Polymorphism of cyanogenesis in Lotus alpinus from Switzerland : 1. Small-scale variability in phenotypic frequencies upon acidic silicare and carbonare

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Polymorphism of cyanogenesis in *Lotus alpinus* from Switzerland. I. Small-scale variability in phenotypic frequencies upon acidic silicate and carbonate.

(Polymorphismus der Cyanogenese bei Lotus alpinus aus der Schweiz. I. Kleinmassstäbliche Verteilungsmuster der Phänotypen-Häufigkeiten auf saurem Silikat- und auf Karbonatgestein)

by

Krystyna URBANSKA

Contents

1. Introduction

Polymorphism of cyanogenesis in *Lotus alpinus* has been found for the first time by the present author in 1974, some preliminary data being published a year later (URBANSKA and WILDI 1975). Since then, phenotypic frequencies were studied in population samples of *L. alpinus* originating from various parts of the Swiss Alps (SCHWANK 1978, URBANSKA 1979, URBANSKA and SCHWANK 1980). Global evaluations carried out in these studies revealed an apparent influence of the substratum type upon the polymorphism of cyanogenesis in *L. alpinus*: population samples from carbonate were characterized by 40.9% of cyanogenic plants, whereas samples from acidic silicate comprised only 16.9% and those from serpentine were predominantly acyanogenic (4.3%). The previous studies suggested as well some relationship between the polymorphism of cyanogenesis and the cytological differentiation occurring within the *Lotus alpinus* group; the preliminary observations (URBANSKA and WILDI 1975) were later corroborated, the global percentage of cyanogenic diploids being twice as high as that of the corresponding tetraploids (URBANSKA 1979, URBANSKA and SCHWANK 1980).

Some field data suggested, however, that the polymorphism of cyanogenesis in *Lotus alpinus* within a given area might be influenced by a local variation. To study this aspect, investigations in a small-scale distribution pattern of phenotypic frequencies were undertaken. The present paper deals with the first results obtained in this subject.

Acknowledgements

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2. The study area, material and methods

The study was carried out in the surroundings of Davos, Grisons (E Switzerland); being geologically heterogeneous, the region was suitable for investigations dealing with influence of the substratum upon variation. All the populations studied were situated upon the timberline, between 2270-2700 m a.s.l. The alpine substrata *Lotus alpinus* was studied from were roughly assigned to two groups viz. acidic silicate and carbonate; either of those groups comprised substrata of various age, sometimes representing different tectonic layers. For instance, the group collectively referred to as the carbonate comprised dolomites, limestones, calciferous schists and so on. For detailed information in this respect, see the Geological Map of Grisons 1:25.000 scale, part B: Davos and D: Landwasser.

All but three populations were sampled for the first time in the course of the present study. In three stations, sampling was repeated to verify the previous incomplete data. The sample size was determined by the actual population size and further influenced by the clonal growth occurring within *Lotus alpinus*; therefore, the samples greatly varied from one station to another (Table 1-2). In particular, colonies inhabiting steep scree slopes at higher altitudes or those occurring within the very contact of two different substrata were exceedingly small and often consisted of only a few individuals; on the other hand, large populations yielded samples of sixty and more plants.

The sampling was concentrated within several restricted areas that usually did not exceed about 1 km^2. Whenever possible, series of samples within a given area were taken in a distance of about 60 m, well-spaced individuals being chosen. Most frequently, small secondary rosettes or stems with numerous leaves were collected from each individual.

The samples were tested for cyanogenesis with the standard sodium picrate paper method and also examined cytologically. Detailed methods used in these studies were described in our previous publications (e.g. URBANSKA and SCHWANK 1980). The HCN-tests permitted to distinguish between two gross phenotypes viz. cynogenic and acyanogenic. The cyanogenic individ-

uals were assigned to four classes viz. very weakly cyanogenic HCN (+), weakly cyanogenic HCN+, strongly cyanogenic HCN++ and very strongly cyanogenic HCN+++. According to semi-quantitative assessments carried out with help of a graded colour table, the HCN(+) class should correspond to 30-50 mg of HCN per Kg fresh weight and the HCN+ one to 75-100 mg. The two classes with strongly positive and very strongly positive reading in the HCN-tests corresponded respectively to 150-200 mg and at least 250 mg of HCN per Kg fresh weight. For comparison purposes, this method proved quite satisfactory in the author's previous studies (URBANSKA 1981).

3. Results

3.1. *Global evaluations of phenotypic frequencies*

3.1.1. *Cyanogenic vs. acyanogenic phenotypes*

On the whole, 1606 plants were examined; 786 individuals from acidic silicate were distributed in 25 samples, whereas 820 plants from carbonate corresponded to 30 samples. No heteroploid samples were observed; in the material from silicate, diploid samples (2n=12) largely prevailed, representing 93.9% (22 samples). The samples from carbonate were invariably tetraploid (2n=24). The results of the cytological control conformed in general to expectations, the distribution of the two chromosomic races in *Lotus alpinus* being strongly influenced by the substratum type as well as the altitude a.s.l. (URBANSKA and WILDI 1975, SCHWANK 1978, URBANSKA 1979, URBANSKA and SCHWANK 1980, URBANSKA unpubl.). Out of the three tetraploid samples originating from acidic silicate, two were found at 2300 m and 2400 m a.s.l., respectively; this altitude bracket corresponds roughly to the contact zone between diploids and tetraploids observed upon the substratum. On the other hand, the tetraploid colony occurring at 2480 m a.s.l. is rather exceptional; its occurrence within the area otherwise inhabited by diploid populations might result from the intensive grazing by cattle.

