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Cyanogenesis in *Ranunculus montanus* s.l. from the Swiss Alps

(*Cyanogenese bei Ranunculus montanus s.l. in den Schweizer Alpen*)

by

Regula DICKENMANN

Contents

1. Introduction

Polymorphism of cyanogenesis on population level was studied so far in only a few taxa (e.g. DADAY 1954a, b, 1965, JONES 1970, 1972, 1973, ARAUJO 1976, URBANSKA 1981, URBANSKA and WILDI 1975, URBANSKA et al. 1979). Relationships between phenotypic frequencies and edaphic factors still remain largely unknown. In some papers, the influence of soil moisture content was referred to (e.g. FOULDS and GRIME 1972a, b, ABBOTT 1981); on the other hand, a distinct influence of substratum type upon the polymorphism of cyanogenesis was described only in *Lotus alpinus* (URBANSKA 1979, 1982, URBANSKA and SCHWANK 1980).

As far as *Ranunculus montanus* s.l. is concerned, preliminary results of HEGNAUER (personal communication) suggested the existence of cyanogenesis polymorphism. The *R. montanus* group comprises several taxa, both diploids and tetraploids being reported (LANDOLT 1954, 1956, HESS, LANDOLT and HIRZEL 1970). As some taxa of *R. montanus* s.l. have distinct edaphic preferences (LANDOLT 1954, 1956, 1971, RUGGLI-WALSER 1976, DICKENMANN 1978, 1980), it was interesting to study cyanogenesis within this group. The geologically heterogenous alpine region of Davos (Grisons) was chosen as the study area. The *R. montanus* group is represented there by *R. grenierianus* Jord. (2n=16) and *R. montanus* Willd. s.str. (2n=32). The former taxon occurs only in acidic silicate soils; the latter one grows mostly in carbonate but occasionally also in acidic silicate substrates, where a unique micro-distribution pattern was found (DICKENMANN 1978, 1980). The present paper deals with cyanogenesis in the two taxa, studied both in rather well-spaced populations as well as in groups of colonies growing in a close neighbourhood.

Acknowledgements

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2. Material and methods

All the plants examined originated from natural populations occurring between 2300 and 2670 m a.s.l. in the region of Davos, on both sides of the Landwasser Valley; 10 - 15 individuals per colony were usually taken. Neighbouring colonies, sampled at intervals of about 50 m, were assigned to larger series, respectively coded as SG1 - SG12 (*R. grenierianus*), SM1 - SM5 (*R. montanus* s.str. from acidic silicate) and CM1 - CM13 (*R. montanus* s.str. from carbonate) (Table 1).

On the whole, 1004 individuals were studied. 384 plants corresponded to *R. grenierianus*, whereas 431 individuals represented *R. montanus* s.str. from carbonate and 189 *R. montanus* s.str. from acidic silicate (Tables 4, 5). A simple qualitative test was used to examine such a large number of plants. The standard sodium picrate paper test (MIRANDE 1909, DAWSON 1941) proved not to be very suitable for *R. montanus* s.l. on account of its rather low HCN content; for this reason, the FEIGL-ANGER test (FEIGL and ANGER 1966, TANTISEWIE et al. 1969) was chosen. This method is known to be very sensitive to low HCN concentrations, the lowest sensitivity level being about 2 mg HCN/kg fresh weight. The tests were carried out with about 0.5 g of fresh leaf blades, a sulfur - free toluene being used as the organic dissolvent. Only leaf blades of adult plants at reproducing or non-reproducing phase were examined. To avoid possible differences, due to seasonal and/or developmental variation, well developed leaves of about the same age were tested. The tests were carried out in 10 cm - long tubes with cork plugs; the test paper was suspended to avoid contact between the material and the paper strip. The tests were read after 24 h incubation at room temperature.

In the FEIGL-ANGER test, acyanogenic materials cause no change in the colourless paper strips, whereas cyanogenic phenotypes are indicated by various shades of blue. With help of a graded colour table, prepared at the Laboratory for Experimental Plant Systematics, University of Leiden, Netherlands, cyanogenic plants were assigned to four classes respectively codified as HCN(+), HCN+, HCN++, HCN+++ (Table 2).

