Polymorphism of cyanogenesis in Lotus alpinus from Switzerland. II. Phemotypic and allelic frequencies upon acidic silicate and carbonate = Polymorphismus der Cyanogenese bei Lotus alpinus aus der Schweiz. II. Phänotypen- und Allelen-Häufigkeit auf saur...

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Objekttyp: **Article**

Zeitschrift: **Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel**

Band (Jahr): **51 (1984)**

PDF erstellt am: **17.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-377727

Ber.Geobot.Inst.ETH, Stiftung Rübel, *51* (1984), 132-163

Polymorphism of cyanogenesis in *Lotus alpinus* from Switzerland. II. Phenotypic and allelic frequencies upon acidic silicate and carbonate

Polymorphismus der Cyanogenese bei *Lotus alpinus* aus der Schweiz. II. Phänotypen- und Allelen-Häufigkeit auf saurem Silikat- und auf Karbonatgestein

by

Krystyna M. URBANSKA

1. Introduction

In the author's previous paper dealing with cyanogenic polymorphism in *Lotus alpinus* (URBANSKA 1979, 1982, URBANSKA and DICKENMANN 1981, URBANSKA and SCHWANK 1980, URBANSKA and WILDI 1975), occurrence of cyanogenic and acyanogenic plants within alpine populations was studied. Both global evaluations as well as data on small-scale variability patterns clearly suggested a strong influence of substratum upon frequencies of the gross phenotypes. Cyanogenic plants occurred much more frequently in population samples from carbonate than in those from acidic silicate, the respective global frequencies being of 63.7% vs. 21.0%. Also a high HCN content did seem to be advantageous upon carbonate, whereas HCN-positive individuals from acidic silicate most frequently were weakly cyanogenic.

Discussing possible rôles of the cyanogenesis, the author suggested that differences in allelic configuration might contribute to different responses of populations of *Lotus alpinus*. It was assumed that acyanogenic plants growing upon carbonate might frequently be glucosidic, whereas other allelic configurations might be favourized upon silicate. The aim of the present study is to verify this hypothesis and to study in detail phenotypic and allelic frequencies in the two alpine substrata.

Acknowledgements

Prof. Dr. R. HEGNAUER (Leiden, The Netherlands) provided valuable advice on methods; his help is greatly appreciated. Thanks are also due to Prof. Dr. H.L. LE ROY (SFIT Zürich) for his constructive comments on some population genetics problems. Ms. Anita HEGI efficiently prepared the test vials and other laboratory equipment, Mr. E. SCHäFFER took care of all necessary reagents. Prof. Dr. E. LANDOLT helped with translations into German. Cordial thanks of the author are addressed not only to those three persons from Geobotanical Institute, but also to members of our Alpine Group who put up with the smell of toluene lingering in rooms of the field-base at Davos-Clavadel.

2. Material and methods

The study was carried out throughout August 1982 in the surroundings of Davos, Grisons, a single sample from Central Swiss Alps (Canton of Wallis, sample code VS/82) being tested in late September. The studied material consisted of ten population samples from either of the two alpine substrata (Table 1). On the whole, 1001 plants were examined from acidic silicate, whereas the material from carbonate comprised 1099 individuals.

Table 1. Origin of the material studied

Herkunft des untersuchten Materials

Sample code	Valley		Exposition	Altitude m a.s.l.
Acidic silicate:				
20/82	Landwassertal	Wannengrat	SW	2500
2/82	Landwassertal	Latschüel	SW	2450
17/82	Landwassertal	Chorbshorn	SW	2570
18/82	Landwassertal	Stafler Berg	SW	2460
19/82	Landwassertal	Bodmen(Schafgrind/Tiejerfürggli)	SW	2540
13/82	Sertigtal	Bargji: opposite Schrattenfluh	W	2400
14/82	Sertigtal	Bargji: central moraine	SW	2460
16/82	Sertigtal	Leidbachhorn	SW	2470
15/82	Sertigtal	below Leidbachfurgga	SW	2650
16/82	Sertigtal	Schwarzhorn	SW	2540
Carbonate:				
3/82	Landwassertal	Casanna	SW	2450
5/82	Sertigtal	Schrattenfluh	SW	2490
7/82	Sertigtal	Aelpli	S	2350
9/82	Sertigtal	Aelpli: upper part	SW	2500
3/82	Ducantal	Männli	SW	2350
8/82	Ducantal	Männli: summit ridge	SW	2450
10/82	Ducantal	ascent towards Fanezfurgga	SW	2350
11/82	Ducantal	below Fanezfurgga	SW	2580
12/82	Ducantal	Bodmen	SW	2400
VS/82	Wallis, Central Swiss Alps	Gemmipass	NW	2370