Phenotypic frequencies observed in the material studied unmistakably

indicate a strong influence of the substratum type upon the cyanogenesis polymorphism in *Lotus alpinus*. The cyanogenic plants occurred far more frequently in samples from carbonate than in those from siliceous soils, the respective global frequencies being 63.2% vs. 21.0%; the increase in frequency corresponded thus to factor 3 (Fig. 1).

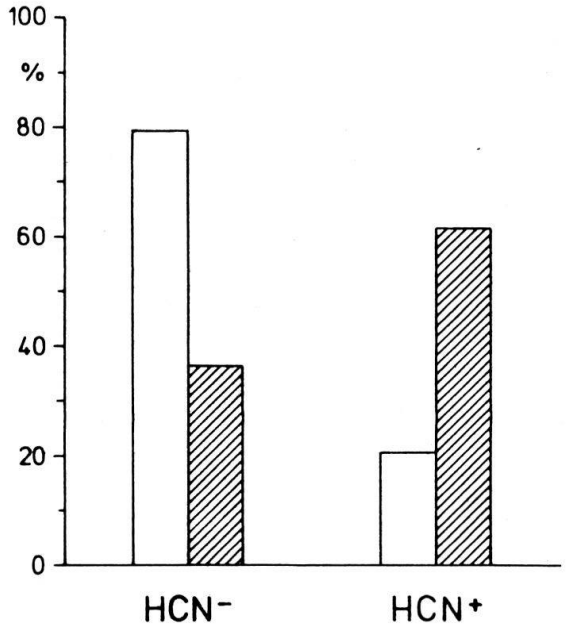

Fig. 1. Global frequencies of cyanogenic and acyanogenic phenotypes in the material from carbonate ▨ and acidic silicate □.
Gesamt-Häufigkeiten der cyanogenen und acyanogenen Phänotypen bei Pflanzen von Karbonat- und saurem Silikatgestein.

3.1.2. *Distribution of particular cyanogenic phenotypes*

The strong influence of the substratum type was reflected as well in another aspect of the cyanogenesis polymorphism in *Lotus alpinus* viz. the distribution patterns of particular cyanogenic phenotypes (Fig. 2). In the samples from siliceous soils, the HCN-positive plants were mostly very weakly cyanogenic i.e. represented the HCN(+) class; their corresponding global frequency was 62.4%. The three remaining classes viz.

HCN+, HCN++ and HCN+++ were represented by the respective global frequencies of 19.4%, 11.5% and 6.7%; the gradual decrease in frequency parallel to the increase in the HCN content in plants was thus clearly observable.

The inverse tendency was found in the material from carbonate, where the very strongly cyanogenic individuals (HCN+++) were the most representative (64.9%). The HCN++ plants and the HCN+ ones occurred in rather low frequencies (8.9% and 6.6%, respectively), whereas the very weakly cyanogenic individuals HCN(+) corresponded to about one-fifth of the material studied, occurring in 19.6% (Fig. 2). The observed patterns of global frequencies suggested thus an advantageous effect of a high HCN content in plants inhabiting carbonate.

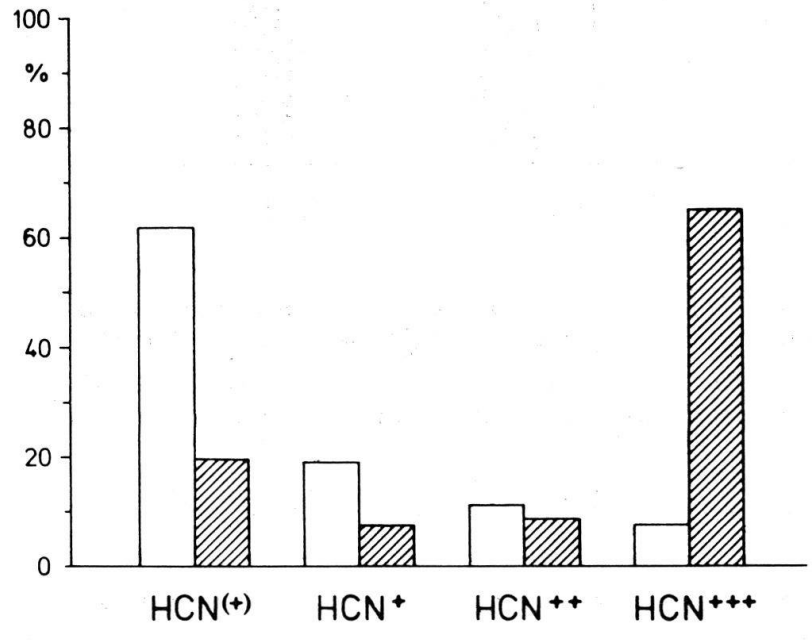

Fig. 2. Global frequencies of particular cyanogenic phenotypes in the material from carbonate ▨ and acidic silicate □.

