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The level of abundance of *Phytodietus griseanae* Kerrich
(Hym. Ichneumonidae) determined by its host *Zeiraphera diniana*
Guenée (Lep. Tortricidae) at high altitude¹

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In the Alps the optimum developmental zone of the larch bud-moth, *Zeiraphera diniana* GUENÉE, is located above 1600 m a.s.l. Its population densities in this zone increase by 20-30 thousandfold within 4 to 6 years and decline during the following 3 to 4 years. Visible damage occurs during 2-3 years only, when needles are destroyed and the colour of the trees turns to brown in July. The feedback mechanisms responsible for these population changes are not fully understood, but larval competition for food and space seems to play a major role. The significance of the large complex of natural enemies associated with the different stages of the moth (about 95 parasitoids and various predators) remains to be defined.

The most common parasitoid of *Z. diniana* during the last phase of population increase of the host and the beginning of population decline is the ichneumonid *Phytodietus griseanae* KERR., which attacks the 4th and 5th larval instars. The degree of parasitization by *P. griseanae* is locally rather high (60%), and because of this the parasitoid has often been considered to have a great impact on the population dynamics of the moth. Recent investigations show, however, that its role in the changes from increase to decrease of *Z. diniana* population densities seems to be of little significance. It even appears that there is a form of regulation action by the host on the parasitoid which is much stronger than that of the parasitoid on its host. When host abundance approaches the level of visible damage, the reproductive capacity of the parasitoid is affected and its population densities decrease at a rate greater than that of the host.

Phytodietus griseanae KERRICH is a larval ectoparasitoid of the larch bud-moth, *Zeiraphera diniana* GUENÉE. In the optimum developmental zone of its host, which is located above 1600 m in the Central European Alps, *P. griseanae* is univoltine and almost monophagous. Its adults emerge in June and the average longevity of the females is about one month. The females feed exclusively on the haemolymph of the host larvae. This feeding activity may be so important that host larvae are killed; in this way *P. griseanae* acts on the population of *Z. diniana* also as a predator, especially during the preoviposition period which lasts about one week. In cage experiments 30% of the larvae were killed by feeding. The fecundity of *P. griseanae* is 40 to 50 eggs in captivity, but it varies considerably, particularly in relation to host density; it is higher when host density increases and this tendency can also be observed under natural conditions. Eggs are laid on the thoracic segments of 4th and 5th instar larvae. When the first egg has been deposited, the females may return to the same host and lay a second egg. Therefore, there is often superparasitism, although only a single parasitoid is able to develop beyond the 1st larval instar. Besides normal eggs which produce males and fe-

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males, *P. griseanae* deposits eggs which have an abnormal chorion and do not hatch. The proportion of such abnormal eggs increases with the degree of superparasitism. Part of the eggs hatch when the parasitized host larva is still on the tree, but larval development of the parasitoid normally occurs in the upper layer of the soil where the host descends to pupate. The mature larvae of the parasitoid diapause from September to the following spring (RENFER, 1975 a, b).

At high altitude *P. griseanae* is considered as the most important parasitoid at maximum density of the host (culmination phase) and of the beginning of the phase of density decline (regression phase) (BALTENSWEILER, 1958). When host population densities are the lowest, it becomes rather rare and its action is taken over by three Eulophids (Fig. 3) (AESCHLIMANN, 1969). *P. griseanae* possesses several attributes which are typical for an efficient parasitoid, as for instance its ecological needs which are very similar to those of *Z. diniana*, its ability to overcome unfavorable situations through egg retention, an increase in fecundity with increasing host density and its predaceous behavior, especially during its preoviposition period. Unfortunately it has other characteristics which hinder its efficiency, as for instance the lack of discrimination between parasitized and unparasitized hosts, its monovoltinism, and a sex-ratio always below 0.5 (RENFER, 1975 b). Several of these characteristics have been investigated in relation to the cyclic change of the host population density and the results obtained are reported in this paper.

METHODS

Most of the experiments have been carried out in the Upper Engadine Valley, Switzerland, at an altitude of 1750 to 2100 m a.s.l. In addition, observations on *P. griseanae* were made in the larch forests of Brienz (1300 m), of the southern slopes of the Simplon Pass (1500–1750 m) and in the Goms Valley (1400 m and above) (all areas in Switzerland), and in the Briançonnais (France) (fig. 1). These localities and the methods used for the experiments have been described by RENFER (1975 b).

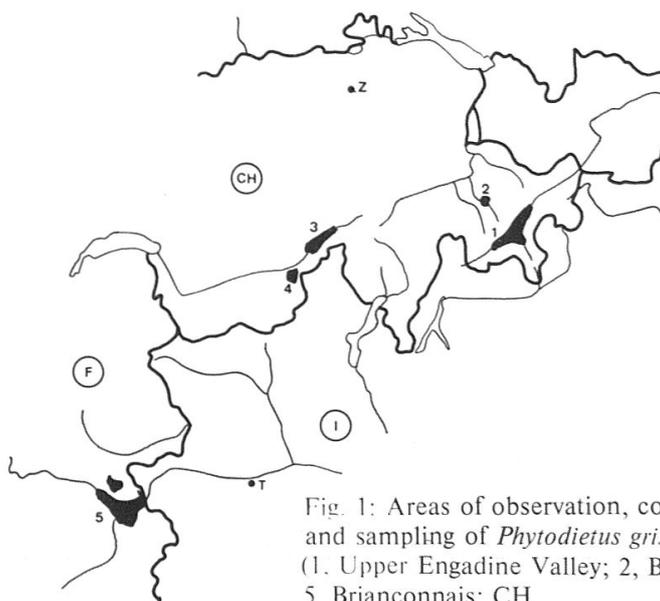


Fig. 1: Areas of observation, collection and sampling of *Phytodietus griseanae* and its host, *Zeiraphera diniana* (1. Upper Engadine Valley; 2, Brienz; 3, Goms Valley; 4, Simplon area; 5, Briançonnais; CH, Switzerland; F, France; I, Italy; z, Zürich).

