

# *r*- and *K*-selection in soil ciliates: a field and experimental approach

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Summary. Previously published field studies have suggested that the concept of r/K selection may be applied to terrestrial ciliates. A census was taken of the dominant groups, the Colpodea and Polyhymenophora, to determine species composition and absolute abundances in climatically unpredictable alpine and predictable lowland sites. In addition, two typical representatives of each of the two taxa (Colpoda aspera and Grossglockneria acuta, and Blepharisma undulans and Gonostomum affine, respectively) were selected for examination under laboratory conditions. Variables investigated were: the C/P index (ratio of Colpodea to Polyhymenophora), fertility, tolerance of altered environmental conditions, incidence in predictable or unpredictable biotopes, opportunism, competitive ability, and body size. Our own observations were supplemented by reference to the literature.

The field census produced a higher C/P index in the unpredictable sites than in the predictable ones. The experiments show that C. aspera and G. acuta are less sensitive to changes in temperature and exhibit a more rapid rise in individual density as well as a higher number of individuals than do B. undulans and G. affine, although the former species have longer generation times at low temperatures. The explosive increase in number of individuals can be ascribed to the special reproductive strategy of the Colpodea (quadripartition in cysts). These results imply that the Colpodea are more r-selected as compared with the Polyhymenophora. That might be an explanation for their wide distribution and high density in unfavourable terrestrial habitats.

No data have previously been available concerning r- and K-selection among soil ciliates. Investigations of some limnic species demonstrate that the concept of r/K-selection does apply to ciliates (Gill 1972; Gill and Hairston 1972; Luckinbill and Fenton 1978; Luckinbill 1979; Taylor 1981, 1983). For soil testaceans, Schönborn (1983) developed an interesting new approach; he classified some species according to four types of strategy. It is not difficult to relate these categories to the r/K continuum (Pianka 1972, 1976). His "optimal type" corresponds to K-selected, his "productive" and "retarded types" to r-selected species.

Field investigations by Foissner (1981, 1985), Foissner et al. (1984) and Petz et al. (1985) have suggested that soil

ciliates also show features of r/K-selection. In colpodid ciliates *r*-selection is indicated by their frequent incidence in extreme and unpredictable habitats (Bamforth 1980; Foissner 1981; Petz et al. 1985) and their special strategy for reproduction and survival (Burt et al. 1941; Wenzel and Meier-Tackmann 1975; Foissner and Didier 1983). For the Polyhymenophora, on the basis of the publications cited, one would expect *K*-selection.

Re-examination of our earlier field data, supplemented by laboratory experiments on two colpodid and two polyhymenophoran ciliate species, has now verified this hypothesis.

#### Materials and methods

#### Source of material and cultivation of specimens

Blepharisma undulans Stein, 1867 (Polyhymenophora, Fig. 1): alluvial soil from the Tullnerfeld, Austria, ca. 180 m  $NN^{1}$  (Foissner et al. 1984). Cultivated as polyaxenic pure culture in lettuce medium (Committee on Cultures 1958) with 3 crushed wheat grains to support bacterial growth. Despite several attempts, no monaxenic culture succeeded.

Gonostomum affine Stein, 1859 (Polyhymenophora, Fig. 2): alpine brown earth from the Schlossalm near Bad Hofgastein, Austria, ca. 1,900 m NN. Culture as for *B. undulans*.

*Colpoda aspera* Kahl, 1926 (Colpodea, Fig. 3): alpine brown earth from the Stubnerkogel near Bad Gastein, Austria, ca. 1,900 m NN (Foissner and Peer 1984). Cultivated as monaxenic culture in lettuce medium with *Escherichia coli* as food bacterium. Every 2 days 1 ml saturated bacterial suspension per 30 ml culture medium was provided (Proper and Garver 1966).