Freshly collected, well-developed leaves were tested according to the sodium picrate method, sulphur-free toluene being used as the organic dissolvent. For each individual, two HCN-tests were carried out parallelly, one with added two drops of A-grade linamarin, the other with added crude linamarase suspension. The glucoside was purchased from CALBIOCHEM, whereas the enzyme suspension was prepared from *Linum* seedlings at the laboratory of the Geobotanical Institute.

The test vials were left for incubation under the electric bulb of 100 W. The test was read after 24 hr and the corresponding allelic configurations were codified. Semi-quantitative differences, observed in the course of the study, were not distinguished between in the present paper.

3. Results

3.1. *Gross phenotypes*

Acidic silicate. The material was predominantly acyanogenic, frequencies

Table 2. Distribution of cyanogenic and acyanogenic individuals in population samples from acidic silicate

Verteilung von cyanogenen und acyanogenen Pflanzen in Populationsproben von saurem Silikatgestein

Sample code	Number of plants HCN^+	HCN^-	Sample size (N)
14/82	2	109	111
19/82	2	104	106
6/82	2	73	75
13/82	3	101	104
16/82	5	95	100
17/82	6	93	99
18/82	6	66	72
2/82	17	141	158
20/82	15	86	101
15/82	13	62	75

Table 3. Frequencies (%) of cyanogenic and acyanogenic individuals in population samples from acidic silicate

Häufigkeit (%) von cyanogenen und acyanogenen Pflanzen in Populationen von saurem Silikatgestein

Sample code	Cyanogenic	Acyanogenic
14/82	1.8	98.2
19/82	1.9	98.1
6/82	2.7	97.3
13/82	2.9	97.1
16/82	5.0	95.0
17/82	6.1	93.9
18/82	8.3	91.7
2/82	10.8	89.2
20/82	14.9	85.1
15/82	17.3	82.7

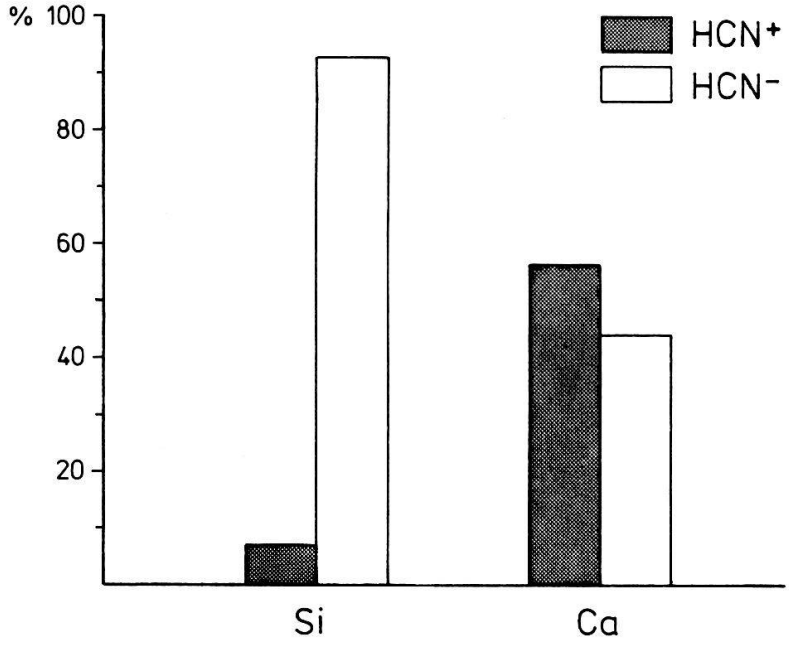

Fig. 1. Global frequencies (%) of gross phenotypes in the material from acidic silicate (Si) and carbonate (Ca)

Gesamt-Häufigkeiten (%) der cyanogenen und acyanogenen Phänotypen bei Material von saurem Silikat-(Si) und Karbonatgestein (Ca)

of cyanogenic plants being mostly less than 10% (Tables 2-3, Fig. 1). Out of the 1001 plants examined, only 71 were cyanogenic; the global frequency of cyanogenic phenotypes was thus of 7.1%, whereas mean frequency corresponded to 17.2%.