RESULTS

Parasitoid-host synchronisation at the level of their populations

P. griseanae parasitizes 4th and 5th instar larvae. The latter are attacked during the feeding active phase only, which is completed about one week before they descend to the ground for pupation. *P. griseanae* rarely oviposits on mature host larvae (1% in 1972 and 1973). Eggs which are deposited too late do not hatch before pupation of the host and are pulled off with the exuvia of the 5th instar larva. As a consequence the embryo dies. The behavior of *P. griseanae* is therefore adjusted to the host development in such a way as to minimize losses of progeny.

In the Upper Engadine Valley parasitization of *Z. diniana* by *P. griseanae* starts in July when about 1/3 of the host larval population has reached the 5th instar and some time before the first host pupae appear. As the average longevity of the females is 33 ± 3 °C (laboratory tests, 50 individuals), the degree of synchronization between the oviposition period of the parasitoid and the vulner-

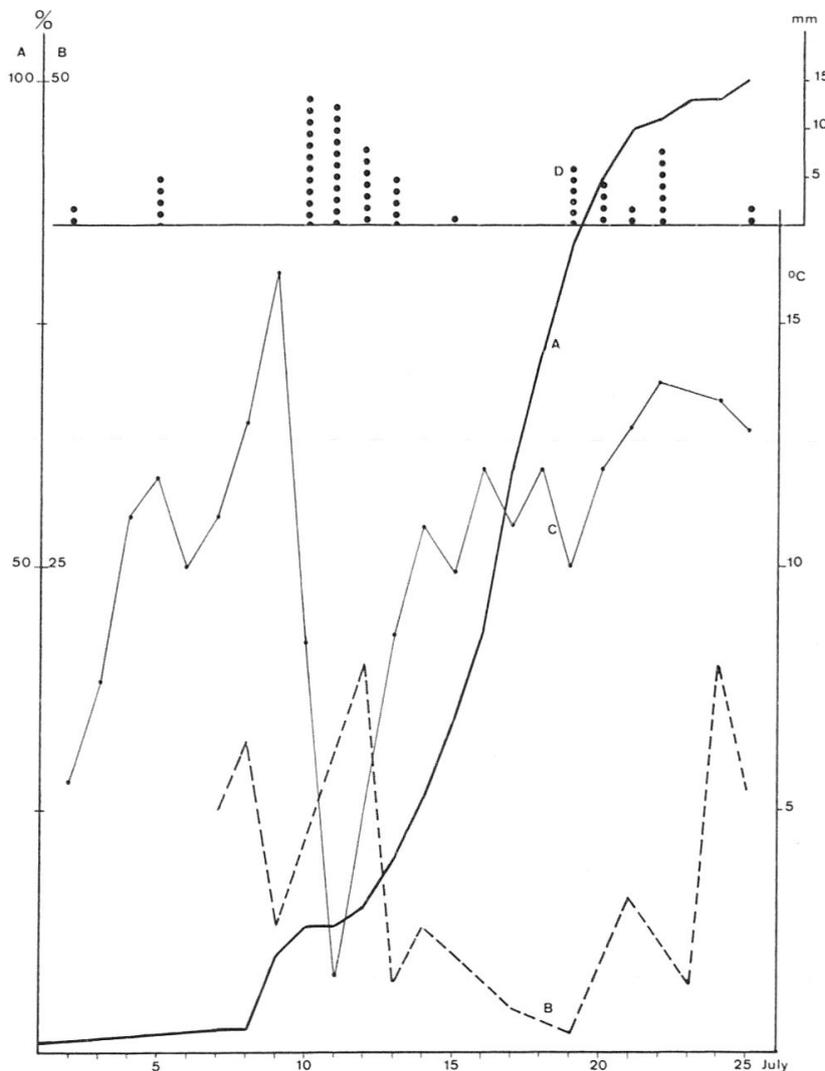


Fig. 2: Rate of parasitization by *Phytodietus griseanae* and larval development of *Zeiraphera diniana* in relation to the climatic conditions at Godin-Pontresina (Upper Engadine Valley) in 1972 (A, cumulative curve for 1196 L₅ of *Z. diniana* fallen to ground; B, rate of parasitization; C, mean daily temperature; D, daily precipitation).

able stages of the host appears to be high. Climatic factors, particularly precipitation (rain or snow) and the associated decline in temperature which are commonplace at high altitude, may modify considerably the degree of synchronization. At a temperature below 10 °C the parasitoid activity ceases whereas the host, whose developmental zero is near 7 °C (BALTENSWEILER, 1966), continues to develop. The parasitization of *Z. diniana* by *P. griseanae* in relation to climate was studied in 1972 in Godin near Pontresina on mature host larvae descending to the ground for pupation (fig. 2). The period of cold weather from 9 to 13 July had a catastrophic effect on parasitization but practically no effect on the activity of the host larvae (curves B and A respectively).

The influence of the stage of the host cycle on the development of P. griseanae

The increase in population density of *Z. diniana* in the optimum developmental area has consequences on the vitality of the species itself (BENZ, 1974; VAČLENA, 1975). When density approaches the threshold at which damage becomes visible (browning of larch trees, about 100 3rd to 4th instar larvae per kg of needle-bearing branches) the intraspecific competition for food and space modifies important biological parameters, as for instance fecundity, longevity, sex-ratio and flight capacity. These parameters are correlated with the pupal weight. The latter decreases progressively with the intensification of the damage and shows the lowest values one generation after maximum population density (1955, 1964, 1974).