Table 1. Origin of the material

Herkunft des Untersuchungsmaterials

Population Code	Station	Altitude m a.s.l	Exposition	Slope %	pH	Remarks
SG1	Jakobshorn	2550	ENE	60	4.5	grassy mounds alternating with SM1
SG2	Chilcherberg	2400-2450	SSE	30-50	4.0	
SG3	Rinerhorn	2460	NW	40	4.0	
SG4	Schwifurgga	2500	SW	45	-	near the boundary to carbonate
SG5	Erezberg	2350-2650	SW-SE	60	4.0	near carbonate
SG6	Geissweidengrat	2320	NE	-	-	
SG7	Vorder Latschüel	2420	S	40	5.0	near the boundary to carbonate
SG8	Jatzhorn	2650	S-SW	40-60	4.0	
SG9	Brämabüel-Jakobshorn	2460-2520	NE-W	40	4.0	
SG10	Bärgji	2320-2400	NE-E	30-40	4.0	
SG11	Weissfluhjoch	2620	SE	60		
SG12	Grüenturm	2360	SE	60	4.5	near the boundary to carbonate
SM1	Jakobshorn	2550	ENE	60	4.5	open scree slopes alternating with SG1
SM2	Chilcherberg	2400	SSE	5	4.0	depression with long-lasting snow cover
SM3	Wannengrat	2360	NE	50	5.0	open scree slope
SM4	V.Latschüel	2380	SE	10	4.0	long lasting snow cover
SM5	Dorftälli	2430	-	0	4.0	long lasting snow cover
CM1	Strela	2350	S	30-60	7.0	
CM2	Schwifurgga	2460-2560	E	50	7.0	open scree slope near the boundary to silicate
CM3	Mitteltälli	2600	S-SE	50	7.0	
CM4	Mitteltälli	2350	W	30	7.0	
CM5	Fanezfurgga (on both sides)	2500	E-W	40	7.0	
CM6	Alteiner, Fürggli,Strel	2490-2540	SE	10	7.0	
CM7	Valbellahorn	2580	SW	50	7.0	long-lasting snow cover
CM8	Uf em Tritt	2350	E	40	6.5	
CM9	Männli	2300-2480	SE	50	6.5	
CM10	Augstberg, Amselboden	2310-2400	SE-E	5-40	7.0	long-lasting snow cover
CM11	Alpli	2410-2480	E	30		
CM12	above Schrättenfluh	2510-2610	NE	40		
CM13	Casanna	2450	SE	50		exceptionally high content of clay

Table 2. FEIGL-ANGER test: Classification criteria and the corresponding codification of the material

FEIGL-ANGER Test: Klassifizierungskriterien und Kodifizierung des Untersuchungsmaterials

sample code	colour of the paper strip	approximate HCN content per kg fresh weight
HCN -	colourless	none
HCN(+)	only part of the paper coloured; light blue	2 - 5 mg
HCN+	light to medium blue	6 - 20 mg
HCN++	medium to deep blue	21 - 50 mg
HCN+++	the deepest blue	over 50 mg*

*The maximum HCN content in *R. montanus* s.l. was not investigated and further studies in this respect are required.

3. Results

3.1. *Global evaluation*

The studied material was first evaluated globally, the sole distinction being made between *R. montanus* s.str. and *R. grenierianus* with no regard to the actual origin of plants (Table 3). Only two gross phenotypes viz. acyanogenic and cyanogenic were taken into consideration.

Acyanogenic phenotypes largely prevailed in the material studied, both in *R. grenierianus* (92.2 %) and in *R. montanus* s.str. (75.2 %). On the other hand, three times more cyanogenic phenotypes were found in *R. montanus* s.str. than in *R. grenierianus* (24.8 % vs. 7.8 %).

The global evaluation seems to indicate a relationship between the taxa and the phenotypic frequencies. However, the two taxa have distinct edaphic preferences, *R. grenierianus* being confined to acidic silicate soils, whereas *R. montanus* s.str. most frequently occurs on carbonate. This fact was taken into consideration when further assessments were made, the studied samples from acidic silicate and carbonate being assigned to separate categories. In this approach, two kinds of evaluations were carried out:

a) No distinction was made between *R. montanus* s.str. and *R. grenierianus*, only substratum type being considered (Fig. 1).

b) In the samples from acidic silicate soils, *R. montanus* s.str. and *R. grenierianus* were evaluated separately, to get more definite patterns of behaviour (Fig. 2).

The results obtained indicate a strong influence of substrate upon the phenotypic frequencies in *R. montanus* s.l. (Fig. 1). Generally, acyanogenic phenotypes prevailed in samples from both substrates; in material from acidic silicate they were more frequent than in samples from carbonate. However, the occurrence of HCN-positive phenotypes was more positively pronounced in the material from carbonate than in the silicate samples (31.6 % vs. 9.1 %). Carbonate soils seem also to favour highly cyanogenic phenotypes (silicate samples 0.9 %, carbonate samples 15.8 %).