Compared to the author's previous study partly carried out within the same area (URBANSKA 1981), a still more pronounced trend towards a low frequency of cyanogenic phenotypes was observed. It was recognizable both in a more limited variation observed in this respect between the population samples (1.8% - 17.3% vs. 0.0% - 53.3%) as well as in a much lower global frequency of cyanogenic plants (7.1% vs. 21.0%).

Carbonate. Cyanogenic phenotypes represented the majority in eight out of ten samples studied (Tables 4-5, Fig. 1. On the whole, 615 cyanogenic individuals were found in the ample material examined (N = 1099); the global frequency of cyanogenic phenotypes was thus of 56.0%, mean frequency being of 58.4%.

The results of the present study confirm generally the author's previous data (URBANSKA 1982), frequencies of cyanogenic plants corresponding to less than 50.0% being found in only two out of the ten samples studied.

Table 4. Distribution of cyanogenic and acyanogenic individuals in population samples from carbonate

Verteilung von cyanogenen und acyanogenen Pflanzen in Populationsproben von Karbonatgestein

Sample code	Number of plants HCN^+	HCN^-	Sample size (N)
3/82	63	104	167
4/82	67	98	165
10/82	47	46	93
9/82	53	48	101
12/82	58	42	100
8/82	57	37	94
7/82	65	36	101
VS/82	55	27	82
5/82	71	27	98
11/82	79	19	98

Table 5: Frequencies (%) of cyanogenic and acyanogenic individuals in population samples from carbonate

Häufigkeit (%) von cyanogenen und acyanogenen Pflanzen in Populationsproben von Karbonatgestein

Sample code	Cyanogenic	Acyanogenic
3/82	37.7	62.3
4/82	40.6	59.4
10/82	50.5	49.5
9/82	52.5	47.5
12/82	58.0	42.0
8/82	60.6	39.4
7/82	64.4	35.6
VS/82	67.1	32.9
5/82	72.4	27.6
11/82	80.6	19.4

The global frequency was lower than the one previously observed (56.0% vs. 63.2%).

The distribution of gross phenotypes followed thus remarkably different patterns in either of the two alpine substrata, cyanogenic individuals being about eight times less frequent upon acidic silicate than in carbonate (Fig. 1). It should be added that frequency variation ranges of cyanogenic plants represented two distinct classes in the material from silicate and that from carbonate, being 1.8 - 17.3 per cent in the former substratum and 37.7 - 80.6 per cent in the latter one.

3.2. *Allelic configurations AcLi, Acli, acLi and acli*

Detailed studies on distribution and frequencies of all four allelic configurations have not been carried out to date in *Lotus alpinus*. For a better assessment of the results obtained, various approaches were chosen:

1. Variation in distribution and frequency of particular configurations were studied in population samples: subsequently, global frequencies were calculated for the whole material examined from silicate (N_{Si} = 1001) and that from carbonate (N_{Ca} = 1099);

2. The acyanogenic material was evaluated separately from the HCN-positive part; the corresponding frequencies of allelic configurations were worked out first for each sample, then globally for N_{Si} = 930 and N_{Ca} = 484;
3. Glucoside carriers respectively representing cyanogenic and acyanogenic phenotype viz. *AcLi* and *Acli* were considered as one group, the frequency in the material from silicate being compared to that from carbonate;
4. The enzymatic plants *AcLi* and *acLi* were treated in the same way as the glucosidic types.

3.2.1. *General distribution of the allelic configurations*

Acidic silicate (Tables 6-7, Fig. 2). The samples varied slightly, but overall pattern was clear. The aglucosidic configurations *acli* and *acLi* were the best represented with the corresponding ranges of frequency variation of 34.3 - 80.2 per cent and 15.8 - 57.6 per cent, respectively. Mean frequency of the *acli* plants carrying both recessive alleles was of 54.1%, whereas that of the enzyme carriers *acLi* corresponded to 36.8%. Glucosidic configurations, on the other hand, occurred most frequently in conspicuously low frequencies, the trend being particularly consistent in the acyanogenic configuration *Acli*. The very narrow range of frequency variation in this type was of 0.9 - 5.3 per cent and its mean frequency corresponded to 1.7%.