The decrease of host pupal weight has consequences on the populations of *P. griseanae*. A morphometric study of the parasitoid males of the first and second generation after host maximum population density (1964 and 1965) reveals that

Table 1: Morphometric study of the males of *Phytodietus griseanae* during the first two years of host population density decline in the Upper Engadine Valley (1964: 123 males; 1965: 71 males).

Origin of the material	Length of thorax (incl. propodeum)		Length of first abdominal segment	
	1964	1965	1964	1965
	+1 ¹	+2 ¹	+1 ¹	+2 ¹
S-chanf	61.61	61.03	25.99	24.77
Sils	59.25	53.15	25.67	24.52
Upper Engadine Valley ²	61.39	56.33	23.90	23.83
Analysis of variance for the interaction of origin and stage of the cycle, F calculated				
		3.17	5.11	
(F _{tab} 0.05=2.29)				

¹ = reference code of AESCHLIMANN (1973): +1 means one generation after density peak of *Z. diniana* in the cycle.

² = localities other than S-chanf and Sils.

there is a reduction of the parasitoid size (table 1). The analysis of variance indicates that for the characters used - length of the thorax and of the first abdominal segment - the difference is significant for the interactions of the origin of the material and the stage of the cycle ($P < 0.001$ in 1964 and $P < 0.05$ in 1965). Because of the small number of females obtained during the above mentioned years or in 1974 and 1975 (same stage of the host cycle), a statistical analysis was not possible. However, dissections of small females which issued from hosts at the beginning of the population density decline revealed a high incidence of atrophied ovaries.

The influence of host «quality» and density of parasitization by, and survival of, P. griseanae

Cage experiments (RENFER, 1975 a, b) were carried out to determine whether host «quality» (i.e. hosts from different stages of the cycle) and host density have an effect on the rate of parasitization by *P. griseanae*, and on the survival of the parasitoid during its larval development. It was expected that the rate of parasitization of 4th instar host larvae collected at the Simplon area and at the Montgenèvre Pass (= second generation of density decline of the host population) and reared on food from the same locality would be different than that of larvae from localities where population density was still increasing (i.e. Brienz). The parasitoids

Table 2: Variation of the rate of parasitization by *Phytodietus griseanae* in relation to the host density and the stage of the host cycle (host larvae caged at 4th instar of development).

Origin of the material and stage of the cycle ¹	Number of replications	Equivalent density of host larvae in nature	Rate of parasitization in %	Larval mortality of <i>P. griseanae</i> ²
Brienz (-2) ³	15	80/kg	50.7	60.3
Godin (-1) ⁴	10	"	51.0	62.3
God God (0) ⁴	16	"	43.8	57.4
Sils (+1) ⁴	10	"	53.1	77.1
Simplon (+2) ⁵	15	"	44.3	75.0
Brienz (-2)	15	600/kg	42.2	49.5
Godin (-1)	10	"	47.7	44.5
God God (0)	15	"	30.1	48.5
Sils (+1)	12	"	41.5	44.6
Montgenèvre (+2) ⁶	14	"	25.7	39.9

¹= reference code of AESCHLIMANN (1973): 0 means maximum density of *Z. diniana* in the cycle.

²= in % of the parasitized larvae of *Z. diniana*.

^{3,4,5,6} see fig. 1 (4 = Upper Engadine, 6 = Briançonnais area)

used were obtained from hosts collected in areas which did not yet show any visible damage by *Z. diniana*; they could therefore be considered as efficient. The results obtained (table 2) prove that the stage of the host cycle doesn't influence the rate of parasitization significantly, although there is a greater numerical response at the 600 larvae level than at that of 80 larvae. Furthermore, the rate of parasitization doesn't increase indefinitely with increasing host density. At a density equivalent to 600 larvae per kg larch branches, the rate of parasitization is significantly ($P < 0.05$) lower than at a density of 80 larvae per kg of needle-bearing branches. The same is true for the mortality of the parasitoid larvae (difference significant at 1‰ level), which seems to be correlated with the increased predation by *P. griseanae* adults at lower host densities. It appears therefore that the rate of parasitization is not influenced by the quality of the host larvae and that the parasitoid seems to be unable to fully exploit the high host densities (up to 717 larvae per kg larch branches – see table 8, God Averts 1973) which are present in many larch stands at the culmination of the cycle.

The influence of host «quality» and density on superparasitism by P. griseanae

The rate of superparasitization indicates the number of hosts which have been parasitized twice or more in relation to the total number of parasitized hosts.

Table 3: Variation of the rate of superparasitization by *Phytodietus griseanae* in relation to the stage of the host cycle.

Origin of the material	Stage of the cycle ¹ and year	Number of host larvae examined	Rate of parasitization in %	Rate of superparasitization ²
Upper Engadine	0 1954	234	9.4	10.0
"	+1 1955	201	31.0	17.6
"	+2 1956	218	31.9	26.1
"	0 1963	2642	18.7	8.9
"	-2 1971 ³	2195	0.61	7.1
"	-1 1972	9798	0.73	8.7
"	0 1973	12025	6.24	5.3
"	+1 1974	1826	21.68	47.4
"	+2 1975	133	11.10	
Simplon	0 1971	289	25.6	1.4
"	+1 1972	108	21.3	34.8
"	+2 1973	206	27.2	64.7

¹= reference code of AESCHLIMANN (1973): 0 means maximum density of *Z. diniana* in the cycle.