Gesamt-Häufigkeiten der verschiedenen cyanogenen Phänotypen bei Pflanzen von Karbonat- und saurem Silikatgestein.

3.2. *Variation within and between population samples*

In general, phenotypic frequencies in population samples from both substrata were very variable (Table 1-2). Except perhaps for exceedingly small samples, this variation did not seem to be much influenced by the sample size; for instance, the same frequency of cyanogenic phenotypes viz. 27.3% was observed in two samples from acidic silicate that respectively consisted of 22 and 117 individuals. No differences that could be specifically attributed to change in altitude and/or exposition occurred as well in the material studied.

Table 1. Cyanogenic and acyanogenic phenotypes in population samples from acidic silicate.

Cyanogene und acyanogene Phänotypen bei Pflanzen von saurem Silikatgestein.

Code No.	2n	Altitude a.s.l.	Total	Acyanogenic phenotypes	Cyanogenic phenotypes	Frequency(%) of cyanogenic plants
8	12	2350 m	15	7	8	53.3
21	12	2270 m	25	12	13	52.0
37	12	2500 m	15	8	7	46.7
49	12	2450 m	64	38	26	40.6
41	12	2650 m	24	16	8	33.3
35	12	2550 m	16	11	5	31.2
61	12	2380 m	50	36	14	28.0
16	12	2500 m	22	16	6	27.3
47	12	2450 m	117	85	32	27.3
42	12	2610 m	19	14	5	26.3
56	12	2400 m	10	8	2	20.0
60	12	2450 m	30	25	5	16.7
36	12	2600 m	7	6	1	14.3
6	12	2460 m	36	31	5	13.9
13	12	2470 m	41	36	5	12.2
9	12	2430 m	17	15	2	11.8
19	24	2300 m	18	16	2	11.1
22	12	2430 m	56	50	6	10.7
43	12	2560 m	25	23	2	8.0
18	12	2550 m	41	38	3	7.3
32	12	2400 m	56	53	3	5.4
17	12	2280 m	19	18	1	5.3
31	24	2400 m	21	20	1	4.8
20	12	2430 m	32	31	1	3.1
33	24	2480 m	4	4	0	0.0

The samples from acidic silicate were polymorphic for cyanogenesis save for a single acyanogenic sample found within the contact zone between silicate and dolomite (Table 1). Most of the various cristalline substrata *L. alpinus* was sampled from did not seem to influence specifically the phenotypic frequencies; for example, the sample with the second highest frequency of cyanogenic plants (52.0%) as well as that with the lowest frequency (3.1%) both originated from quartz-porphyry. The only exception observed so far was the amphibolite, nearly all samples collected upon this substratum being characterized by very low or low frequencies of cyanogenic plants (5.3% to 12.2%) and only a single sample containing 20.0%. More attention should be paid to this aspect in future investigations dealing with plants from siliceous soils.

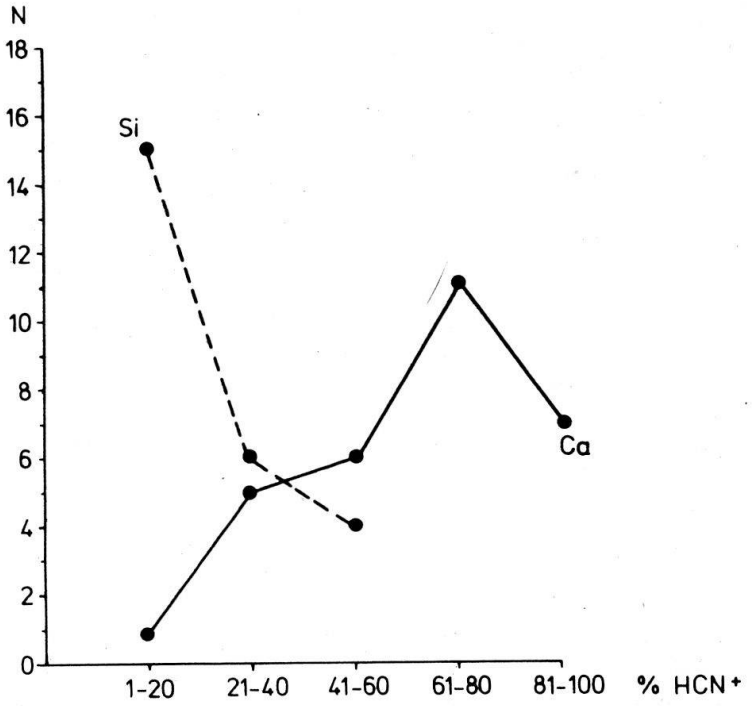

Fig. 3. Distribution of samples with various phenotypic frequencies within the material studied.