Carbonate (Tables 8-9, Fig. 2). The configuration *AcLi* comprising both dominant alleles represented most frequently more than 50 per cent in a given sample, mean frequency being of 58.7%. Frequencies of the *Acli* configuration corresponding to acyanogenic glucosidic individuals varied from 6.1 to 48.4% with a mean value of 21.0%. Acyanogenic enzyme carrying plants represented by the *acLi* configuration were remarkably rare, missing altogether in four out of the ten samples studied; only in a single sample did their frequency slightly exceed ten per cent (10.9%, Table 9). Frequencies in the *acli* configuration comprising both recessive alleles were very variable (1.1-42.5%), mean frequency being of 16.3%.

Differences in general distribution patterns of allelic configurations

observable in population samples from acidic silicate and carbonate were particularly pronounced in global evaluations (Table 10, Fig. 2).

The material from acidic silicate was characterized by largely prevailing aglucosidic plants that most frequently corresponded to a double-recessive configuration *acli*. The second-best represented category was that

Table 6. Allelic configurations in population samples from acidic silicate

Allel-Konfigurationen in Populationsproben von saurem Silikatgestein

Sample code	N of plants				Total
	AcLi	Acli	acLi	acli	
14/82	2	1	34	74	111
19/82	2	2	17	85	106
6/82	2	1	35	37	75
13/82	3	3	49	49	104
16/82	5	1	31	63	100
17/82	6	2	57	34	99
18/82	6	0	29	37	72
2/82	17	2	25	114	158
20/82	15	2	49	35	101
15/82	13	4	26	32	75

Table 7. Frequencies (%) of particular allelic configurations in samples of acidic silicate

Häufigkeit (%) verschiedener Allel-Konfigurationen in Proben von saurem Silikatgestein

Sample code	AcLi	Acli	acLi	acli
14/82	1.8	0.9	30.6	66.7
19/82	1.9	1.9	16.0	80.2
6/82	2.7	1.3	46.7	49.3
13/82	2.9	2.9	47.1	47.1
16/82	5.0	1.0	31.0	63.0
17/82	6.1	2.0	57.6	34.3
18/82	8.3	0.0	40.3	51.4
2/82	10.8	1.3	15.8	72.1
20/82	14.8	2.0	48.5	34.7
15/82	17.3	5.3	34.7	42.7

of enzyme-carrying acyanogenic individuals *acLi*. Glucosidic plants were rare, glucoside-carrying acyanogenic individuals *Acli* occurring in exceedingly low frequencies (Table 10, Fig. 2).

Contrary to this trend, the material from carbonate was recognizable above all by prevailing glucosidic plants. The double-dominant allelic

Table 8. Allelic configurations in population samples from carbonate

Allel-Konfigurationen in Populationsproben von Karbonatgestein

Sample code	N of plants				Total
	AcLi	Acli	acLi	acli	
3/82	63	33	0	71	167
4/82	67	40	13	45	165
10/82	47	45	0	1	93
9/82	53	27	11	10	101
12/82	58	35	0	7	100
8/82	57	15	3	19	94
7/82	65	9	7	20	101
VS/82	55	5	3	19	82
5/82	71	7	5	15	98
11/82	79	17	0	2	98

Table 9. Frequencies (%) of particular allelic configurations in samples from carbonate

Häufigkeit (%) verschiedener Allel-Konfigurationen in Proben von Karbonatgestein

Sample code	AcLi	Acli	acLi	acli
3/82	37.7	19.8	0.0	42.5
4/82	40.6	24.2	7.9	27.3
10/82	50.3	48.4	0.0	1.1
9/82	52.5	26.7	10.9	9.9
12/82	58.0	35.0	0.0	7.0
8/82	60.6	16.0	3.2	20.2
7/82	64.3	8.9	6.9	19.8
VS/82	67.1	6.1	3.6	23.2
5/82	72.4	7.1	5.1	15.3
11/82	80.6	17.3	0.0	2.0

configuration *AcLi* was the most frequent, the next highest frequency being that of glucosidic acyanogenic plants *Acli*. As far as the aglucosidic types are concerned, *acli* individuals with neither glucoside nor enzyme corresponded to about one-fifth of the material studied from carbonate; on the other hand, enzyme-carrying acyanogenic plants *acLi* represented only 3.8% (Table 10, Fig. 2).