*Grossglockneria acuta* Foissner, 1980 (Colpodea, Fig. 4): spruce forest soil near Aigen-Schlägl, Austria, 540 m NN. Pure culture in Knop solution, with fungal hyphae (*Mucor mucedo*) as food supply (Petz et al. 1985).

All species were raised as clone cultures in the dark. Growth rate as a function of temperature was determined in petri dishes, each containing 30 ml medium for *B. undulans*, *G. affine*, and *C. aspera*, and 15 ml medium for *G. acuta*.

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<sup>&</sup>lt;sup>1</sup> NN = Normalnull; i.e., above mean sea level by the Amsterdam standard



Figs. 1–4. Living appearance of experimental species: 1 Blepharisma undulans, Right lateral view; 2 Gonostomum affine, Ventral view; 3 Colpoda aspera, Right lateral view; 4 Grossglockneria acuta, Left lateral view. Fig. 4 from Petz et al. (1985)

#### Experiments

Temperatures employed were 5° C, 10° C,  $21 \pm 2^{\circ}$  C, and 30° C. For each species and temperature three dishes were inoculated from cultures in the log phase (Browning et al. 1952). The density at inoculation was 1 individual per ml. Every 1–3 days a count was made of 1 ml of the cultures.

Since the shortest generation times occured within the first 3 days after inoculation, the medium was not renewed. The daily shock of fresh medium might well affect the results more than a non-constant medium would (Taylor 1981). Besides, the non-renewed medium may approach the natural conditions in the soil more closely. The generation times we observed are roughly consistent – as far as comparisons are possible – with the data of other authors (Giese 1973; Proper and Garver 1966).

The division rate r was calculated by the formula r = g/t, where  $g = (\log N_1 - \log N_0)/\log 2$  or  $g = (\log N_1 - \log N_0)/\log 4$ , depending on whether bipartition (*B. undulans, G. affine*) or quadripartition (*C. aspera, G. acuta*) occured. Here g = number of divisions in time t,  $N_0 =$  number of individuals at time  $t_0$ ,  $N_1 =$  number of individuals at time  $t_1$ . The generation time d is the reciprocal of r (Vater-Doberstein and Hilfrich 1982).

## Field studies

Investigations took place in 1977–1982 (sites F, G), 1980–1982 (sites A–E, H), and 1982 (site I). From sites A–E 10 samples each were taken; from F and G, 8 each; from I, 3 each; all at 0–10 cm soil depth.

Species and individual numbers were ascertained by the culture method of Buitkamp (1979) and the petri-dish method of Foissner and Peer (1984). These counts were used to calculate the ratio of Colpodea to Polyhymenophora, the C/P index.

Sites in Tullnerfeld (lower Austria):

A) Xerothermic site, Althann. Soil type: brown alluvial soil. Humus type: mor. Vegetation: dry grassland (*Xerobrome-tum*). Average (=av.) soil water content 22%. Av. summer temperature 16.5° C. 180 m NN

B) Xerothermic site, Vogelsang. Soil type: brown alluvial soil. Humus type: mull. Vegetation: *Xerobrometum*. Av. soil water content 19%. Av. summer temperature 16.5° C. 190 m NN

C) Dry oak-beech forest, Baumgarten. Soil type: decalcified loose-sediment brown earth. Humus type: morish mull. Vegetation: *Asperulo-Fagetum*. Av. soil water content 25%. Av. summer temperature 16.5° C. 260 m NN

D) Bottom land, Althann. Soil type: gray alluvial soil. Humus type: mull. Vegetation: *Phalaris arundinacea-Phragmites australis-Salix alba* community. Av. soil water content 37%. Av. summer temperature 16.5° C. 180 m NN

E) Bottom land, Vogelsang. Soil type: gray alluvial soil. Humus type: mull. Vegetation: *Phalaris arundinacea-Urtica dioica-Salix alba* community. Av. soil water content 42%. Av. summer temperature 16.5° C. 180 m NN

Sites in the Austrian Alps (Grossglockner region):

