

SEED PRODUCTION AND CONE-FEEDING INSECTS OF PINUS PUMILA ON THE KAMTCHATKA PENINSULA: ASPECTS OF COEXISTENCE

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INTRODUCTION

Insects attacking seeds and cones of trees are significant for their economic consequences as well as for the ecological role in vegetation dynamics. Currently much is known about seed and cone insects feeding on upright trees (see Roques, this volume), but almost nothing is known about cone inhabitants of prostrate pines *Pinus pumila* (Pall.) Rgl., *P. albicaulis* Engelm., *P. mugo* Tur. These three vicariant species from young mountain systems of the northern hemisphere have evolved in unfavorable environments which have favored peculiar patterns of seed production and insect-host relations. Cone insect populations are strictly determined by well known periodicity of seed production which often causes the evolution of diapause in cone-feeding insects. This phenomenon occurs in upright trees and is perfectly illustrated by *Lasiomma melania* on *Larix kamtchatica* on the Kamtchatka Peninsula. Unlike *Larix*, *Pinus pumila*, whose seeds develop over 2 years, has peak crops every 2 to 3 years but in fact produces some cones every year. This happens because seeds are produced on mosaically dispersed local patches of trees varying in micro-climate and other environmental factors. There are small, contiguous patches of good seed production in almost each region. Another important feature of the stochasticity of seed production is that seed dispersal is affected by the nutcracker, *Nucifraga caryocatactes* L., which leads to wide exchange of genetic material, and, consequently, to high ecological valency of the tree species. In sharp contrast to the typical strong antibiosis towards xylophagous insects: the trees apparently tolerate parasitic-commensal relationships with the seed and cone feeding species.

On the other hand, the plant is highly vulnerable to the attack of highly specialized insects. *Pinus pumila* cones, growing on the Kamtchatka Peninsula, are damaged by only two insect species--*Cecidomyia pumila* Mamaev et Efremova sp.n. (Diptera: Cecidomyiidae) and *Eupithecia abietaria* Goeze (Lepidoptera: Geometridae).

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

Seed Yields of *Pinus pumila*

Pinus pumila on the Kamtchatka Peninsula produces seeds along the whole altitudinal profile of its range, from the sea coast almost up to the timber-line (about 1350 to 1400 m. above sea level). It can occur practically in all sites (Fig. 1), if not overshadowed for more than 50 percent.

Cone size (length and diameter) declines with increasing altitude more definitely than their mass (correspondingly $r.l = -0.73$; $r.d. = -0.79$; $r.m. = -0.41$). Cumulative seed quantity increases very definitely with altitude ($r = 0.76$), mainly owing to increasing numbers of imperfect seeds. Seed output per cone (seed mass percent of cone mass) is practically invariable at each altitude ($r.o = -0.11$). Cone mass and seed quantity achieve their maximum between 300 and 700 m above sea level. Here one can observe the highest stability of crops and large numbers of mosaically dispersed patches of different seed producing levels. Mean characteristics of *Pinus pumila* seed production in central and eastern Kamtchatka (Table 1, data from 30 sites, confidence level 95 percent, coefficient of variation doesn't exceed 28 percent) are as follows: cone length = 42 mm (range: 25 to 62), cone diameter = 27 mm (range: 18 to 37), mean air-dry full cone mass = 7.3 g (range: 4.4 to 10.0), mass of a thousand of seeds--84.4 g (range: 52 to 116), percent of nuclei mass--48 to 54 percent. A typical cone includes about 45 seeds, about 39 (range: 26 to 52) seed scales, 11 (5 to 18) of which are undeveloped and don't contain seeds.

Conophagous Insects on *Pinus pumila* at Kamtchatka

Pinus pumila cones in general, for unknown reasons, are not damaged by a polyphagous cone feeders (at least not at Kamtchatka). This may be caused by specific physical and chemical characteristics of tree resin which is, in particular, a well-known defense for polyphagous xylobionts.

Biology of *Cecidomyia pumila* Mamaev et Efremova sp.n.

This insect was first recorded on *Pinus pumila* by L.S. Efremova in 1969, but serious difficulties in collecting adults and other reasons prevented it from being described as a new species until 1990. The description has been made by B.M. Mamaev (in press). The species has never been recorded on

Table 1. Average properties of *Pinus pumila* cones at different altitudes in the central and eastern Kamtchatka

Cone trait	Height above sea level--m											
	4	200	400	400	600	650	700	750	900	940	950	1,000
CM	5.7	5.6	6.7	9.0	9.4	10.0	9.3	9.0	6.6	4.4	5.8	5.7
SMP	44	45	43	49	45	43	51	55	50	42	46	32
SSS	35	26	42	31	38	43	43	52	42	38	39	40
SWS	12	6	12	5	10	13	18	14	12	10	12	11
SQT	26	27	40	42	50	46	45	68	54	47	47	50
SMT	73	100	84	116	94	100	109	78	67	52	75	65