Verteilung der Proben mit verschiedenen Phänotypen-Häufigkeiten innerhalb des gesamten untersuchten Pflanzenmaterials.

The whole spectrum of variation observed in the material from acidic silicate was rather broad, phenotypic frequencies ranging from 0.0% to 53.3% (Table 1). However, out of the 25 samples studied, 15 were characterized by low frequencies of cyanogenic phenotypes (Fig. 3); in addition to the diploids, the tetraploid samples belonged to this group, their respective frequencies comporting 4.8% and 11.1%; the only acyanogenic sample was also tetraploid.

Table 2. Cyanogenic and acyanogenic phenotypes in population samples from carbonate.

Cyanogene und acyanogene Phänotypen in Populationsproben von Karbonatgestein.

Code No.	Altitude a.s.l.	Total	Acyanogenic phenotypes	Cyanogenic Phenotypes	Frequency(%) of cyanogenic plants
40	2350 m	29	0	29	100
48	2390 m	3	0	3	100
53	2390 m	6	0	6	100
55	2450 m	20	1	19	95.0
1	2600 m	15	2	13	86.7
52	2330 m	40	5	35	85.4
29	2700 m	17	3	14	82.3
28	2600 m	14	3	11	78.6
59	2350 m	22	5	17	77.3
27	2700 m	4	1	3	75.0
2	2500 m	23	6	17	73.9
4	2300 m	20	6	14	70.0
57	2530 m	40	13	27	67.5
54	2340 m	49	16	33	67.3
10	2420 m	45	15	30	66.7
26	2520 m	20	7	13	65.0
50	2350 m	71	25	46	64.8
11	2370 m	60	22	38	63.3
58	2450 m	40	16	24	60.0
45	2300 m	25	11	14	56.0
12	2300 m	38	17	21	55.3
51	2350 m	63	30	33	52.4
25	2560 m	33	16	17	51.5
24	2500 m	8	4	4	50.0
39	2350 m	10	6	4	40.0
44	2400 m	42	26	16	38.1
3	2400 m	11	7	4	36.4
38	2670 m	30	21	9	30.0
23	2470 m	14	11	3	21.4
46	2370 m	8	7	1	12.5

The materials from carbonate were polymorphic for cyanogenesis except for three samples which were uniformly cyanogenic (Table 2). No differences between samples collected upon various carbonate-bearing substrata were noted. On the whole, variation in phenotypic frequencies was still more pronounced than in the material from acidic silicate, the corresponding minimal and maximal frequencies of cyanogenic individuals being respectively 12.5% and 100% (Table 2). However, a distinct trend towards high frequencies of HCN-positive plants was observed in the material studied: in more than two-thirds of the samples studied from carbonate, frequencies exceeding 50.1% were observed, those between 60.1% and 80.0% being the best represented (Fig. 3).

Table 3. Distribution of particular cyanogenic phenotypes in samples from acidic silicate.

Verteilung verschiedener cyanogener Phänotypen in Proben von saurem Silikatgestein.

Code No.	2n	Number of cyanogenic phenotypes				Total N
		HCN(+)	HCN+	HCN++	HCN+++	
42	12	0	1	0	4	5
41	12	0	1	4	3	8
22	12	2	3	0	1	6
16	12	1	2	2	1	6
9	12	1	0	0	1	2
8	12	0	2	5	1	8
21	12	5	3	5	0	13
49	12	22	3	1	0	26
19	24	1	0	1	0	2
6	12	2	2	1	0	5
47	12	25	7	0	0	32
61	12	11	3	0	0	14
43	12	0	2	0	0	2
31	24	0	1	0	0	1
32	12	2	1	0	0	3
18	12	2	1	0	0	3
37	12	7	0	0	0	7
35	12	5	0	0	0	5
60	12	5	0	0	0	5
13	12	5	0	0	0	5
33	24	2	0	0	0	2
56	12	2	0	0	0	2
17	12	1	0	0	0	1
20	12	1	1	0	0	1
36	12	1	0	0	0	1

Distribution of particular cyanogenic phenotypes within the population samples varied within either of the two groups studied (Table 3-4); in spite of this variation, influence of the substratum type was distinct. In the material from acidic silicate, the very weakly cyanogenic plants HCN(+) and the weakly cyanogenic ones (HCN+) largely prevailed, the former type being observed in 20 samples, the latter - in 14 (Table 3). Only 9 samples, however, comprised both these types. The strongly cyanogenic phenotypes HCN++ were found in 7 samples; the very strongly cyanogenic

Table 4. Distribution of particular cyanogenic phenotypes in samples from carbonate.

Verteilung verschiedener cyanogener Phänotypen in Proben von Karbonatgestein.

