south	low	−0.9	0.3 **	−3.1	−4.7
	south	high	0.6 *	3.3	1.2 **	−2.6 **
Average	north	low	−3.3 *	0.9	−7.4	−3.1
	north	high	−1.8 **	4.0	−2.3	−1.1 **
	south	low	−5.1	−3.4 **	−3.1	−3.5
	south	high	−3.6 *	−0.4	2.1 **	−1.5 *
High	north	low	−7.4 **	−2.8	−6.6	−2.0
	north	high	−5.9 **	0.3 *	−1.4	0.02 *
	south	low	−9.2 **	−7.1	−2.2	−2.4
	south	high	−7.7 *	−4.1	3.01 **	− 0.4

* and ** denote coefficients differing significantly from 0 with $0.05 \geq P > 0.001$ and $P \leq 0.001$, respectively.
Note that 'seeds per cone' refers to one surface of the longitudinal section of a cone.

model results, the most important and significant negative effects due to insect presence occurred at high altitude in the Jura, irrespective of aspect and total seed number.

The presence of insects in a cone does not necessarily signify lower yield of viable seeds, if compared with uninfested cones. According to table 6 infested cones may even present significantly higher yield. This indicates that a single qualitative dichotomous predictor (i.e. presence/absence) may be an incomplete representation of the effect of seed-feeding insects (cf. discussion).

4 Discussion

The analyses of the infestation rates as well as seed losses per cone showed highly significant differences between the sample sites. In contrast to Wermelinger et al. (1995), who investigated the frequencies of insects emerging from spruce cone insects in Switzerland, the differentiation into the five geographical regions (Jura, Central Plateau, North, Central and South Alps) did not contribute significantly to the observed variance. This is also true if the fluctuations in the 2 years under study are taken into account. Although there are considerable differences among the regions concerning altitudinal range, topography, climate and vegetation type, factors acting on a local scale seem to be more important for variability of the infestation rates. One reason for the lack of differences among the regions may be the fact that seed losses are essentially due to two species (*C. strobilella, P. abietina*) obviously showing no restriction in occurrence throughout the geographical distribution area of their host species (Roques, 1983).

The chosen geographical classification mainly corresponds to the five forest production regions in Switzerland, which are characterized, among others, by factors such as main vegetation type, growth conditions for the main crop trees, production potential (Brassel and Brändli, 1999). The differences found in the total number of seeds per cone among these regions were highly significant. Thus, a differentiation at this level may have some explanatory value concerning the yield formation process of the host tree. As an interaction seems to exist between the seed quantity of a cone and insect infestation as shown in table 5, a regional effect on insect attack rates and seed loss, mediated by the seed content, may not be completely excluded. Unfortunately, the structure of the collected data did not allow for testing this hypothesis.

According to Turgeon et al. (1994) the temporal fluctuations in cone production is one of the most important mechanism regulating the population dynamics of many conophyte insects (i.e. insects that can feed or develop only in cones). Substantial annual variations in larval populations generally reflect the yearly changes in crop size. The prevailing pattern is a negative correlation between insect infestation levels and cone abundance (Turgeon et al., 1994). In addition to this temporal heterogeneity the cone setting of coniferous trees may exhibit a considerable spatial variability. Thus, the interpretation of the results from short-term studies covering a geographically diverse country such as Switzerland must take into consideration the effects caused by temporal and spatial fluctuations of food and breeding resources.

The present study covers 2 years with crop sizes varying from poor to moderate. At most sites the crop size was smaller in the second year, giving evidence that samples were taken in a phase of crop production decreasing from masting towards sparse or even no cone setting. As may be expected with the observed crop sizes, infestation rates by seed-feeding insects were relatively high. The spatial variability was reflected by the significant differences among the sites within the five regions. However, the reasons for infestation differences may not only arise from the varying supply in spruce cones. The heterogeneity of the regions and sites has probably also affected the population dynamics of the seed predators, for example, through differences in the local climates.

A common trait of the species association of Norway spruce cones reported in the literature was the dominance of the spruce cone moth *C. strobilella* (Skrzypczyńska, 1982; Skrzypczyńska and Roques, 1987). Likewise for Switzerland, Wermelinger et al. (1995) showed that this species outnumbers all other seed-feeding insects when reared from spruce cones harvested in the five production regions. The results of the present study on the quantitative impact confirms the role of *C. strobilella* as the most important member of the guild of insects feeding on seeds of Norway spruce in Switzerland.

At least in some parts of Switzerland, infestation rates of *P. abietina* equalled or exceeded those of *C. strobilella*, but this gall midge caused only about half of the absolute and relative seed losses per cone. In other countries such as Finland (Annila, 1966), France (Roques, 1983) or Poland (Skrzypczyńska, 1989), *P. abietina* is referred to as a rather rare species with infestation rates sporadically rising up to 20%. Annila (1984) found, that this species exploits seeds only during years of heavy to medium crop, whereas in Switzerland the crop size was quite small in the two years under study. Insects are considered the most important seed predators during the predispersal phase of seed development (Turgeon et al., 1994). Fenner (1985) ranked seed predation among the four main causes of mortality of ovules and seeds. It was even postulated that, under certain conditions, the natural regeneration potential of coniferous tree species may be significantly reduced by insect seed predators (Roques, 1988; Mosseler et al., 1992).

In the present study a regression analysis was carried out to identify important factors affecting the variability of seed yield in Norway spruce. For Switzerland, the results of the analysis imply that in the two years under study, the site and tree conditions had a greater impact on seed yield than seed-feeding insects. Taking into account the above considerations on the relationship between the temporal fluctuations of crop size and insect infestation levels, the fraction of variation due to seed predators would probably be even smaller under conditions of larger cone production.

The proposed regression model included only predictor variables whose values could be easily measured or collected during one or two visits to the sampling sites. Thus, the important mortality factors during cone and seed development (pollination and developmental failure, resource deficiency, weather; Fenner, 1985) could not be measured directly. In the present case, site and tree variables were considered as proxy variables for these factors. The relatively low proportions of the overall variance explained by the model may be attributed to the fact that the variables in the model only partly represent the influences which in reality determine the seed yield of a cone.

The analysis of the marginal effect of insect attack shows that insect presence in a cone may be correlated with higher contents of viable seeds compared with uninfested cones. This positive correlation occurred mainly in cones with total seed numbers that were higher than average. On the one hand, it is probably an effect of insects selecting cones with high seed content offering optimal conditions for preimaginal development. On the other hand, the variable 'presence or absence of insects' neither contains information on the number of eggs deposited in a cone nor on the survival of the offspring. Combinations of high seed content with small numbers of eggs laid and/or low survival of the seed predators may lead to an apparent positive effect of insect attack on seed yield.

The present analyses were based on a data set covering two years of cone production. However, the reproduction of trees as well as insect dynamics are also influenced by biotic and abiotic factors acting on a multiseasonal scale. Thus, long-term studies will be necessary to confirm the results and conclusions presented and such studies will provide additional insight into the relevant processes which determine the amount of viable seeds in a cone.

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