²= in % of the rate of parasitization.

³= 1971 to 1975 in selected biotopes (see table 7).

Superparasitism by *P. griseanae* is observed during the whole cycle of the host. Its rate is rather low during the phase of host population density increase until the appearance of the damage to the larch trees and increases rapidly during the phase of host density decline. Its maximum is observed in general 2 generations after host density peak, when the host population density is about 1 larva per kg of needle-bearing branches with needles (table 3). In the following generation it is no longer possible to collect enough material for the comparison of data.

The influence of host «quality» and density on sex-ratio of P. griseanae

When host larvae are offered continuously to females of *P. griseanae* in captive rearings, the sex-ratio of the progeny remains almost constant, and is near 0.35. This value is influenced very little by variations of host densities and is obtained under natural conditions when parasitoids are reared during the last phase of host population increase (RENFER, 1975 b). When host larvae are offered discontinuously (1 day out of 4) the sex-ratio increases up to a maximum of 0.52.

The sex-ratio increases with the age of the female. Young females produce twice as many males as females, while in females older than 10 days this relationship is reversed. This occurs independently of the continuous or discontinuous offering of host larvae.

The sex-ratio varies during the cycle of the host. Table 4 summarizes all the data obtained from the Upper Engadine Valley, the Simplon area, the Goms Valley and the zone of Montgenèvre during the last two cycles of the host. It is clear that the phase of the host population density decline is characterized by a decrease of the sex-ratio down to 0.25 one generation after host density peak and to 0.15 two generations after the same peak. The increase of the rate of superparasitism during the phase of host density decline is perhaps one of the most important phenomena contributing to the decrease in the sex-ratio of *P. griseanae*, as it is shown in table 5. Although the difference between successive sex-ratios are not significant, there is a clear tendency in sex-ratio decrease which drops from 0.46 (monoparasitism) to 0.11 (5 eggs/host larva). It could not be established whether the decrease of the sex-ratio is due to a differential mortality at the larval stage of the parasitoid, e.g. the elimination of the female larvae in superparasitized hosts, like in *Bracon hebetor* SAY (BENSON, 1973), or simply to arrhenotoky. It is only possible to say that the decrease of the sex-ratio is not related to the size of the host (which tends to decrease as the host population declines) as shown by PURINGTON & ULEMAN (1972) for the chalcid *Hyssopus thymus* GIRAULT. To know whether host size influences the sex ratio of *P. griseanae*, 3rd, 4th and 5th larvae from areas with host peak densities were parasitized and reared separately. The results are summarized in table 6 and demonstrate that *P. griseanae* doesn't select bigger larvae in which to deposit fertilized (i.e. female generating) eggs.

The influence of forest stand type on the total rate of parasitization of Z. diniana, and on parasitization by P. griseanae

The development of the total rate of parasitization of *Z. diniana* and of the rate caused by *P. griseanae* were studied during 5 years in 4 to 6 forest stands of 2 to 4 ha size each, located in the Upper Engadine Valley between 1750 and 2100 m of altitude. To appreciate the influence of environmental factors on the action of

Table 4: Variation of the sex-ratio of *Phytodietus griseanae* in relation to the stage of the host cycle.

Stage of the cycle ¹	Composition of the progeny		
	♀	♂	sex ratio
-2	33	56	0.37
-1	98	223	0.30
0	557	874	0.39 ^a
+1	240	705	0.25 ^b
+2	18	104	0.15 ^c

¹ = reference code of AESCHLIMANN (1973): 0 means maximum density of *Z. diniana* in the cycle.

^{a to c} = differences significant between a and b ($P < 0.001$) and between b and c ($P < 0.05$).

Table 5: Variation of the sex-ratio of *Phytodietus griseanae* in relation to superparasitism.

Degree of super-parasitization ¹	Number of replications	Composition of the progeny		
		♀	♂	sex ratio
1 (parasitism)	612	201	237	0.46
2 eggs/host	361	41	71	0.38
3 eggs/host	286	20	35	0.36
4 eggs/host	35	4	20	0.17
5 eggs/host	13	1	8	0.11

¹ = "abnormal" eggs were not considered.

Table 6: Variation of the sex-ratio of *Phytodietus griseanae* in relation to the parasitized host stage and size.

Parasitized host stage	Host number	Sex ratio of the progeny of <i>P. griseanae</i>
L ₃ (small)	38	0.30 ^a
L ₄ (medium)	145	0.22 ^a
L ₅ (large)	208	0.38 ^a

^a = differences not significant.

Table 7: Main characteristics of six forest stands in the Upper Engadine Valley where the development of parasitism by *Phytodietus griseanae* was followed from 1969 to 1976.

Localities ¹	Altitude in m	Stand composition			Exposure	Forest stands	Understory
		Larch	Norway spruce	Arrolla pine			
Pradatsch (Madulain)	1750-1850	5/10	4/10	1/10	NW	predominatly small trees	shrubby
Morteratsch (Pontresina)	1860-1950	6/10	1/10	3/10	SW	predominatly small trees	shrubby
God-God (S-chanf)	1950-2100	6/10	1/10	3/10	SE	old big trees widely spaced	shrubby
God Averts (Zuoz)	1760-1900	10/10	-	-	NW	young small trees, dense	shrubby
Sils-Schadenherd (Sils)	1850-1900	10/10	-	-	SE	old big trees widely spaced	pasture
Christolais (Samedan)	1900-2040	10/10	-	-	SE	old big trees dense	pasture

¹= in brackets the name of the village where stands are located.