Note: CM - cone mass, g; SMP - yield (seed mass percent from cone mass), %; SSS - seed scale quantity; SWS - quantity of the scales without seeds; SQT - seed quantity in a cone; SMT - mass of seed thousand, g; (data are taken from various parts of the central and eastern Kamtchatka)

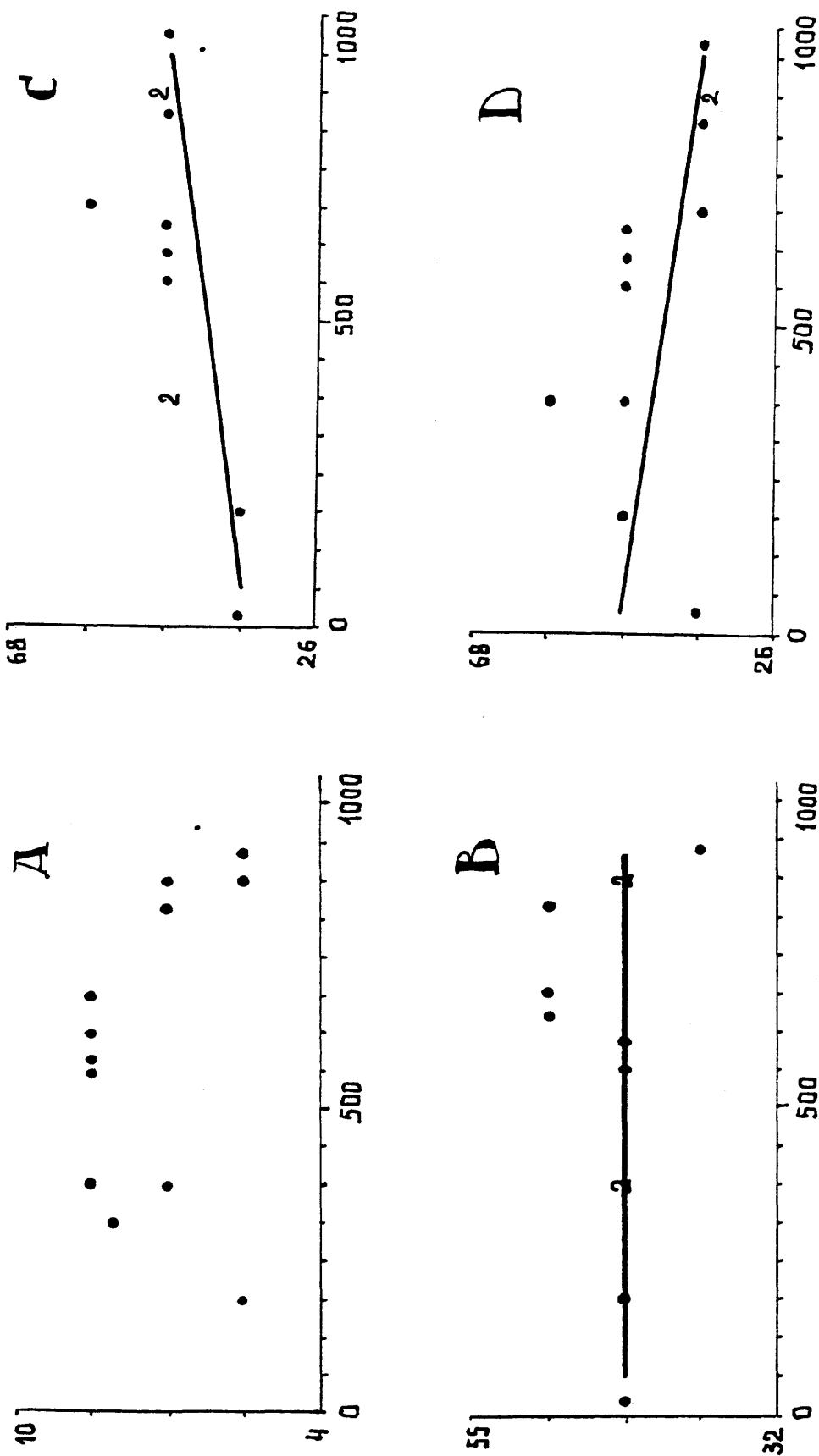


Figure 1. Seed production dynamics in changing ecotope disposing altitudes (combined data from various parts of Kamtchatka Peninsula). Horizontal axis - height above sea level, m. Vertical axis - (A) cone mass, g.; (B) seed yield, %; (C) seed quantity in a cone; (D) thousand nuclei mass, g.