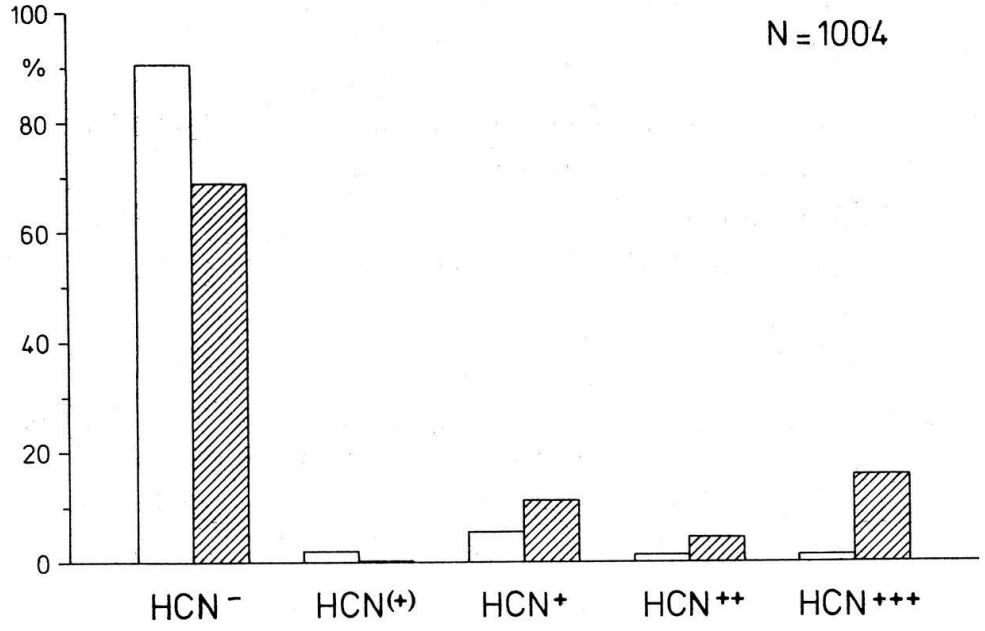

Fig. 1. Phenotypic frequencies in samples from acidic silicate (□) and carbonate (▨), no distinction between *R. grenierianus* and *R. montanus* s.str. being made.

Häufigkeit der Phänotypen in Proben von saurem Silikat (□) und Karbonat (▨) ohne Unterscheidung von R. grenierianus und R. montanus s.str.

Differences of phenotypic frequencies between *R. montanus* s.str. and *R. grenierianus* from silicate were in general negligible (Fig. 2).

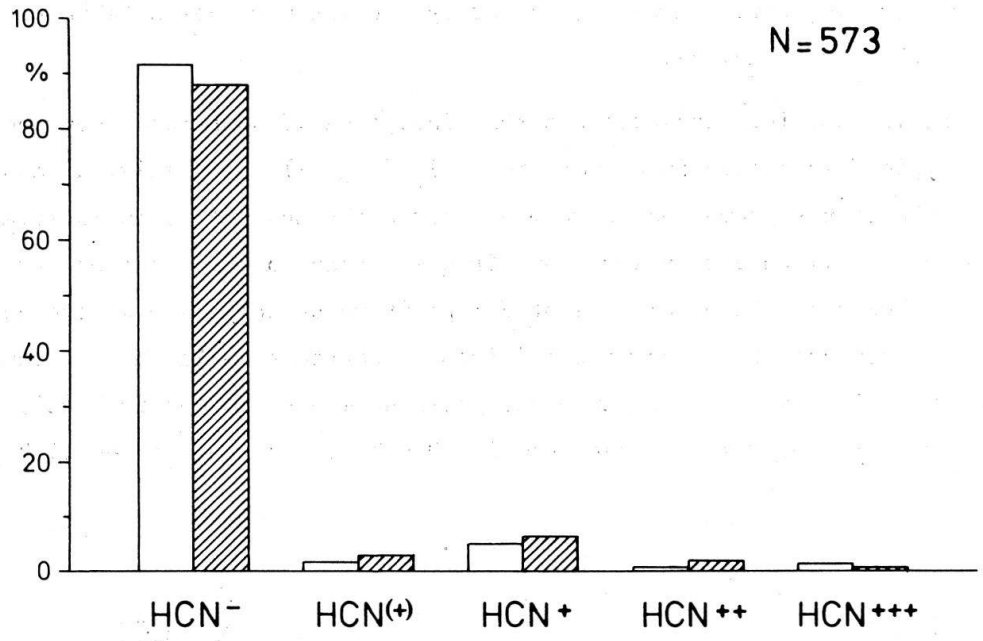

Fig. 2. Phenotypic frequencies in samples from acidic silicate

□ *R. grenierianus* (2n=16)

▨ *R. montanus* s.str. (2n=32)

Häufigkeit von Phänotypen in Proben von saurem Silikat

Table 3. Phenotypic frequencies in *R. grenierianus* (2n=16) and *R. montanus* s.str. (2n=32) without regard to substrate type.

Häufigkeit der Phänotypen bei R. grenierianus (2n=16) und R. montanus s.str. ohne Berücksichtigung des Substrattypes.

	R. grenierianus		*R. montanus* s.str.	
	Number of individuals	Frequency (%)	Number of individuals	Frequency (%)
acyanogenic	354	92.2	470	75.2
cyanogenic	30	7.8	155	24.8

3.2. *Variation on population level*

Both inter- and intrapopulational variation was found in the material studied from both substrates. It did not seem to be much influenced by differences in the sample size due to collective presentation of neighbouring colonies (see Table 1 and also the remarks on sampling methods).

