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Short note

Insect damage to cones and other mortality factors limiting natural regeneration potential of Swiss stone pine (*Pinus cembra* L) in the northern French Alps

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Summary — A seed cone population of Swiss stone pine was surveyed from flower bud burst to cone maturation during 1992–1993. The potential seed crop was estimated to decrease by 84 % of the initial value. Mortality was mainly caused by abiotic factors during the first year of cone development while cone insects caused most damage to second-year cones. The cone entomofauna only included three phytophagous species, and largely differed from the fauna observed in cones of other Alpine conifers.

***Pinus cembra* / regeneration / cone insect / seed loss**

Résumé — Les dégâts d'insectes des cônes et autres facteurs de mortalité limitant les potentialités de régénération naturelle du pin cembro dans les Alpes françaises du Nord. Un suivi démographique de cônes de pin cembro sur un cycle reproductif complet a été réalisé en 1992 et 1993. Au total, 84 % de la production potentielle de graines a été détruite. La majorité des pertes a été causée par des facteurs abiotiques la première année, et par des insectes pour les cônes de deuxième année. L'entomofaune ne comprend que trois espèces phytophages et diffère largement de celle observée dans les autres essences des conifères alpins.

***Pinus cembra* / régénération / insecte des cônes / perte en graines**

INTRODUCTION

Insects exploiting seed cones are known to limit the potential of natural regeneration in high altitude conifer forests. In larch, such insects may currently reduce the annual number of seeds by 50 to 80% in the French Alps, and even by 100% in mountains of northeastern China (Roques, 1993). However, insects exploiting seed cones of Swiss stone pine (*Pinus cembra* L.) have received little attention (Coslop and Masutti, 1978; Roques, 1983). Moreover, the decrease in seed yield that results from insect damage during the seed predispersal phase has never been quantified. Our study thus aimed to assess the species composition and biology of the entomofauna feeding on seed cones of *P. cembra*, and then to measure the respective impact of insects and other mortality factors on the potential of natural regeneration of stone pine forests. Insect damage has usually been measured using periodic dissections of cones collected at successive dates. By contrast, we intended to survey the same reproductive structures over their whole development, from flower bud burst to seed maturation.

MATERIALS AND METHODS

The survey was carried out in the forest of Tuéda, near Méribel-Les-Allues (45°21'N, 6°38' E), in the northern French Alps. The Tuéda forest ranges from 1 700 to 2 000 m, and is the largest pure stand of *P. cembra* in the region although mixed with spruce at low altitude. In June 1992, 20 cone-bearing trees were randomly selected throughout the forest. Six branches bearing both conelets and second-year cones were selected per tree and tagged. The position of the conelets and cones was mapped, and the branches were then surveyed according to the methods developed by Ebel and Yates (1974) and Rauf *et al* (1985). A total of 500 conelets were surveyed over a complete reproductive cycle, from June 1992 to September 1993, while 480 second-year cones (ie, initiated in 1991) were surveyed from June

to September 1992. In September 1992 and 1993, the surviving second-year cones were harvested for seed extraction. All seed lots were X-rayed to measure the respective number of filled, insect-damaged and aborted seeds. In 1992 and 1993, 10 cone-bearing trees were additionally sampled nearby the trees considered earlier. A monthly collection of 5 cones per tree was performed on these trees from June to September. The sampled cones were immediately dissected in order to identify the damaging larvae and to assess the type and importance of damage (Roques, 1983). Insects were either preserved in 70% alcohol or raised to the adult stage.

RESULTS

Cone entomofauna of Swiss stone pine

Three phytophagous species were observed to attack the seed cones of Swiss stone pine. The weevil *Polydrusus atomarius* Olivier (Coleoptera: Curculionidae) had never been recorded to attack conelets of *P. cembra* until our observations. Adults fed on external surfaces and attack usually resulted in conelet abortion. Larvae of the midge *Cecidomyia pini* De Geer (Diptera: Cecidomyiidae) developed in tissues and resin of first-year cones. Midge attack resulted in a typical twisted shape of the subsequent second-year cones in which most of the seeds aborted. Larvae of the cone pyralid, *Diorctria abietella* Denis and Schiffermüller (Lepidoptera: Pyralidae), entered the second-year cones and fed on cone tissues (scales, cone axis). A few were found preying seeds. The three species were already known to attack twigs, shoots and other cone species (Roques, 1983).