other Kamtchatka conifers. Flying imago appear in the early July and can be rarely seen in the early September even though you can find young and mature larvae in the same cone. Insects feed on the first-year cones where adults usually lay about 1 to 5 eggs. In the case of abundant crop, about 70 percent of cones are occupied by one larva, 20 percent by two, and 10 percent by three larvae. It has been noticed that in 50 percent of cases, insects occupy the middle part of the cone, in 30 percent of cases--the upper, and in 20 percent--the lowest part. After the hatching a larva bores into the seed scale causing the appearance of resin drops on scale surface or between the scales which serve as galls. The resin spots are quite visible, and the next year the cone damage is clearly indicated by the surface deformation and retarded development of some seed scales. Larvae leave the cones in the middle of August and pupate in the soil litter. The insect has a one generation per year. The adult has an orange body, with dark thorax and dark, almost black eyes. Male body length is about 2 to 3 mm, that of female--3 to 5 mm, the length of wings and legs is about 3 and 5 mm, respectively. Male antennae are about half as long as the body. In the laboratory, adults live for about 2 days, both with and without food. Insects don't like bright light, they usually die under the lamp heat and prefer semi-shadowed sites. Larvae of this genus have cherry-orange or red-orange color, and are 3 to 4.5 mm long and 1 to 1.5 mm thick. The pupal stage takes about 4 to 5 days in laboratory conditions at room temperature.

Biology of *Eupithecia abietaria* Goeze.

This species was first recorded on the Kamtchatka Peninsula by L.A. Ivliev and D.G. Kononov (1962). It has not been recorded on other conifers (*Larix kamtchatica*, *Picea ajanensis*). This fact and some other reasons cause us to suspect that the Kamtchatka population of *Eupithecia* is a new species because *Eupithecia abietaria* is well known throughout the palearctic as an oligophagous insect of conifers (Stadnitsky et al. 1978). Adults fly from the middle of June, larvae appear in the middle of July. Insects feed on the second-year cones. In the year of large crop, a cone is occupied by one larva, but in the year of low crop--by two or three larvae. Damaged cones are easily distinguished by visible holes and abundant excrements. Larvae feed on seed scales, cone stem, etc., but never on mature seeds. They pupate in soil litter in September, and the pupa overwinters. The insect has one generation per year.

Seed Damage by Insects

Cecidomyia pumila occupies about 70 percent (50 to 100) of *Pinus pumila* first-year cones in various sites and altitudes (Table 2).

Table 2. *Cecidomyia pumila* occupation of *Pinus pumila* cones at central and eastern parts of Kamtchatka peninsula

Cone trait	Height above sea level--m						Mean
	5 ¹	100 ²	400 ²	600 ³	950 ³	1000 ²	
Percent damaged	60-100	50-70	50	65	100	60	70

Note: Sites: ¹ - sea shore; ² - subcontinental climatic conditions;
³ - continental climatic conditions (all within the Kamtchatka).

All estimates are certainly rough because of great variety of habitat conditions, weather, and crop yield. Nevertheless, two features were revealed. Firstly, cone damage by *Cecidomyia pumila* varies insignificantly between sites. Second, in the many moderately shaded sites both on the seashore and continental climatic conditions, in spite of altitude, the cone damage is substantial in nearly all cases. *Cecidomyia pumila* larvae destroy seed scales thus preventing normal seed development without their direct injury to seeds. Defective seed quantity often amounts 20 to 30 percent in a cone. But it has been demonstrated that the mean seed quantity in normal and deformed cones appeared to be the same. Neither are mean cone diameter and length seriously influenced by the insect injury. *Eupithecia abietaria*, in contrast as has been stressed above, occupies cones during the second summer, in the final 2 to 3 months of cone development. Very often it chooses cones previously damaged by *Cecidomyia pumila*. The occupation rate is significantly lower than of the previous species and varies from 5 to 10 percent in the year of large crops to 40 percent in the years of low crop. *Eupithecia abietaria* prefers plains and foothill sites, being rather rare in middle and high mountain sites, i.e. in the main *Pinus pumila* habitats. Its injury does not significantly influence the seed output and cone size.

CONCLUSION

Perhaps the main conclusion is that neither insect species damages seeds directly and hence cannot seriously influence the seed yields despite their high level of cone occupation. Assuming coevolution between producer and consumers, we believe that those cone feeders demonstrate both parasitic and commensal relations with the host plant as a whole: parasitic relations prevailing in the case of *Cecidomyia pumila* and commensal one prevailing in the case of *Eupithecia abietaria*. In general, the tree species show sharp antibiosis towards all insects, and only resin-gall species *Cecidomyia pumila* has managed to overcome this threshold very successfully. The main thing is that neither this nor the second cone feeding species causes significant injury to the seeds and therefore does not influence tree fitness. Taking into account the origin of *Pinus pumila* in unfavorable and even extreme abiotic conditions, it is not surprising to see the host specific gall-forming insect being the only one which is apparently fully adapted. Here we see support of the "harsh environment" hypothesis (Fernandes and Price 1988), which states that harsh environments favor the evolution of gall-forming plant-insect relationships probably due to hydrothermal stresses facing herbivores. The "harsh environment" hypothesis seems to favor other kinds of concealed feeders, e.g. xylophages *Urocus gigas* L. (Hymenoptera, Siricidae) and *Pissodes gyllenhali* Gyll. (Coleoptera, Curculionidae) which feed in dying trunks in the mountain habitats. We admit that *Pinus pumila* is a young species and hence coadaptation with its herbivores and plant neighbors is far from complete.

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