F) Cushion-plant level, Hochtor/Nord. Soil type: alpine rendzina. Humus type: mor. Vegetation: Cushion-plants. Av. soil water content 40%. Av. summer temperature 4.5° C. 2,500 m NN

G) Alpine grassland, Wallackhaus. Soil type: alpine pseudogley. Humus type: mull-like mor. Vegetation: *Caricetum curvulae*. Av. soil water content 38%. Av. summer temperature 4.5° C. 2,300 m NN

Sites H and I:

H) "normal sites" A–E, Tullnerfeld (see above)

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Figs. 5–8. Growth curves at various temperatures. 5a Blepharisma undulans: 5° C, 10° C. 5b Blepharisma undulans: 21° C, 30° C. 6 Gonostomum affine: 10° C, 21° C. 7a Colpoda aspera: 5° C, 10° C. 7b Colpoda aspera: 21° C, 30° C. 8a Grossglockneria acuta: 5° C, 10° C. 8b Grossglockneria acuta: 21° C, 30° C. Figure 8a, b from Petz et al. (1985)

I) 5 high alpine pasture sites at the Stubnerkogel (Central Alps, Austria). Soil type: alpine pseudogley. Humus type: mull-like mor/mor. Av. summer temperature 4.5° C. 1,800 m NN

More detailed soil and vegetation data are given by

Foissner (1981), Foissner and Peer (1984), and Foissner et al. (1984).

On the basis of the climatic factors and the vegetation, A–E can be classified as "temperate or predictable" sites and F and G as comparatively "extreme or unpredictable"

Table 1. Boo	ly size, shorte	t generation tim	e, and maxima	l individual c	density at	5° C,	10° C.	, 21°	C and 3	0° C <sup>a</sup>
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Species	Size $(\bar{x})^{\circ}$	Shortest	Shortest generation time (h)				Max. individual density (ml <sup>-1</sup> )				
	(n = 10)	5° C	10° C	21° C	30° C	5° C	10° C	21° C	30° C		
Colpoda aspera	28×18.3	19.2	14.2	9.6	4.1	35,700	37,500	29,500	5,840		
Grossglockneria acuta <sup>b</sup>	$40.1 \times 16.3$	35.8	18.2	4.8	3.8	12,900	1,500	3,200	3,900		
Blepharisma undulans	$170.4 \times 51.2$	11.5	11.5	8.9	7.2	120	1,200	9,300	4,200		
Gonostomum affine	$64.5 \times 16.5$	Death	13.4	10.6	Death	0	2,300	3,800	0		

<sup>a</sup> Arithmetic mean of 3 replicates

<sup>b</sup> From Petz et al. (1985)

<sup>c</sup> Measurements from protargol impregnated specimens

Table 2. Air temperature and relative humidity, measured daily at Salesen Station (Stubnerkogel), representative for sites I, and Langenlebarn Station, representative for sites A–E. All values from 1977

Month	Air tempe	Air temperature (in 0.1° C)							Relative humidity (in %)						
	Salesen			Langenlebarn			Salesen			Langenlebarn					
	$V_{\min}$	V <sub>max</sub>	V	V <sub>min</sub>	V <sub>max</sub>	V	V	Min	Max	V	Min	Max			
7	57.8	34.8	52.2* 41.5** 39.0***	18.2	11.3	14.4* 17.3** 16.3***	21.4* 30.6** 26.8***	43 34 40	98 99 99	13.0* 35.9** 30.2***	59 28 30	98 93 96			
8	46.4	39.9	46.3 44.3 40.3	22.6	14.8	17.3 17.7 16.5	24.2 32.7 28.4	40 26 35	97 93 94	8.2 24.2 16.4	77 38 52	98 87 95			
9	149.2	68.2	112.8 78.3 91.5	52.8	33.1	46.3 35.4 35.6	26.4 37.4 29.0	25 23 34	98 98 98	8.7 27.7 17.7	64 35 52	99 99 96			
10	103.1	45.5	70.3 47.2 55.8	42.7	27.5	33.5 29.0 32.8	46.4 47.3 39.9	14 17 22	96 93 95	6.3 25.5 16.5	77 41 48	99 99 96			