P. griseanae, the stands were selected taking into account their composition and exposition (table 7).

The results obtained are summarized in table 8 and concern the period of maximum density of the host cycle (from 2 years before to 2 years after density peak). First of all it appears that the rate of total parasitization (incl. all larval and larvo-pupal parasitoid species attacking *Z. diniana*) is not influenced either by the stand composition (pure larch stand - mixed stand) or by the altitude. Not even the age, the size and the density of the trees, the type of understory vegetation and the exposure seem to influence the rate of total parasitization, although in stands with old, big, widely spaced trees, shrubby understory and SE exposure (God-God and Sils, table 7 and 8: 1972, 1973, 1975) larvae of *Z. diniana* seem to be more heavily parasitized than in stands with other characteristics. Secondly, table 8 shows the importance of *P. griseanae* in relation to the other parasitoids attacking larvae of *Z. diniana*. Whatever the characteristics of the stands may be, the relative importance of *P. griseanae* increases - although weakly - with the density of the host (1971 to 1973) and may locally exceed 90% (God Averts, 1973). It then decreases from 1974 or 1975 with the host density decline.

PRESENCE OF *P. GRISEANAE* IN THE HOST CYCLE

The relative abundance of the larval and larvo-pupal parasitoids of *Z. diniana* for the period 1969 to 1975 and for the localities mentioned in table 7 is illustrated in fig. 3. The relative abundance of the Eulophids (A, 3 species) decreases with the increase of the host population density (1969 to 1973) and increases when the host population density declines (1973-1975). The relative abundance of the ichneumonids (D and E) develops in the opposite way and increases from less than 10% to more than 80%, its maximum coinciding with the host density peak. The same trend may be observed for the relative abundance of *P. griseanae* (E) which reaches its maximum (nearly 60%) at host density peak (1973) and/or one year later. It appears, therefore, that within the parasitoid complex attacking larvae or pupa of the larch bud-moth, *P. griseanae* is the most important entomophagous species when host densities approach the damage threshold which is about 100 larvae per

Table 8: Development of the rate of parasitization by *Phytodietus griseanae* in six forest stands of the Upper Engadine Valley from 1971 to 1975 and importance of *P. griseanae* in relation to the larval and larvo-pupal parasitoid complex associated with *Zeiraphera diniana* (A, density of 5th instar larvae of *Z. diniana* per kg twigs; B, rate of total parasitization of *Z. diniana* in %; C, relative importance of *P. griseanae* in % of B).

Localities (Table 7)	1971 (-2)			1972 (-1)			1973 (0)			1974 (+1)			1975 (+2)		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Pradatsch	4.6	8.2	10	76.4	16.2	3.2	506.1	7.2	55.4	109.6	49.4	27.9	3.5	46.2	20
Morteratsch ¹	4.1	0.9	0	26	2.3	0	80.7 ²	7.5	10	166.6	23.3	80.8	3.1	42.1	25
God-God	8.3	0.4	0	201.6	8.9	0	374.1	17.5	49	28.4	52.1	66.2	2.8	88.2	20
God Averts	7.6	2.5	60	243.2	13	27.9	717.9	8	92.1	abandoned			abandoned		
Sils-Sch.	40.7	18.8	7	570.4	0.4	47.1	435.9 ³	22.2	60.9	24.6	46.7	31.4	1.9	90	0
Christolais	29.8	1.6	6.7	192.4	2.6	1.9	384.4	10.4	28.8	37.6	40.1	36	11.3	57.4	34.3

¹= after 1973: Alp Staz, about 6 km W-direction.

²= late fluctuation type of *Z. diniana*, one generation in arrear (1973 = -1, 1974 = 0) (BALTENSWEILER et al., 1977).

³= early fluctuation type of *Z. diniana*, one generation in advance as compared with other stands (1972 = 0, 1973 = +1).

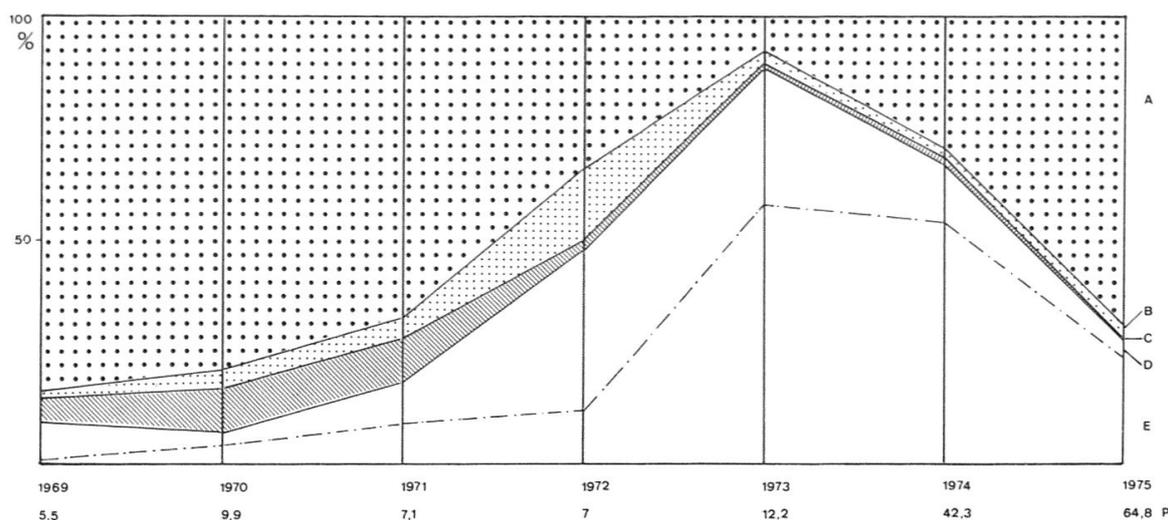


Fig. 3: Relative abundance of the parasitoids attacking the larvae of *Zeiraphera diniana* in 6 localities of the Upper Engadine Valley during 7 years of the host cycle (1973 = maximum density of the host) with particular reference to *Phytodietus griseanae* (A, Eulophids; B, Tachinids; C, Braconids; D, Ichneumonids, excl. *P. griseanae*; E, *P. griseanae*; P, rate of total parasitization in %).

kg of needle-bearing branches (average of 2 larvae per m branches). The complex of *P. griseanae*-Eulophidae (3 species) is responsible for 40 to almost 90% parasitization of the *Z. diniana* population during the entire fluctuation cycle.