Table 10. Global frequencies (%) of particular allelic configurations in the material from acidic silicate (N=1001) and carbonate (N=1099)

Häufigkeit (%) verschiedener Allel-Konfigurationen im Material von saurem Silikat- (N=1001) und Karbonatgestein (N=1099)

Substratum	AcLi	Acli	acLi	acli
Si	7.1	1.8	35.2	55.9
Ca	56.0	21.2	3.8	19.0

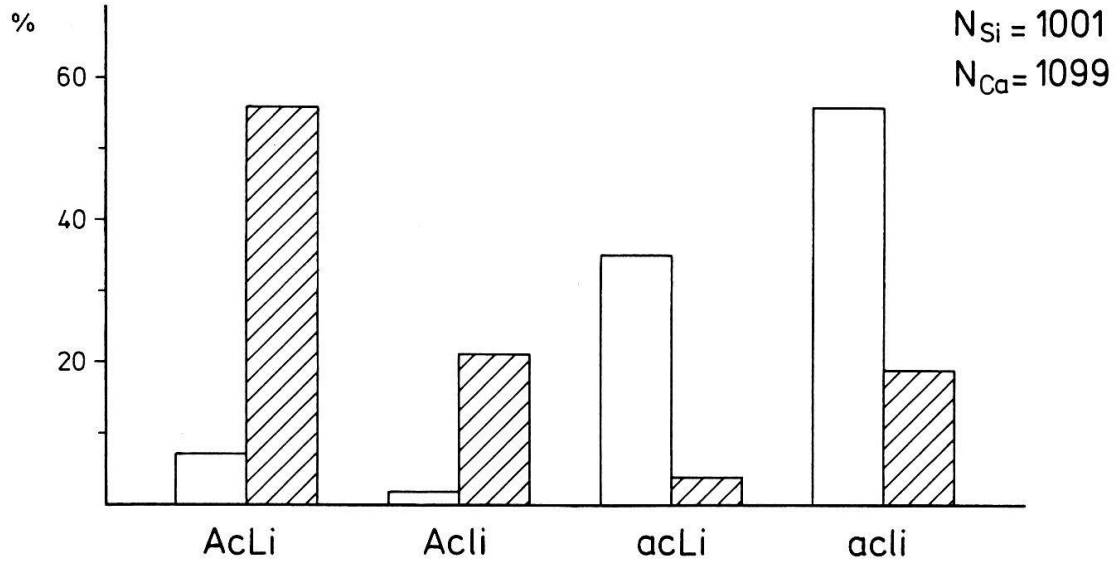

Fig. 2. Global frequencies (%) of particular allelic configurations in the material from acidic silicate and carbonate

Häufigkeit (%) verschiedener Allel-Konfigurationen im Material von saurem Silikat- und Karbonatgestein

silicate
Silikatgestein

carbonate
Karbonatgestein

3.2.2. *Allelic configurations in the acyanogenic material*

Acidic silicate. Configurations comprising the recessive allele *ac* were representative of the material (Table 11, Fig. 3). Frequencies of the *acli* individuals were mostly high, mean frequency being of 58.1%. The

Table 11. Frequencies (%) of allelic configurations in acyanogenic samples from acidic silicate

Häufigkeit (%) der Allel-Konfigurationen in den acyanogenen Proben von saurem Silikatgestein

Sample code	Acli	acLi	acli	Total HCN^-
18/82	0.0	43.9	56.1	66
14/82	0.9	31.2	67.9	109
16/82	1.1	32.6	66.3	95
2/82	1.4	17.7	80.9	141
6/82	1.4	47.9	50.7	73
19/82	1.9	16.4	81.7	104
17/82	2.1	61.3	36.6	93
20/82	2.3	57.0	40.7	86
13/82	3.0	48.5	48.5	101
15/82	6.5	41.9	51.6	62

Table 12. Frequencies (%) of allelic configurations in acyanogenic samples from carbonate

Häufigkeit (%) der Allel-Konfigurationen in den acyanogenen Proben von Karbonatgestein