As far as acidic silicate is concerned (Table 4), over 50 % of the investigated samples (total N = 17) were completely acyanogenic. The polymorphic samples were very variable, both as to the ratio: cyanogenic/acyanogenic phenotypes as well as to the particular frequencies of various cyanogenic types. Bar a single sample, however, a general trend towards low frequencies of HCN-positive individuals was observed. There

Table 4. Cyanogenesis polymorphism in population samples from acidic silicate

Polymorphismus in der Cyanogenese in Populationsproben von saurem Silikat

Sample code	N of sub-samples	Total sample-size	Cyanogenic plants N	Cyanogenic plants %	N of particular cyanogenic types HCN(+)	HCN+	HCN++	HCN+++
SG1	8	67	0	0	-	-	-	-
SG2	3	37	5	13.5	2	3	-	-
SG3	1	12	0	0	-	-	-	-
SG4	2	29	3	10.3	-	3	-	-
SG5	4	52	0	0	-	-	-	-
SG6	1	10	0	0	-	-	-	-
SG7	3	34	19	55.9	-	13	2	4
SG8	3	51	0	0	-	-	-	-
SG9	2	45	0	0	-	-	-	-
SG10	2	19	3	15.8	3	-	-	-
SG11	1	14	0	0	-	-	-	-
SG12	1	14	0	0	-	-	-	-
SM1	12	143	17	11.9	6	10	1	-
SM2	1	12	2	16.7	-	-	2	-
SM3	1	10	0	0	-	-	-	-
SM4	1	11	3	27.3	-	2	-	1
SM5	1	13	0	0	-	-	-	-
$\bar{x}$		33.7	3.1	9.1	0.7	1.8	0.3	0.3

Table 5. Cyanogenesis polymorphism in population samples from carbonate

Polymorphismus in der Cyanogenese in Populationsproben von Karbonat

Sample code	N of sub-samples	Total sample size	Cyanogenic plants N	Cyanogenic plants %	N of particular cyanogenic types HCN(+)	HCN+	HCN++	HCN+++
CM1	4	69	29	40.6	-	12	2	15
CM2	2	23	5	21.7	-	1	4	-
CM3	2	22	10	45.5	-	4	-	6
CM4	1	12	4	33.3	-	2	-	2
CM5	2	27	6	22.2	-	3	-	3
CM6	4	55	19	34.6	-	7	1	11
CM7	1	14	1	7.1	-	1	-	-
CM8	2	31	9	29.0	-	5	2	2
CM9	2	26	4	15.4	-	2	-	2
CM10	5	78	23	29.5	-	10	5	8
CM11	2	31	6	19.4	-	2	2	2
CM12	2	28	5	17.9	-	-	3	2
CM13	1	15	15	100.0	-	-	-	15
$\bar{x}$		33.2	10.5	31.6	0	3.8	1.5	5.2

was also a pronounced tendency towards a low HCN content: Strongly cyanogenic phenotypes not only represented a minor fraction of the studied material (altogether 5 individuals) but also were confined to two population samples.

All the 13 samples studied from carbonate (Table 5) comprised cyanogenic individuals in various proportions, low frequencies occurring rather seldom. As far as frequencies of particular cyanogenic types are concerned, the strongly HCN-positive phenotypes were largely prevailing. In this respect the material from carbonate positively differed from the samples collected upon acidic silicate.

3.3. *Examples of a small-scale variation pattern*

The results presented in former parts of the present paper indicate a pronounced general trend towards higher frequencies of cyanogenic phenotypes on carbonate vs. lower frequencies of HCN-positive individuals on acidic silicate. It is interesting to note that a small-scale distribution pattern of phenotypic frequencies not only corroborates the general