Code No.	Number of cyanogenic phenotypes				Total N
	HCN(+)	HCN+	HCN++	HCN+++	
50	13	2	1	30	46
40	0	0	0	29	29
52	3	0	4	28	35
10	3	0	3	24	30
11	6	1	11	20	38
57	9	0	0	18	27
2	0	0	2	15	17
12	1	2	4	14	21
44	0	0	2	14	16
45	0	0	0	14	14
55	0	5	0	14	19
26	1	0	0	12	13
51	15	6	0	12	33
1	2	0	0	11	13
28	1	0	0	10	11
29	0	0	4	10	14
58	11	3	0	10	24
25	1	4	3	9	17
4	4	0	2	8	14
59	7	2	0	8	17
53	0	0	0	6	6
54	16	6	7	4	33
3	0	1	0	3	4
23	0	0	0	3	3
24	0	0	1	3	4
27	0	0	0	3	3
38	7	0	0	2	9
39	1	2	0	1	4
46	0	0	0	1	1
48	1	0	2	0	3

individuals HCN+++ not only were scarce (altogether 11 plants observed) but also occurred solely in 6 samples out of the 25 studied (Table 3). The HCN++ types and the HCN+++ ones were found together only in three samples.

In the material from carbonate, the very strongly cyanogenic phenotypes HCN+++ were found in all samples but one (Table 4) and usually prevailed over other cyanogenic plants. The strongly cyanogenic and weakly cyanogenic individuals HCN++ and HCN+ were observed in less than a half of the samples studied (13 and 11 samples, respectively); only in five samples did they occur together. The very weakly cyanogenic plants HCN(+) were observed in 18 samples; their number varied from one sample to another but usually was rather low (Table 4).

The influence of the substratum type upon the polymorphism of cyanogenesis in *Lotus alpinus* was particularly distinct in areas where acidic silicate and carbonate occurred in a close neighbourhood. A fairly instructive example represented in this respect the adjacent areas of Leidbachhorn-Erezberg and Alplihorn-Fanezfurgga, situated SW of Davos (Fig. 4).

The siliceous area of Rinerhorn-Leidbachhorn-Erezberg and the carbonate group of Alplihorn-Strel-Chrachenhorn form a part of the mountain group limited from NW by the Valley of Landwasser, from NE by the Valley of Sertig and from SW by the Valley of Ducan. The area of Leidbachhorn-Erezberg comprises mostly various types of gneiss (Silvretta-ortho-gneiss, granite-gneiss, paragneiss, biotite-gneiss) and the amphibolite. The area of Alplihorn-Fanezfurgga consists of dolomites (e.g. Arlberg-dolomite, Altein-dolomite, "Hauptdolomite"), limestones (e.g. upper-Rhaetian limestone, Recoaro-limestone) as well as some carbonate-bearing schists. Large moraine fields occur in either of the two areas, the development of the soil being usually much advanced only at lower altitudes. The zone of contact between silicate and carbonate is clearly visible in steep slopes, whereas the bottom parts of small side-valleys sometimes consist of mixed moraine containing both substrata.

The areas were sampled throughout summer 1981. It should be noted parenthetically that the few colonies of *Lotus alpinus* marked on both sides