In the localities mentioned in table 7 the rate of total parasitization increased from 5.5% in 1969 to 12.1% in 1973 (host peak density), then to 42.3% in 1974 (5 localities only), 64.8% in 1975 and 60% in 1976 (4 localities only, J.-R. HERREN, pers. comm.). The rate of parasitization by *P. griseanae* increased by 4 fold in one host generation when host density begins to decline (1974). This tendency was not restricted to the mentioned localities, but could be observed everywhere in the Upper Engadine Valley and in the Simplon area (table 9) and can be retraced on the basis of previous publications and observations (BALTENSWEILER, 1958 and pers. comm.; AESCHLIMANN, 1965, 1969 and pers. comm.). The rate of parasitization by *P. griseanae* increases considerably at host density peak when the host reproduction rate is already tending to decrease (table 9, 3rd column) and doubles (1964) or triples (1955) or even quadruples (1974) during the first year of host density decline.

The increase of the rate of parasitization of *Z. diniana*, and especially that attributable to *P. griseanae* and (later) the Eulophids, is determined by the numerical relation between parasitoids and host which is favorable to the parasitoids beginning from the last host generation of population density increase (1954, 1963, 1973). The high rate of parasitization by *P. griseanae* remains then more or less constant as long as the host density doesn't decrease beyond 2 or 3 larvae per kg branches, i.e. during the first, or the first 2 host generations of the phase of host density decline. When the host density falls below 2 or 3 larvae per kg of needle-bearing branches, *P. griseanae* populations crash and the parasitoid almost disappears.

The densities of the viable eggs of *P. griseanae* per 1 kg of needle-bearing branches (= base for *Z. diniana* densities) give a better idea of the relationship between the parasitoid and its host during the phase of maximum host densities. With these values (table 9, 6th column) it is possible - using the life-tables of RENFER (1975 b) - to estimate the number of *P. griseanae* females per kg branches

Table 9: Density of the populations of *Phytodietus griseanae* in the Upper Engadine Valley (UEV) (1954-1975) and in the Simplon area (1971-1973).

Locality and year	Density of <i>Z. diniana</i> ¹	<i>P. griseanae</i>						
		Rate of parasitization in % ²	Degree of superparasitization ³	Rate of abnormal eggs ⁴	Density of viable eggs ⁵	Rate of survival ⁶	Density of females ⁵	Mean fecundity of females ⁷
UEV								
1954	331.76	9.4	1.15	6.79	33.422	11	3.6 (1955)	12.7 (1955)
1955(+1)	126.54	31	1.35	13.04	45.864	5.7	2.6 (1956)	3.3 (1956)
1956	21.28	31.9	1.69	21.26	8.862	5.7 ⁹	0.5 (1957)	1.6 (1957)
1957	2.25	25.5	2.25	31.30	0.881			
1958	0.085							
1959	0.080							
1960	0.37							
1961	1.64							
1962	22.88							
1963	248.82	18.7	1.09	5.23	48.065	11	5.2 (1964)	14.7 (1964)
1964(+1)	184.27	36.1	1.35 ⁸	13.04 ⁸	78.092	5.7	4.4 (1965)	0.33 (1965)
1965	3.12	34.4	1.69 ¹⁰	21.26 ¹⁰	1.43	5.7 ⁹	0.08 (1966)	
1966	0.02	1.5			0.001			
1967	0.002	0.6			0.001			
1968	0.06	?						
1969	0.20							
1970	2.67	0.81	1.01	3.27	0.021	?	0.003 (1971)	30.67 (1971)
1971	14.16	0.61	1.07	4.76	0.092	?	0.015 (1972)	112 (1972)
1972	225.01	0.73	1.14	6.54	1.68	16	0.27 (1973)	94.44 (1973)
1973	400.83	6.24	1.08	5	25.50	11	2.81 (1974)	6.33 (1974)
1974(+1)	73.04	21.08	1.32	12.50	17.79	5.7	1.01 (1975)	0.55 (1975)
1975	4.52	11.10	1.40	21.26 ¹⁰	0.553	5.7 ⁹	0.03 (1976)	0.17 (1976)
1976	0.05	6.60	2.25 ¹¹	31.30 ¹¹	0.005			
Simplon								
1971(+1)	321.11	25.6	1.02	3.65	79.61	5.7	8.7 (1972)	4.5 (1972)
1972	50.4	21.3	1.36	13.14	12.57	?	0.7 (1973)	3.1 (1973)
1973	6.58	27.2	1.52	15.75	2.26	?	0.13 (1974)	

¹= number of larvae per kg larch branches with needles: data from AUER (1976) until 1969, from selected biotopes (table 7) after 1970

²= multiparasitism of Eulophids not included

³= mean number of eggs of *P. griseanae* per host larva

⁴= in % of all eggs deposited

⁵= per kg of needle-bearing branches (calculated)

⁶= from egg to adult stage, females only (RENFER, 1976)

⁷= only viable eggs considered

⁸= taken from 1955

⁹= as for preceding generation (5.7)

¹⁰= taken from 1956

¹¹= taken from 1957

Table 10: Comparison of the rates increase of *Zeiraphera diniana* and *Phytodietus griseanae* during parts of the cycle in the Upper Engadine Valley (UEV) and in the Simplon area.