Factors of mortality acting during seed cone development (table I)

During the first year of development, 66% of the conelets disappeared, mainly because

Table 1. Life table for the 1992–1993 cone crop of Swiss stone pine from bud burst to seed maturation, forest of Tuéda, northern French Alps.

Development stage	Date	No of survivors	No/branch	Mortality factor	Death (no)	Mortality quotient	Survival rate
Flower bud burst	16 VI 92	500	4.16				
0.5-month conelet	30 VI 92	453	3.77	Development lacking	47	9.4	90.6
1-month conelet	14 VII 92	444	3.70	<i>Polydrusus</i>	9	1.98	98.1
1.5-month conelet	30 VII 92	343	2.85	Abortion <i>Polydrusus</i>	79 22	17.7 4.9	77.2
					101	22.8	
2-month conelet	16 VIII 92	280	2.33	Disappeared Abortion <i>Polydrusus</i>	42 1 20	12.2 0.2 5.8	81.6
					63	18.4	
3-month conelet	14 IX 92	227	1.89	Disappeared	53	18.9	81.1
11-month cone	25 V 93	167	1.39	Disappeared Frost	20 40	8.8 17.6	73.6
					60	26.4	
12-month cone	20 VI 93	167	1.39		0	0	100
15-month cone	8 IX 93	70	0.58	<i>Cecidomyia</i> <i>Dioryctria</i>	53 44	31.7 26.3	41.9
					97	58.0	

of abiotic factors (85% of the losses), but 11.8% of the conelets aborted following the attack of *P. atomarius*. Conelet attack by the midge *C. pini* could only be quantified during the second year of development because no damage was visible from outside during the early stages of cone development. Mortality of the second-year cones was predominantly caused by insects, involving larvae of *C. pini* and *D. abietella* that attacked 32 and 26% of the cones, respectively.

Relative importance of mortality factors in decreasing the potential seed crop (fig 1)

A sound cone yielded an average of 41 ± 15 seeds (max: 78, min: 14; $n = 50$). The potential seed crop expected to result from the 500 conelets tagged in June 1992 was therefore extrapolated to 20 500 seeds, on the average. X rays showed that aborted and undeveloped seeds averaged $8.9 \pm 6.1\%$ in sound mature cones ($n = 50$) but

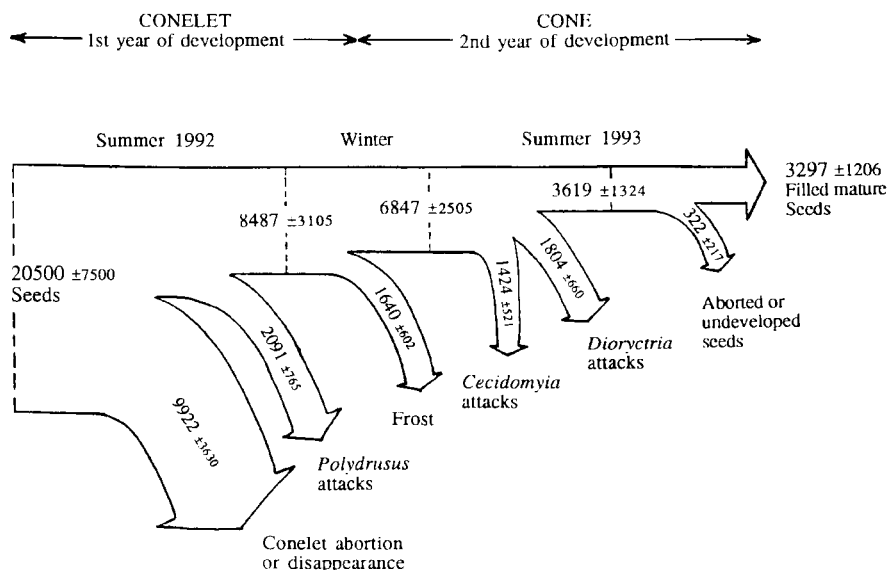


Fig 1. Mortality factors of *Pinus cembra* seed cones and estimation of their seasonal impact during a reproductive cycle 1992–1993, forest of Tuéda, northern French Alps (average number of seeds $\pm$ SD).