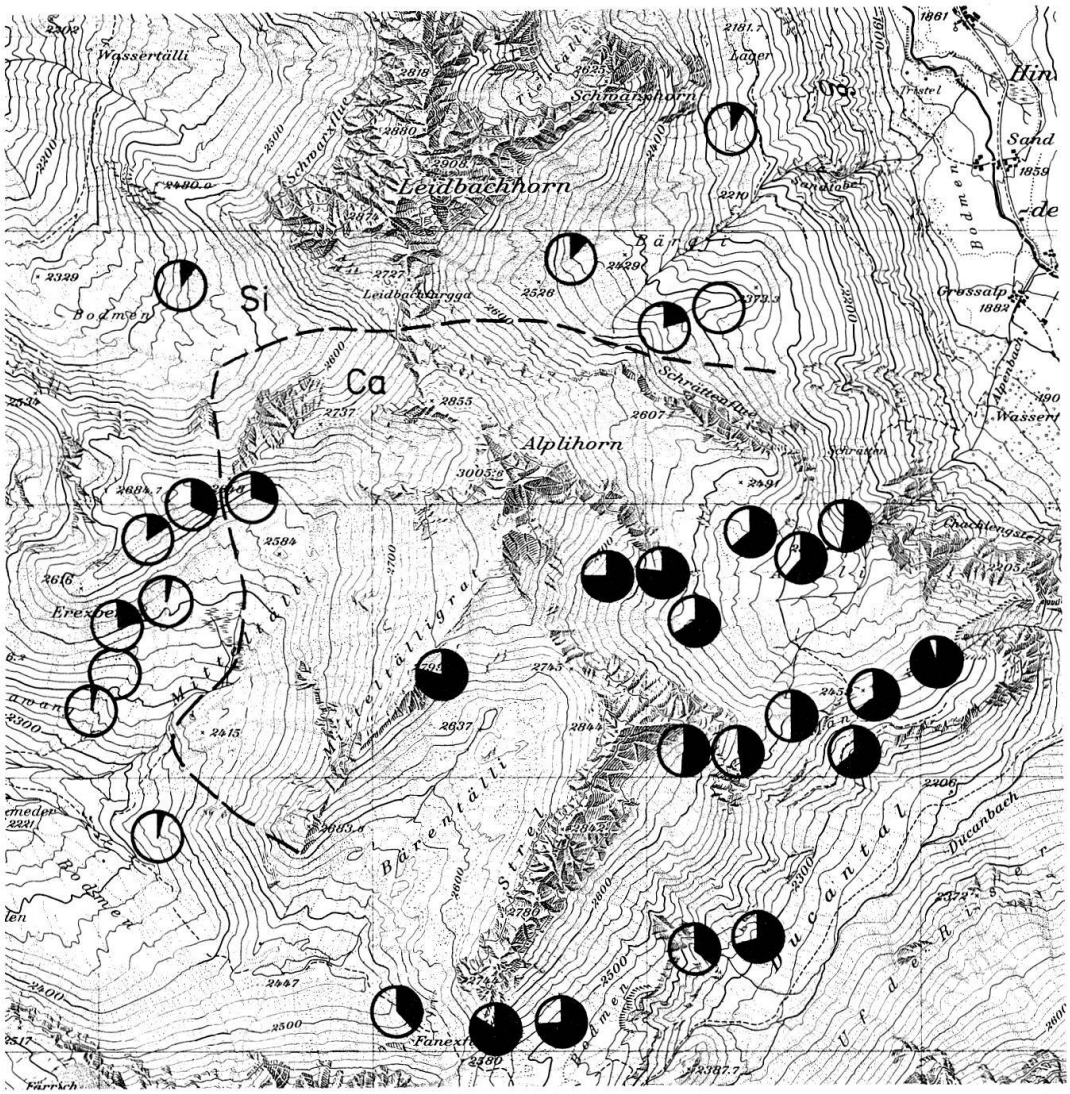

Fig. 4. The adjacent areas of Leidbachhorn-Erezberg and Alplihorn-Fanezfurgga. Map of Switzerland 1:25.000 scale No. 1217: Scalettapass. Reference grids: 780.700-784.300/174.000-178.000. Reproduced by permission of the Swiss Federal Office of Topography from December 18, 1981.

Si = acidic silicate; Ca = carbonate. Broken line refers to the substratum contact zone. Black sections (pies) correspond to percentages of cyanogenic phenotypes.

Umgebung des Gebietes Leidbachhorn-Erezberg und Alplihorn-Fanezfurgga. Landkarte der Schweiz 1:25.000, Nr. 1217: Scalettapass.

Si = saures Silikatgestein, Ca = Karbonatgestein. Die gestrichelte Linie zeigt die Gesteinsgrenze an. Die schwarzen Kreisausschnitte entsprechen dem Prozentsatz der cyanogenen Phänotypen.

of the predominantly amphibolitic Leidbachhorn correspond to the actual sparse occurrence of the taxon in this area; it is rather doubtful that much more material should be found there, except perhaps for an odd colony or two in the upper part of the Wassertälli (N slope). The phenotypic frequencies found in the area show, on the one hand, the pronounced general influence of the substratum type upon the polymorphism of cyanogenesis in *Lotus alpinus*; on the other hand, variation in phenotypic frequencies occurring over short distances within either of the two substrata studied is observable.

4. Discussion

The present investigations show that phenotypic frequencies in *Lotus alpinus* are generally related to distinct substrata notwithstanding a local variation that may appear over short distances within a given substratum. In this respect, observations carried out in restricted areas corroborate our previous, more general data on the polymorphism of cyanogenesis in *L. alpinus* from various parts of the Swiss Alps (URBANSKA and WILDI 1975, SCHWANK 1978, URBANSKA 1979, URBANSKA et al. 1979, URBANSKA and SCHWANK 1980). Furthermore, the present study bring about the evidence of an apparently strong influence of the substratum type upon the HCN content in cyanogenic plants. In alpine siliceous soils, cyanogenic phenotypes not only occur in low frequencies but also mostly have a low cyanide content; contrary to this pattern, not only the very occurrence of cyanogenic phenotypes but also their high HCN content seem to be favoured upon carbonate.

Polymorphism of cyanogenesis was recently studied also in *Ranunculus montanus* s.l. (DICKENMANN 1982) within the same restricted area as *Lotus alpinus* the present paper deals with. It is of a particular interest that the pattern of phenotypic frequencies observed in *R. montanus* was virtually the same as that in *L. alpinus*. This is the first case when plants belonging to two very distant families respond to a given set of environmental conditions in nearly the same way as far as the phenotypic frequencies are concerned; previously, no single trend for HCN compounds could

have been discerned even in two related taxa of *Lotus* (BAND et al. 1981).