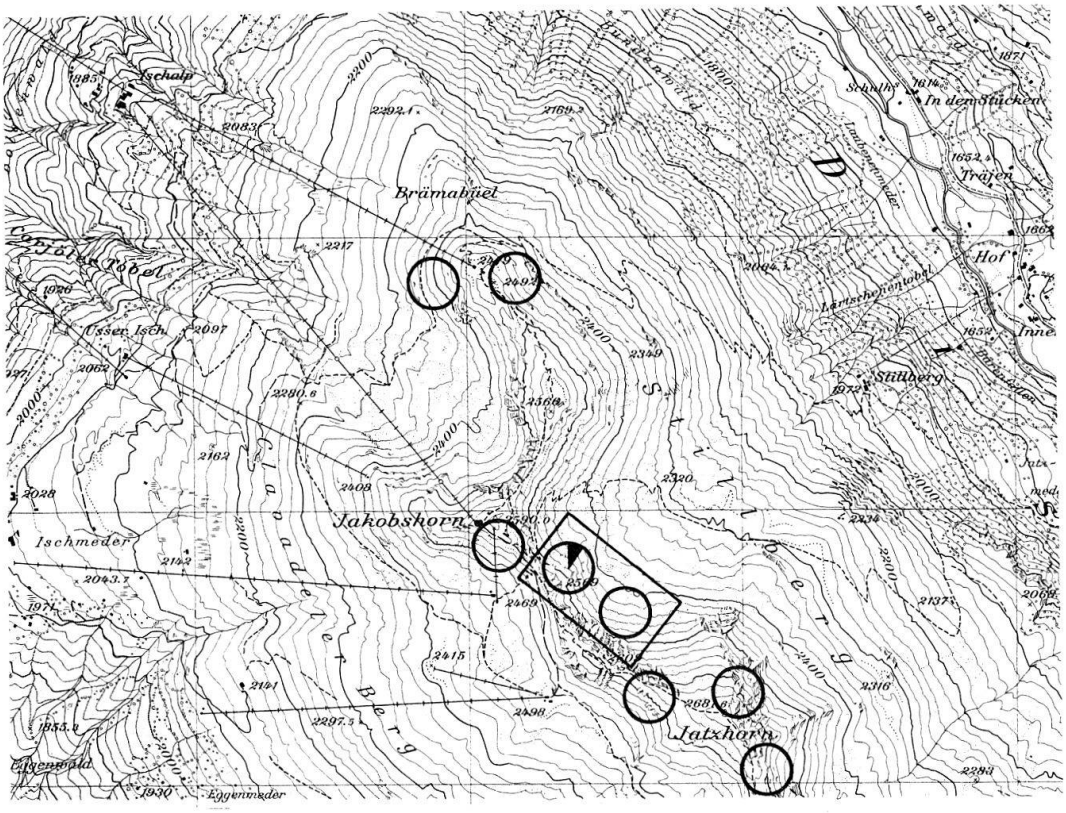

Fig. 3a. The neighbouring colonies of *R. montanus* s.l. studied within the area of Jatzhorn-Jakobshorn-Brämabüel. Framed area refers to Fig. 3b.

○ = *R. grenierianus* ◔ = *R. montanus* s.str.

(Map reproduced with permission of the Swiss Federal Office of Topography from December 18, 1981).

Benachbarte R. montanus s.l.-Kolonien vom Jatzhorn-Jakobshorn-Brämabüel-Gebiet. Die eingerahmte Fläche bezieht sich auf Abb. 3b.

data, but also sometimes indicates apparently strong selective pressures operating within or between closely adjacent colonies. Two regions within the study area offered particularly instructive examples in this respect.

The region of Jatzhorn-Jakobshorn-Brämabüel (Fig. 3a) belongs to the acidic silicate mountains that form southern side of the Landwasser Valley. In this area, *R. grenierianus* is virtually the only taxon of the group, the only exception being the ENE slope of Jakobshorn, where small colonies of *R. grenierianus* alternate regularly with those of *R. montanus* s.str. following the microrelief (DICKENMANN 1978, 1980). The frequencies of cyanogenic phenotypes corresponded to this pattern, the only HCN-positive plants being found in scree slope "stripes" inhabited by *R. montanus* s.str., whereas *R. grenierianus* samples from grassy mounds were all acyanogenic (Fig. 3b). The frequencies of HCN-positive plants in *R. montanus* s.str. varied from 6.7 to 23.1 %, the average frequency being 11.7 % (Table 6).

The region: Augstberg-Altein Plateau is localised on northern side of the Landwasser Valley. The substrate is exclusively calciferous (e.g. dolo-

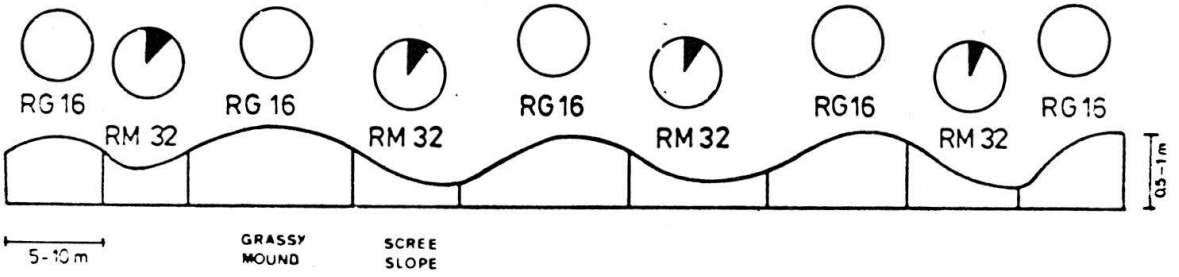

Fig. 3b. Fragment of microdifferentiation pattern, cross-section of the ENE slope of Jakobshorn.
RG16 = *R. grenierianus*, RM32 = *R. montanus* s.str.
Black sector of the circles represent frequencies (%) of cyanogenic plants in the respective sector.
(After DICKENMANN 1980, altered and completed)

Fragment des Mikrodifferenzierungsmusters, Querschnitt durch den ENE-Hang des Jakobshorns.

mite, limestone) and so far only *R. montanus* s.str. was found there. Two series of six and five neighbouring colonies, respectively, studied from this area showed a consistent pattern of cyanogenic polymorphism in particular as far as to the ratio: HCN-/HCN+, the frequencies varying only slightly (Fig. 4).