65% of the potential seed content aborted when a first-year cone was attacked by *C. pini*. Infestation of second-year cones by *Dioryctria* larvae also resulted in a loss of the entire seed content because such cones with visible frass were always forsaken by the nutcracker, and seeds were thus unable to escape the serotinous cones and be dispersed. Finally, the potential seed crop was estimated to decrease by 84% of the initial value, insect damage accounting for 31% of the decrease.

DISCUSSION

The seed cone entomofauna of *P. cembra* appeared markedly different from that observed in cones of other Alpine conifer species (Roques, 1983, 1993). Cones of larch, spruce, fir and mountain pine generally host a larger number of species (nine

to 17 according to tree species) and show greater insect damage (Roques, 1993). Moreover, most cone insects are host-specific and highly specialized in exploiting cone resource, a given number of species being fully adapted to seed exploitation (ie, spermatophages) (Turgeon *et al*, 1994). In contrast, the exploitation of the cone niche appeared incomplete in Swiss stone pine. No spermatophagous insect was noted, and none of the 3 insect species was apparently specialist of *P. cembra* cones. Additional cone collections performed all over the Alps during 1994 confirmed these preliminary results (Dormont and Roques, unpublished observations). The cone entomofauna was similarly limited in two related pine species of the *cembrae* subsection, *P. pumila* Regel (Khomentovsky and Efremova, 1991) and *P. sibirica* Du Tour (Florov, 1951). In both cases, the fauna consisted of two or three insect species that are taxonomically and

ecologically close to those attacking cones of *P. cembra*. These similarities lead to assume that specific physical and/or chemical barrier, as well as biotic barrier – seed predation by nutcracker – may limit insect colonization of stone pine cones (Dormont, 1993).

Similar phenological relationships between seed cone development and action of mortality factors, especially insect attack, have been observed in *Pinus* spp other than stone pines (Ebel and Yates, 1974; Roques, 1977; Mattson, 1978; Rauf et al, 1985). However, stone pines differ because of the additional harvest of the surviving second-year cones by the spotted nutcracker, *Nucifraga caryocatactes* L. The nutcracker–stone pine relationships are considered both coevolved and mutualistic, the bird action allowing wingless seeds to escape from indehiscent cones, and to disseminate and colonize new areas (Mattes, 1982; Crocq, 1990; Khomentovsky and Efremova, 1991). The nutcracker harvests and hides pine seeds by the end of summer, and stored seeds not used during the following winter may thus germinate in sites very suitable for germination (Mattes, 1982; Crocq, 1990). On the other hand, Crocq (1990) reported that all of the hidden seeds were recovered afterwards by the spotted nutcracker during poor crop years. The combined action of bird and insects could thus hinder pine recruitment in most years because good cone crops usually occur only every 5–6 years in *P. cembra* stands (Contini and Lavarello, 1982; Mattes, 1982). Moreover, additional seed predators such as squirrels, small rodents and other seed-eating birds were not taken into consideration (Smith and Balda, 1979). Difference in insect damage to seeds between larch and Swiss stone pine may also influence the development of forests where the two species are mixed. The higher damage to larch seeds could be speculated to result in the faster development of Swiss stone pine that is

usually observed in mixed stands (Piuksi, 1994). However, insect impact on both species was only compared at the cone or tree level (Roques, 1993). Further studies will have to supply accurate measures of the respective number of filled seeds dispersed per tree species and per surface unit.

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