The genetic background of the cyanogenesis polymorphism is reasonably well understood. In *Trifolium repens* and *Lotus corniculatus*, the mechanisms involved are essentially the same, the synthesis of cyanogenic glycoside(s) and that of the corresponding β-glucosidase(s) being respectively controlled by two dominant alleles *Ac* and *Li*. The cyanogenic phenotypes have accordingly a double dominant status as far as the two unlinked loci are concerned (ATWOOD and SULLIVAN 1942, CORKILL 1940, 1942, DAWSON 1941, JONES 1972, 1973, JONES et al. 1978, MELVILLE and DOAK 1940, NASS 1972). Various quantities of HCN released on injury to the tissue by particular cyanogenic individuals are apparently controlled by modifying genes that influence the expressivity of the dominant allele *Ac* (DAWSON 1941, JONES 1973); on the other hand, differences in the amount of the β-glycosidase(s) produced seem rather to remain under influence of an allelic dosage (MAHER and HUGHES 1973). The acyanogenic phenotype corresponds to three possible allelic configurations viz. *Acli* resulting in the presence of glycoside but the absence of enzyme, *acLi* (enzyme but not glycoside) as well as the double recessive status *acli* reflected in the absence of both components. As far as *Lotus alpinus* is concerned, no detailed investigations on genetical basis of cyanogenesis were carried out to date; it seems, however, that the above described genetic systems determining cyanogenesis may well apply to the whole group of *Lotus corniculatus* s.l. The present results indicate an interesting relationship between the substratum type and distribution of both dominant alleles as well as the expressivity modificators: cyanogenic plants comprising strong expressivity modificators seem to be given preference upon carbonate, whereas weak expressivity is apparently representative of cyanogenic plants occurring in low frequencies upon acidic silicate.

Any discussion on factors involving in cyanogenesis polymorphism inevitably relates to possible function of the cyanogenesis, none of the currently advanced hypotheses being universally applicable as the sole explanation. It seems, however, that the rôles ascribed to the cyanogenesis viz. a defence against herbivores as well as a function in the nitrogen economy of plants (e.g. ROBINSON 1930, JONES 1972) are not mutually exclusive; they may either represent independently operating strategies or

constitute two aspects integrated into the whole life pattern of a given plant.

Both circumstantial and direct evidence of the defensive rôle of cyanogenesis has been provided in some cases (for references, see e.g. JONES 1972, 1978). It appears that cyanogenic compounds affording some protection against generalist herbivores might be particularly valuable for ephemeral tissues, as suggested by RHOADES and GATES (1976). The author's recent observations on cyanogenesis polymorphism in the annual *Eschscholzia mexicana* (URBANSKA 1981) support this theory. The seasonal variation in content of cyanogenic glycosides within leaves of *Heteromeles arbutifolius* (DEMENT and MOONEY 1974) also indicates a possible defence against herbivores in young tissues of a perennial species. The results obtained in *Lotus alpinus* do not, however, suggest the defence against herbivores being the principal aspect involved in the cyanogenesis in this taxon. Were this the case, the pattern of phenotypic frequencies upon carbonate should reflect a particularly strong herbivore pressure correlated with a differential predation of acyanogenic plants. However, the alpine vegetation upon carbonate is well known for being much less grazed than the neighbouring siliceous areas. Furthermore, it is not very probable that herbivores should rigorously keep to a restricted carbonate surface and never move over short distances into neighbouring siliceous slopes predominantly inhabited by acyanogenic individuals.

Some rôle of cyanogenesis in the nitrogen economy of *Lotus alpinus* seems a more plausible explanation for the observed patterns of phenotypic frequencies. The available data on the nitrogen budget in plants as well as pathways of the nitrogen metabolism specific to the legumes are still far from being fully known and appreciated (see e.g. PATE 1976, SHANMUGAN et al. 1978). However, it seems that endogenous HCN has some function in the nitrate reductase regulation (ECK and HAGEMANN 1972, SOLOMONSON and SPEHAR 1977). On the other hand, cyanogenic glycosides apparently may serve as nitrogen storage structures accumulated in conditions favourable for rapid N-cycling and later used by plants when the nitrogen becomes limiting (DEMENT and MOONEY 1974). The particular ionic composition of the soil apparently may influence the cyanogenesis; BOYD and his collaborators (1938) observed an exceedingly high HCN content in *Sorghum*

vulgare var. *sudanense* grown in soil low in available phosphorus but containing 50 lbs of NO_3-N per acre.

No coherrent pattern emerges so far from the few reports on cyanogenesis polymorphism that contain as well data on the substratum type and/or the ionic composition of a given soil. However, carbonate soils within the alpine vegetation belt contain NO_3-N, whereas the bound nitrogen in soils upon acidic silicate occurs as NH_4-N. Alpine soils tend to be low in an available phosphorus. The water régime in carbonate, particularly in dolomite, is generally considered as unfavourable; on the other hand, soils upon acidic silicate are regarded as relatively well-balanced (GIGON 1971). The strongly cyanogenic plants of *Lotus alpinus* as well as those of *Ranunculus montanus* (DICKENMANN 1982) prevailing upon carbonate are apparently well-adapted to particular conditions occurring in this substratum. It might be assumed that most of their cyanogenic glycoside(s) would be rapidly accumulated early in summer, when the soil moisture allows soil organisms to become active in N-cycling thus increasing the available nitrogen. The stored glycoside(s) might then serve, on the one hand, as a possible source of nitrogen during periods when its sufficient amount is not available but need for it in plant life processes is high; on the other hand, the plants would have a source of an endogenous HCN if needed in regulation of the nitrate uptake from the soil. Conditions in acidic silicate soils might require different strategies (e.g. biosynthesis of nitrogen compounds different from cyanogenetic glycosides, regulation of the ammonium uptake from the soil following different pathways than that of the nitrate); should they indeed occur, cyanogenesis would not be an important aspect.