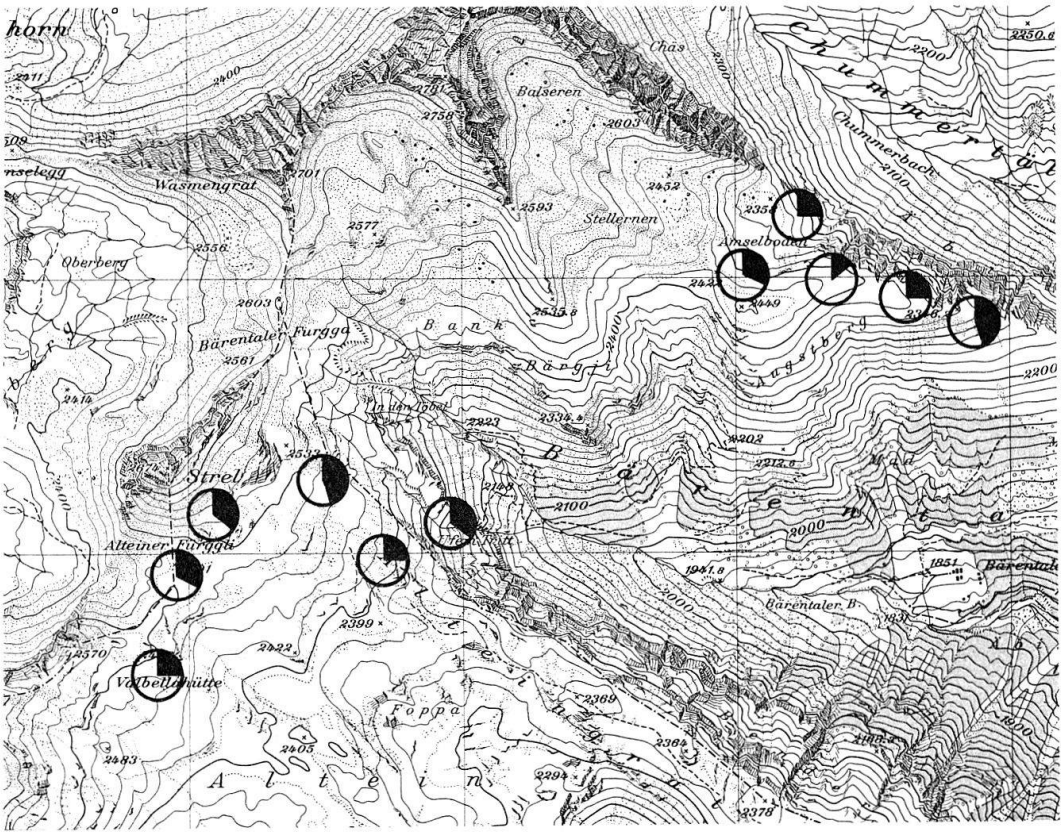

Fig. 4. The neighbouring colonies of *R. montanus* s.str. studied within the area of Augstberg-Altein.
Black sectors: frequencies (%) of cyanogenic phenotypes.
(Map reproduced with permission of the Swiss Federal Office of Topography from December 18, 1981)

Benachbarte R. montanus s.str.-Kolonien vom Augstberg-Altein-Gebiet.
Schwarze Sektoren: Häufigkeit (%) der cyanogenen Phänotypen.

Tab. 6. Cyanogenesis polymorphism in the colonies of *R. montanus* s.str. from the ENE-slope of Jakobshorn.

Polymorphismus in der Cyanogenese in R. montanus s.str.-Kolonien vom ENE-Hang des Jakobshorns.

colony*	sample size	cyanogenic plants	
		N	%
1	10	1	10.0
2	11	1	9.1
3	15	1	6.7
4	13	3	23.1
5	11	1	9.1
6	16	2	12.5
7	10	1	11.1
8	10	1	11.1
9	11	1	9.1
10	13	2	15.3
11	11	1	9.1
12	12	2	16.6

*Colonies 1-12 collectively codified as SM1 in Table 4.