Localities and years	Stage of the cycle ¹	<u>Z. diniana</u>		<u>P. griseanae</u>	
		Density of larvae ²	Rate of increase	Density of viable eggs	Rate of increase
UEV					
1954	0	331.76	0.38	33.42	1.37
1955	+1	126.54	0.17	45.86	0.19
1956	+2	21.28	0.1	8.86	0.1
1957	+3	2.25		0.88	
1963	0	248.82	0.75	48.06	1.62
1964	+1	184.27	0.016	78.09	0.02
1965	+2	3.12	0.006	1.65	0.0006
1966	+3	0.02		0.001	
1970	-3	2.67	5.3	0.021	4.38
1971	-2	14.16	15.89	0.092	18.26
1972	-1	225.01	1.78	1.68	15.18
1973	0	400.83	0.18	25.5	0.7
1974	+1	73.04	0.06	17.79	0.031
1975	+2	4.52	0.011	0.563	0.009
1976	+3	0.05		0.005 ³	
Simplon					
1971	+1	321.11	0.15	79.61	0.16
1972	+2	50.40	0.13	12.57	0.18
1973	+3	6.58		2.26	

¹ = reference code of AESCHLIMANN (1973): 0 means maximum density of *Z. diniana* in the cycle.

² = per kg larch branches with needles (according to AUER, 1976, until 1966; from selected biotopes - table 7 - after 1970).

³ = rate of superparasitization and rate of abnormal eggs unknown, taken from 1975 (table 9).

of the following year and also the mean fecundity per female. It appears clearly that the fecundity of *P. griseanae* decreases considerably beginning from the host density peak and that the highest density of *P. griseanae* females exists only at host density peak and one host generation later (table 9, 8th and 9th column). The rate of increase of *P. griseanae* develops more or less in the same way as that of its host (table 10).