V =coefficient of variation

 $V_{\min(\max)} =$  coefficient of variation of a month's minima (maxima)

Measured at: \* 7 h; \*\* 14 h; \*\*\* 19 h

sites (Table 2). By the same criteria, biotopes A–C are more unpredictable than D and E, because they are subject to more pronounced aperiodic desiccation.

## Results

The generation times, as expected, become shorter the higher the temperature (Table 1). However, the highest temperature employed is above the optima of the species; at 30° C the populations never achieve high densities and soon collapse (Figs. 5b, 7b, 8b). For G. affine this temperature is lethal. It is evident from the growth curves and the maximum numbers of individuals at  $5^{\circ}$  C and  $10^{\circ}$  C that B. undulans is less well adapted to low temperatures than C. aspera and G. acuta, which reach the highest densities of individuals at these temperatures, although population growth is slow (Figs. 5a, 7a, 8a; Table 1). G. affine behaves about the same at 10° C as at 21° C, but at 5° C it dies within a day (Fig. 6, Table 1). At almost all temperatures C. aspera and G. acuta reach considerably higher densities than B. undulans and G. affine (Table 1). The densities always become maximum later in the polyhymenophoran species than in C. aspera and G. acuta (Figs. 5-8). The colpodid species exhibit an explosive increase in individual numbers at 21° C, though this is followed by a rapid collapse of their populations (Figs. 7b, 8b).

The field censuses indicate relative dominance of Colpodea in the "unpredictable" sites A-C, F, G, and I. The C/P index for sites A-C is 0.92 for species numbers and 5.58 for individual numbers; the corresponding values for sites F and G are 5.25 and 44.18. Thus, the dominance of colpodid ciliates is most conspicuous in the alpine soils. The temperate sites D and E, on the other hand, favor the polyhymenophoran species (C/P = 0.67 and 0.53, respectively, Fig. 9). When the data from all the "normal" sites are combined, the C/P values obtained are 0.55 for species and 3.84 for individuals. Comparison with five "extreme and unpredictable" biotopes in the Austrian Alps, together designated I, again shows that alpine soils contain relatively more colpodid ciliates than do more climatically moderate biotopes (C/P=0.79 for species and 8.75 for individual numbers, Fig. 9, Table 2).

## Discussion

C. aspera and G. acuta meet many of the criteria for rstrategists. In comparison, B. undulans and G. affine fit several of the known requirements for K-selection (MacArthur



**Fig. 9.** Ratio of Colpodea to Polyhymenophora at different sites and climates. A-E: Sites-Tullnerfeld, "comparatively predictable", A-C are more "extreme" than D and E, because they desiccate aperiodically. F, G: Alpine sites – Grossglockner region, "comparatively unpredictable". H: Sites A-E combined. I: 5 alpine sites – Stubnerkogel. Values <1 indicate dominance of polyhymenophoran species (dotted area). SM = soil moisture

and Wilson 1967; Pianka 1970, 1972, 1976; Southwood et al. 1974; Luckinbill 1979).

*Reproduction strategy. C. aspera* and *G. acuta* divide in cysts which produce four individuals (Petz et al. 1985). By this means they soon reach high densities of individuals despite their relatively long generation time (Table 1). At 21° C their populations rapidly overshoot the equilibrium point, oscillate for some time, and then quickly collapse or encyst (Figs. 7b, 8b). This is a strategy that offers a good alternative to that of "equilibrium strategists", given high individual densities and the consequent opportunity for expansion in an open system (Taylor 1981). The polyhymenophorans can be considered rapidly growing ciliates, for their size (Table 1), as is also indicated by the very small micronuclei relative to the size of the animal (Taylor 1981): ca. 1  $\mu$ m in *B. undulans*, and ca. 2  $\mu$ m in *G. affine* (Figs. 1, 2). Since they reproduce only by bipartition, they are inferior to the colpodid ciliates with respect to fertility.