4. Discussion

Polymorphism of cyanogenesis is known to date only in a few plant families. Most of the investigations dealing with various populations of a given taxon were carried out in the family of *Leguminosae*, viz. in *Lotus corniculatus*, *Trifolium repens* (e.g.ABBOTT 1977, 1981, ARAUJO 1976, DADAY 1954a, b, 1965, JONES 1970, 1972a, b, URBANSKA and WILDI 1975) as well as in *Lotus alpinus* (URBANSKA 1979, 1982, URBANSKA and SCHWANK 1980). Recently, URBANSKA (1981) found polymorphism of cyanogenesis in the annual *Eschscholzia mexicana* of the *Papaveraceae* family. The present study revealing polymorphism of cyanogenesis on population level in *Ranunculus montanus* s.l. represents the first investigation of the kind within the buttercup family; therefore, it brings about a further contribution to the general knowledge of the occurrence and distribution of cyanogenesis in the Angiosperms.

One of the possible basic functions of cyanogenesis is a defense against herbivores. Studies in natural populations and laboratory experiments

indicated a protective function, acyanogenic plants being sometimes selectively eaten (e.g. JONES 1962, 1966, CRAWFORD-SIDEBOTHAM 1972, ANGSEESING and ANGSEESING 1973, ELLIS et al. 1977a, b). On the other hand, various animals have detoxification mechanisms and are able to eat cyanogenic plants. The cyanogenesis as a defense mechanism is thus not absolutely efficacious. As far as *R. montanus* s.l. is concerned, no experiments with regard to a protective function of cyanogenesis were carried out. However, a selective eating of acyanogenic phenotypes does not seem to be helpful for explaining the observed pattern of phenotypic frequencies. It is rather unlikely that in the study area slugs and snails should inhabit only carbonate sites and never migrate over a few-meter distance into neighbouring acidic silicate soils. It should be added that all individuals of *R. montanus* s.l., cultivated in the experimental garden in Zurich, were eaten by slugs and snails, no distinction between acyanogenic plants and cyanogenic ones being observed. The usually low HCN content in *R. montanus* s.l. might have no pronounced effect upon herbivore behaviour, but this problem remains open to verifications.

Another possible function of cyanogenesis is a rôle in the nitrogen metabolism. ABROL et al. (1966) showed an active turnover of cyanide in *Lotus* sp. and *Nandina domestica* and SOLOMONSON and SPEHAR (1977) as well as ECK and HAGEMAN (1974) found a possible rôle of endogenous HCN in nitrate reductase. Recent observations of DEMENT and MOONEY (1974) suggest as well that cyanogenic glycosides might serve for nitrogen storage. Unfortunately, information on this subject is, in general, rather fragmentary and so are data on edaphic conditions in reports on cyanogenesis in natural populations. Only in *Lotus alpinus* from the Swiss Alps a strong influence of substratum upon cyanogenesis polymorphism was found (URBANSKA 1979, 1982, URBANSKA and SCHWANK 1980). Recent studies of URBANSKA (1982) on a small-scale distribution pattern of *L. alpinus* were carried out in the same area as the present author's investigation on *R. montanus* s.l.. The patterns of behaviour found in *L. alpinus* and *R. montanus* s.l. are strikingly similar, cyanogenic phenotypes being in both cases about three times as frequent upon carbonate as on acidic silicate. The families of *Ranunculaceae* and *Leguminosae* obviously stay far apart from each other as far as the phyletic relationships are concerned; it should also

be kept in mind that the HCN-tests in *R. montanus* s.l. were carried out with a method different from that used in *L. alpinus*. Last but not least, HCN content in the studied taxa of *R. montanus* s.l. is, in general, much lower than in that of *L. alpinus*. Given all these circumstances, the similarity of the general trends of cyanogenesis polymorphism is truly amazing; to the best of the author's knowledge, this is the first time when very similar phenotypic frequencies were observed in two different plant families within the same restricted area.

Carbonate and acidic silicate soils differ from each other as to the prevailing form of bound nitrogen: carbonate soils contain mainly NO_3-N, whereas in acidic silicate soils NH_4-N is predominant. It is possible that these differences influence the nitrogen metabolism in plants from either substrate; distinct patterns of cyanogenesis polymorphism observed in acidic silicate and carbonate might partly reflect this influence and accordingly suggest a relationship between cyanogenesis and the nitrogen metabolism. It should be most desirable to carry out further studies on cyanogenesis polymorphism within the same alpine region *R. montanus* s.l. and *L. alpinus* were studied from, looking also for other groups of closely related taxa.

Another edaphic factor possibly influencing polymorphism of cyanogenesis is the soil moisture, but also in this case no unequivocal patterns appear so far. FOULDS (1977) and FOULDS and GRIME (1972a, b) found soil moisture stress acting against cyanogenic phenotypes in *Trifolium repens* and *Lotus corniculatus*. Their results support the opinion of DADAY (1965), that the gene locus concerned with cyanogenic glycoside production might be genetically linked to genes concerned with fitness. Also BAND et al. (1981) found a decrease of cyanogenic *L. halophilus* individuals towards more arid areas in Israel. ABBOTT (1977, 1981) found a correlation between decreasing soil moisture content and lower frequencies of cyanogenic phenotypes of *L. corniculatus* on Birsay Links in Orkney. His results from other links in Orkney did not suggest, however, such a correlation, for the frequency of cyanogenic phenotypes was always high independently from the soil moisture content. BOYD and his collaborators (1938) observed that in *Sorghum vulgare* drought possibly operated as an indirect factor for increasing the HCN content by lessening the availability of phosphorus.