The speculative remarks presented above obviously do not attempt to explain the actual cyanogenesis polymorphism in *Lotus alpinus*. They have been offered nevertheless to point out aspects that urgently need to be investigated for getting a better understanding of selective factors involved in the maintaining of polymorphic populations. RHOADES and GATES (1976) postulate that "secondary compounds must have a net positive effect on plant fitness, since if they did not, metabolic costs associated with their production and sequestration should cause the elimination of geno-

types producing these substances". The previous data and the present results suggest that gross phenotypes are directly selected; possible interpretations are, however, easier for the cyanogenic phenotype than for the acyanogenic one if the precise allelic structure of the latter is not known. Differences in allelic configuration might well contribute to different responses of cyanogenic plants to given environmental factors; alternatively, the same overall selective effect may involve plants representing various allelic combinations. FOULDS and GRIME (1972) observed soil moisture stress acting as a selective force in *Trifolium repens* and *Lotus corniculatus*. In *Trifolium repens*, a reduction in the frequency of the glycosidic (*Ac*) plants was found, but in *Lotus corniculatus* fewer enzyme (*Li*) plants occurred in the droughted populations. As far as *Lotus corniculatus* is concerned, acyanogenic plants from various substrata have to be studied in detail; it should be particularly important to know whether acyanogenic phenotypes from carbonate do comprise *Ac* allele or are aglucosidic.

Selection results not only in a differential survival but also in a differential reproduction. JONES (1962) observed previously in *Lotus corniculatus* a better seed output in acyanogenic plants than in cyanogenic ones. In *L. alpinus*, reproductive performance of acyanogenic individuals seems also be better than that of cyanogenic plants, some differences being observed as well in germinating behaviour of plants from various substrata (URBANSKA et al. 1979, URBANSKA unpubl.). It should be most desirable to study these aspects.

Summary

Polymorphism of cyanogenesis in *Lotus alpinus* was studied in populations from acidic silicate and carbonate. The small-scale distribution pattern of phenotypic frequencies is sometimes influenced by a local variation, but general differences between either of the two substrata remain distinct. Not only the very presence of cyanogenic phenotypes but also the HCN content in cyanogenic plants are apparently influenced by the type of substratum: in acidic siliceous soils, cyanogenic plants occur in low frequencies and mostly have a low HCN content, whereas upon carbonate cyanogenic phenotypes prevail and their HCN content is usually high. It may therefore be assumed that both dominant alleles as well as expressivity modificators are involved in selection of cyanogenic plants influ-

enced by the substratum type. Selection of acyanogenic plants might be more complex, depending of their precise allelic structure.

Two principal rôles ascribed to the cyanogenesis viz. a defence against herbivores and a function in plant nitrogen economy are not mutually exclusive; they may either represent independently operating strategies or constitute two aspects integrated into the whole life pattern of a given plant.

Zusammenfassung

Bei *Lotus alpinus* wurde der Polymorphismus der Cyanogenese in Populationen von saurem Silikat- und von Karbonatgestein untersucht. Das kleinmassstäbliche Verteilungsmuster der Phänotypen-Häufigkeiten wird manchmal durch lokale Variation beeinflusst; indessen sind die allgemeinen Unterschiede zwischen den Pflanzen der beiden Gesteinsunterlagen sehr deutlich. Nicht nur das Auftreten von cyanogenen Phänotypen sondern auch der Gehalt an HCN in den cyanogenen Pflanzen wird durch das unterschiedliche Substrat beeinflusst: auf den sauren Silikatböden sind die cyanogenen Pflanzen nicht häufig und besitzen einen niederen Gehalt an HCN, während auf Karbonatböden cyanogene Phänotypen mit normalerweise hohem HCN-Gehalt vorherrschen. Es kann deshalb angenommen werden, dass sowohl dominante Allele wie auch Modifikatoren der Expressivität an der Selektion der cyanogenen Pflanzen, die durch die beiden Gesteinsunterlagen beeinflusst werden, beteiligt sind. Die Selektion der acyanogenen Pflanzen ist möglicherweise komplizierter und hängt von deren genauen Allel-Struktur ab.

Die beiden der Cyanogenese zugeschriebenen Bedeutungen, d.h. Schutz gegen Herbivoren und Rolle im pflanzlichen Stickstoffhaushalt, schliessen sich nicht unbedingt aus; sie können entweder voneinander unabhängig wirkende Strategien sein oder zwei verschiedene Aspekte darstellen, die im Gesamtleben der einzelnen Pflanze integriert sind.

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Corrigenda:

S. 52, 5. Zeile von oben:

Differences in allelic configuration might well contribute to different responses of acyanogenic plants to given .....