Tolerance to changed environmental conditions. C. aspera and C. acuta adapt well to changed temperatures, whereas B. undulans and G. affine adapt poorly (Figs. 5–8, Table 1). This is an astonishing finding in the case of G. affine, because this is a very common and widespread soil ciliate (Foissner 1981). Giese (1973) reports a low tolerance of B. undulans with respect to temperature changes, toxic substances, and antibiotics. By contrast, the studies of K racht (1982) on Colpoda cucullus show broad limits with respect to pH and high salinity.

Incidence. According to Southwood et al. (1974), the selection type of a species is determined by the predictability and permanence of a habitat. Successful K-strategists are found in temperate, uniform habitats, whereas r-strategists tend to inhabit ecosystems with variable climate, less intense competition, and more free resources, whereby periodic recolonization after severe disturbances is required (McNaughton 1975). The findings of Buitkamp (1979), Münch (1970), Kracht (1982), and Foissner et al. (1982) show that higher population densities of the colpodids Cyrtolophosis and Colpoda develop only under extreme environmental conditions, when competition is reduced. The results of our field studies are consistent with these findings (Fig. 9).

*Competitive ability*. Very rapid population growth is negatively correlated with competitive ability (Luckinbill 1979). Therefore in homogeneous habitats, where the ability of individual organisms to compete is decisive, the Colpodea give way to the Polyhymenophora (Fig. 9). In soil samples that are air-dried and re-moistened, colpodid ciliates appear after only a few hours (Buitkamp 1979). Not until some days have elapsed do polyhymenophoran species appear (mainly hypotrichs), and crowd out the Colpodea (Foissner unpublished). The experiments of Maguire (1963) and Münch (1970) also indicate that the Colpodea are not vigorous competitors. The hypothesis that *K*-strategists are better competitors than *r*-strategists, regarded as controversial in some quarters (Pianka 1970; Gill 1972; Luckinbill 1978; Taylor 1981), is thus supported by our results.

*Body size. B. undulans* and *G. affine* are larger than the colpodid species (Figs. 1–4). This observation can certainly be generalized, for almost all terrestrial Colpodea are unusually small (Foissner 1985).

From the data presented here it can be concluded that the terrestrial Colpodea are more *r*-selected than the Polyhymenophora. Our results give no information as to whether soil ciliates in general are more *r*-selected than limnic ones. Since the C/P index is a measure of the characteristics of a habitat, it can usefully be employed as an indicator of the level of disturbance of a biotope. We hope to study this subject further in a later paper.

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Material and methods.

Saidy: Skiel's Studies were performed an several bouteher in the Republic of Punamir (Fig. 1). In the following carreler ence will be made to the locations accordup of the above viations given here.

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The composition of the entomolatura (e.g. Nentwig 1982b) and the previot of the entomolatura (e.g. Nentwig 1982b) 1965; Nytelef and Bensi 1978; Netheler 1982; Nentwig neri 1981; Nentwig 1982b) are well known the temperate zone. The math conclusion to be drawn are that size and available around the web. Most prey items are that size and the web has the effect of selecting the smaller insects from the available spectrum, while the spaller insects that the available spectrum, while the spaller insects the trace from the web catal. In generally phytophagous



# Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone

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Summary. The actual prey in the orb webs of four araneid spiders (Nephila clavipes, Eriophora fuliginea, Argiope argentata, and A. savignyi) and the relative abundance of their potential prey (pitfall traps, yellow traps, and sweep-netting) was investigated over 1 year at different locations in Panama. The relative abundance of insects and spiders depends on seasonal fluctuations (Fig. 2) which are reflected by corresponding variations in the effectiveness of the webs. The main prey groups are Nematocera (50%–68%), winged Formicoidea (6%-15%) and Hymenoptera, Coleoptera, and Brachycera (4%-10% each) (Fig. 4-6). The remaining 10%-17% of the prey comes from up to 26 other groups (Table 2). Differences in prey size and prey composition between the spider species are small (Fig. 7). Most prey items are 1-2 mm long: only a few insects exceed 30 mm body length (Figs. 9-12). Relative to the available prey, some groups (e.g. Nematocera, Aphidoidea, Psocoptera) are caught selectively, while other groups (e.g. Heteroptera, Coleoptera, Brachycera, Orthoptera) are underrepresented in the prey spectrum and obviously avoid orb webs (Table 7). The differences in prey composition between araneids of the tropics and of the temperate zone are discussed (Table 8) and compared to those recorded in other studies (Tables 9, 10). Most of these report large numbers of big prey items (Odonata, Lepidoptera, wasps/bees). It is pointed out that those studies do not take into account the total available prey in a spider's web but only that part which the spider selects from the web (mainly according to size). The importance of small prev items even for large spiders is explained and an obvious lack of niche partitioning among coexisting araneids is discussed (Table 11).

The composition of the entomofauna (e.g. Nentwig 1982b) and the prey of orb-weaving spiders and their webs (Kajak 1965; Nyffeler and Benz 1978; Nyffeler 1982; Nentwig 1983a), and also the distribution of insect size (e.g. Remmert 1981; Nentwig 1982b) are well known in the temperate zone. The main conclusion to be drawn are that size and prey composition in a spider's web depend on the insects available around the web. Most prey items are very small. The web has the effect of selecting the smaller insects from the available spectrum, while the spider itself selects the larger items from the web catch. In general, phytophagous and detritophagous insects are disproportionately represented in the web, while pollinating, predatory and parasitic insects avoid the web (Nentwig 1982a).

Corresponding data for the actual and potential prey of orb-weaving spiders of tropical countries is scarce and it is not clear whether or not the generalisations which have been derived from temperate-zone studies can be applied to the tropics. A few studies have been conducted on the prey of tropical orb-weaving spiders (Robinson and Robinson 1970, 1973; Shelly 1983), but those of Robinson and Robinson report high percentages of large insects (many wasps, beetles, butterflies, no midges) in the spiders' diet. The size of insects in the tropics has been investigated several times (Williams 1941; Janzen and Schoener 1968; Elton 1973: Janzen 1973a, b; Janzen et al. 1976): the most numerous are small arthropods. Various trapping methods (Smythe 1982; Erwin 1983; Sutton 1983) showed high percentages of Nematocera, Cicadina, Psocoptera, and other small insects in the entomofauna. The question arises: Do tropical Araneidae not catch these small insects? In order to answer this question a 1-year study in Panama was carried out on four araneid species at different locations. The potential prey of the spiders was established by means of extensive trapping using three different methods and was then compared to the actual prey of the spider according to size and composition. The following paper contains a discussion on the differences in prey composition between tropical and temperate-zone araneids.

## Material and methods

*Study sites*. Studies were performed at several locations in the Republic of Panama (Fig. 1). In the following text reference will be made to the locations according to the abbreviations given here.

1) On the access road (approx. 3 km in length) to Cerro Galera (CG), a hill near the Pacific Ocean, 5 subsites (CG 1 to CG 5) were selected, each about 20 m of road length (CG 1 behind the gate to CG, CG 5 at the summit).

2) Cerro Pelado (CP), a hill near Gamboa, with one access road (1 km long) to a transmitting station (CP 1) and another road (500 m long) to the watertank of Gamboa (CP 2).

3) Several study sites were selected on the first 8 km of Pipeline Road (PR), a road leading from Gamboa to the NE end of Lake Gatun.