They found that a high level of available nitrogen and a low level of available phosphorus in the soil tended to increase the HCN content in plants. Recent observations of URBANSKA (1981) who found high frequencies of cyanogenic phenotypes of *Eschscholzia mexicana* in semi-arid habitats of Arizona and Southern California might corroborate the data of BOYD et al. (1938), but her preliminary report did not contain any data on the actual soil components. In other cases, soil moisture seemed to have no influence (JONES 1973, ELLIS et al. 1977).

As far as the study area is concerned, the water régime was on the whole much less favourable on carbonate than on acidic silicate (GIGON 1971), though the water supply depended on the development of the soil and the vegetation.

Acidic silicate is generally regarded as a more favourable, "well-balanced" substrate. The frequencies of cyanogenic phenotypes in *R. montanus* s.l., especially as far as the carbonate substrate is concerned, suggest that water stress might favour cyanogenic phenotypes. However, in the siliceous ENE slope of Jakobshorn, the water régime apparently is more favourable in scree slopes and moist depressions partly inhabited by *R. montanus* s.str., whereas on grassy mounds the acyanogenic *R. grenierianus* are more liable to water stress. This situation might be partly attributed to the taxonomic background of particular taxa within the *R. montanus* group. LANDOLT (1954) suggested that *R. montanus* s.str. (2n=32) is an allotetraploid with the putative parents *R. grenierianus* (2n=16) and *R. carinthiacus* (2n=16). As far as the cyanogenesis polymorphism is concerned, *R. montanus* s.str. is in general rather frequently represented by cyanogenic phenotypes, whereas *R. grenierianus* is mostly acyanogenic (Fig. 2). More precise data on *R. carinthiacus* are not available so far, but the few HCN-tests carried out by the present author indicated cyanogenesis polymorphism; *R. carinthiacus* usually grows on carbonate substrates, it should be interesting to investigate cyanogenesis in this taxon.

The knowledge of cyanogenesis polymorphism, its causes and effects is obviously far from being complete. Some authors suggested that general hypotheses explaining cyanogenesis polymorphism should be tested only at specific level within the regional frame (JONES 1977, BAND et al. 1981).

The present results support this opinion but also point out that more attention should in future be paid to some finely balanced habitat components, edaphic factors being of a particular interest. Evolutionary relationships between closely related taxa should also be considered.

Summary

Polymorphism of cyanogenesis was studied on population level in *R. grenierianus* (2n=16) and *R. montanus* s.str. (2n=32) in the alpine region of Davos (Grisons). Inter-populational variation in frequencies of cyanogenic/acyanogenic phenotypes, as well as intra-populational variation in HCN content of the cyanogenic individuals was found. A pronounced influence of substratum type was observed: Cyanogenic phenotypes were more than three times more frequent on carbonate soils than on acidic silicate soils (31.6 % vs. 9.1 %). Moreover, carbonate soils seemed to favour strongly cyanogenic phenotypes (samples from carbonate 15.8 %, those from acidic silicate 0.9 %). *R. grenierianus* and *R. montanus* having distinct edaphic preferences, the observed patterns of cyanogenesis polymorphism might be partly related to evolution of the *R. montanus* group.

In conclusion, possible causes and effects of cyanogenesis are briefly discussed.

Zusammenfassung

Polymorphismus in der Cyanogenese wurde bei *R. grenierianus* (2n=16) und *R. montanus* s.str. (2n=32) in der alpinen Stufe bei Davos auf Populationsebene untersucht. Neben einer Variation der Häufigkeit von cyanogenen und acyanogenen Phänotypen zwischen den verschiedenen Populationen, konnte auch innerhalb von Populationen eine Variation des HCN-Gehaltes der cyanogenen Individuen festgestellt werden. Es wurde ein deutlicher Einfluss des Substrattypes beobachtet: Auf Karbonat waren cyanogene Phänotypen mehr als dreimal häufiger als auf saurem Silikat (31.6 % vs. 9.1 %). Zudem schienen Karbonatböden stark cyanogene Phänotypen zu begünstigen (Karbonatproben 15.8 %, Silikatproben 0.9 %). Da *R. grenierianus* und *R. montanus* s.str. meist unterschiedliche edaphische Areale besiedeln, könnte die beobachtete Verteilung des Cyanogenese-Polymorphismus in Beziehung stehen zur Evolution der *R. montanus* Gruppe. Abschliessend werden mögliche Ursachen und Wirkungen der Cyanogenese kurz diskutiert.

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