Sample code	Acli	acLi	acli	Total HCN^-
VS/82	18.5	11.1	70.4	27
7/82	25.9	19.4	55.6	36
5/82	25.9	18.5	55.6	27
3/82	31.7	0.0	68.3	104
8/82	40.5	8.1	51.4	37
4/82	40.8	13.3	45.9	98
9/82	56.3	22.9	20.8	48
12/82	83.3	0.0	16.7	42
11/82	89.5	0.0	10.5	19
10/82	97.8	0.0	2.2	46

Table 13. Global frequencies (%) of allelic configurations in acyanogenic material from acidic silicate (N=930) and carbonate (N=484)

Häufigkeit (%) der Allel-Konfigurationen im cyanogenen Material von saurem Silikat- (N=930) und Karbonatgestein (N=484)

Substratum	Acli	acLi	acli
Si	1.9	37.8	60.2
Ca	48.1	8.7	43.2

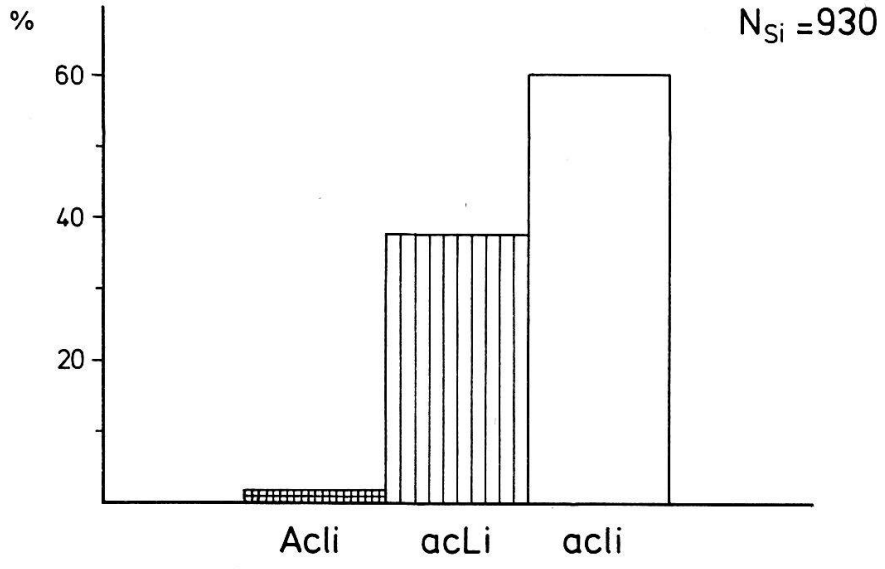

Fig. 3. Global frequencies (%) of allelic configurations in the acyanogenic material from acidic silicate

Häufigkeit (%) der Allel-Konfigurationen im acyanogenen Material von saurem Silikatgestein

acLi plants were also well represented with mean frequency of 39.8%. Glucosidic individuals *Acli*, on the contrary, were exceedingly scarce and their mean frequency corresponded to 2.1%.

Carbonate. Glucosidic individuals *Acli* occurred in various proportions, mean frequency being of 51.0%. Distribution of the enzyme-carrying plants *acLi* was very irregular: they were completely missing in some samples, whereas in others frequencies exceeding 10% were observed (Table 12). Mean frequency was of 9.3%. The *acli* types occurred in mean frequency of 39.7%.

Global evaluations clearly demonstrated differences in allelic constitution of acyanogenic plants occurring in either of the two alpine substrata. Of a particular interest were the glucoside plants *Acli* that represented nearly a half of the whole acyanogenic material from carbonate but were virtually missing upon acidic silicate (Table 13, Figs 3-4).