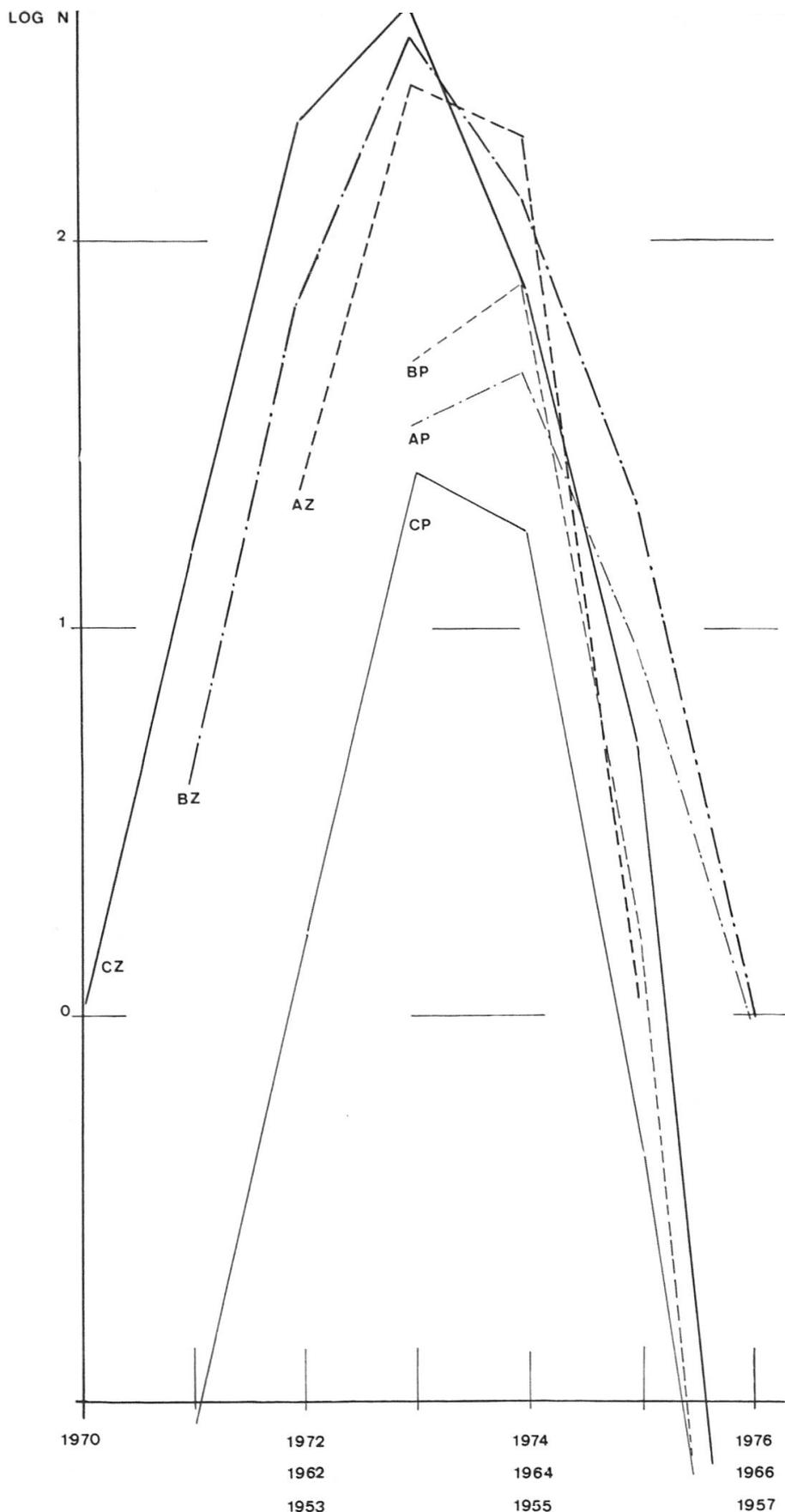


Fig. 4: Development of the densities of the populations of *Zeiraphera diniana* and *Phytodietus griseanae* in the Upper Engadine Valley during the last phase of population density increase and the beginning of the subsequent decline (N = number of larvae of *Z. diniana* [Z] and of L_5 with viable eggs of *P. griseanae* [P], both per kg of needle-bearing larch branches; A, B and C = phases of population density increase and decline culminating respectively in 1954, 1963 and 1973 for the host, and in 1955, 1964 and 1973 for the parasitoid).

DISCUSSION

The cyclic change of the population densities of *P. griseanae* is modelled on that of its host, *Z. diniana* (fig. 4). The amplitude of the cycle remains, however, unknown because the densities of the parasitoid populations can not be estimated with enough accuracy at lowest host densities. The rate of parasitization of *Z. diniana* (either by the total complex attacking host larvae or by *P. griseanae* only) is almost negligible (table 9 and fig. 3) as long as the rate of increase of the host remains high; it tends to augment as soon as the host enters a stress situation (fig. 4: 1953-4, 1962-3, 1972-3), i.e. at host density peak, and becomes gradually more important at the beginning of the phase of host density decline. The first major conclusion is that the density of the host plays a minor role in the build-up of the parasitoid populations. This is confirmed by cage experiments (table 2) and also by observations in Val Aurina (Italy) where the *Z. diniana* population density remained almost stationary (4 to 7 larvae per kg of needle-bearing branches) during 4 years without any remarkable increase of the rate of parasitism (OMLIN & HERREN, 1976). In 1971 the density of *Z. diniana* (L₅) in selected biotopes (table 7) of the Upper Engadine Valley was 14.16 and the rate of parasitization by *P. griseanae* 0.61%, in 1972 the corresponding values were 225.01 and 0.73%.

A second conclusion is that the development of *P. griseanae* populations appears to be entirely conditioned by the physiological status of its host. This can best be followed by comparing the densities of the two species (viable eggs for *P. griseanae* and larvae for *Z. diniana*) before and after host density peak (fig. 4). However, for this comparison it is necessary to make a time adjustment of the two curves as the densities of viable eggs of *P. griseanae* (reported in table 9, 6th column) refer to the parasitoid females issued from the preceding host generation. In other words, the density estimation of the *P. griseanae* population at the egg stage has not to be related to the parasitized host generation, but to the preceding one which has influenced the preimaginal stage of the parasitoid. If this delayed influence of the host is taken into account it will be easy to note on fig. 4 that the stress situation, in which the host happens to be when visible damage on larch appears, has immediate repercussions on the rate of increase of the parasitoid. The curves AP, BP and CP of fig. 4 should therefore be moved left by one year in order to place the densities of the parasitoid and of its host in a position which is correct from a standpoint of population dynamics. The deterioration of the environment (food and possibly space) which play an essential role in the cyclic change of the population densities of *Z. diniana* (BALTENSWEILER *et al.*, 1977) is largely (may be entirely) responsible for the fluctuation of *P. griseanae* population densities. Because of the inability of the parasitoid to build up important populations during the phase of host density increase and the existence of feedback mechanisms induced primarily by the deterioration of the environment, *P. griseanae* seems to be of little value in the biological control of *Z. diniana* in the optimum zone of development of its host.

RESUME

Induction de la gradation de *Phytodietus griseanae* KERRICH (Hym. Ichneumonidae) par son hôte *Zeiraphera diniana* GUENÉE (Lép. Tortricidae) en haute montagne.

La zone optimum de développement de la Tordeuse grise du mélèze, *Zeiraphera diniana* GUENÉE, se situe dans les Alpes au dessus de 1600 m d'altitude. Dans cette zone les densités des popu-

lations de la Tordeuse augmentent de 20 à 30 mille fois en 4 à 6 ans et diminuent ensuite pendant environ 4 ans. Lorsque les densités sont les plus élevées les dégâts se manifestent par un brunissement des mélèzes en plein été. La période des dégâts visibles ne dure que 2 à 3 ans. Les mécanismes de feedback de la gradation sont encore assez mal compris, mais il semble que la compétition des chenilles pour la nourriture et l'espace joue un rôle déterminant. Le rôle que joue le complexe des nombreux antagonistes (environ 95 parasitoïdes et nombreux prédateurs) associés aux différents stades de développement de la Tordeuse reste à préciser.

L'Ichneumonide *Phytodietus griseanae* KERR. est le parasitoïde de *Z. diniana* le plus commun en phase de progression-culmination. Il attaque les chenilles de 4e et 5e stade. Le degré de parasitisme est assez élevé (60%) par endroit et le parasitoïde est censé avoir une influence sur la dynamique des populations de son hôte. Son action n'est toutefois pas responsable du retour des populations de *Z. diniana* aux faibles densités. Il apparaît même que la gradation du parasitoïde est calquée sur celle de l'hôte et induite par ce dernier, c'est-à-dire que l'action régulatrice de l'hôte sur le parasitoïde est beaucoup plus forte que celle du parasitoïde sur son hôte. Lorsque la phase de progression de *Z. diniana* approche du seuil des dégâts visibles, la capacité de reproduction du parasitoïde s'affaiblit en même temps que celle de l'hôte et le taux de diminution des densités de ses populations est même plus élevé que celui de son hôte.

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