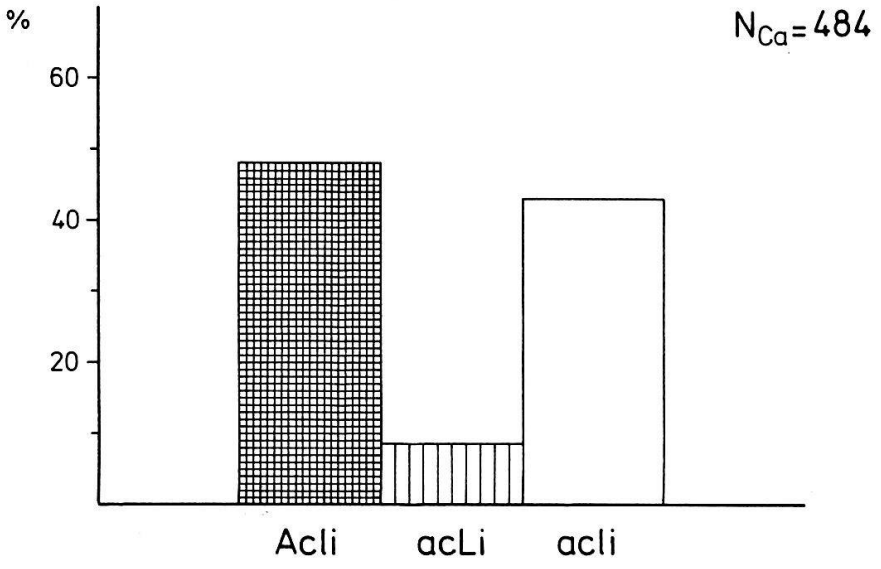

Fig. 4. Global frequencies (%) of allelic configurations in the acyanogenic material from carbonate

Häufigkeit (%) der Allel-Konfigurationen im acyanogenen Material von Karbonatgestein

3.2.3. *Glucosidic plants*

Acidic silicate (Table 14). The samples were rather variable, but frequencies of less than 10% prevailed in the material studied. On the whole, glucosidic plants were scarce: out of the 1001 plants examined, only 89 viz. 8.9% belonged to this category (Fig. 5).

Table 14. Frequencies (%) of glucosidic plants AcLi and Acli in samples from acidic silicate

Häufigkeit (%) der glukosiden Pflanzen AcLi und Acli in Proben von saurem Silikatgestein

Sample code	Frequency (%)
14/82	2.7
19/82	3.8
6/82	4.0
13/82	5.9
16/82	6.0
17/82	8.1
18/82	8.3
2/82	12.0
20/82	16.8
15/82	22.7

Table 15. Frequencies (%) of glucosidic plants AcLi and Acli in samples from carbonate

Häufigkeit (%) der glukosiden Pflanzen AcLi und Acli in Proben von Karbonatgestein

Sample code	Frequency (%)
3/82	57.5
4/82	64.8
VS/82	73.1
7/82	73.3
8/82	76.6
9/82	79.2
5/82	79.6
12/82	93.0
11/82	97.9
10/82	98.9

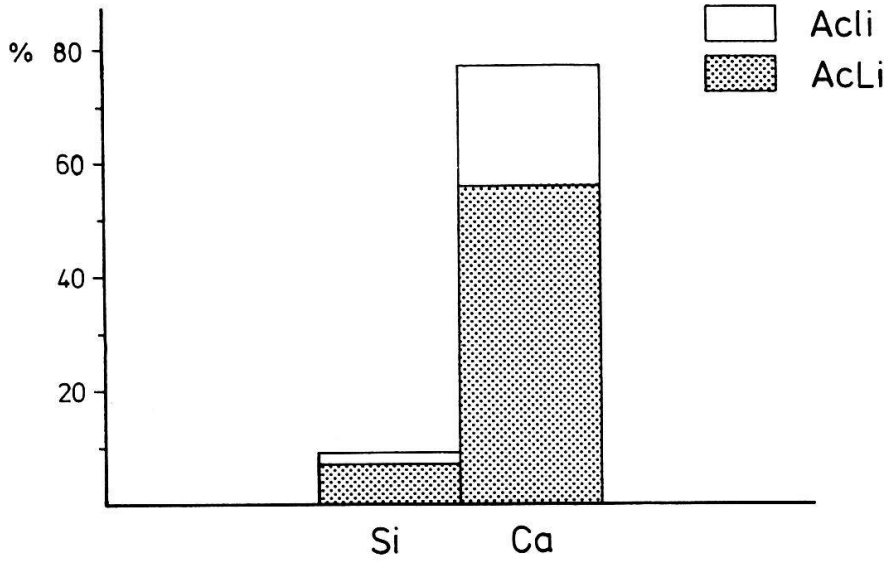

Fig. 5. Global frequencies (%) and allelic configurations of glucosidic plants in the material from acidic silicate (Si) and carbonate (Ca)

Häufigkeit (%) und Allel-Konfigurationen bei glukosiden Pflanzen von saurem Silikat-(Si) und Karbonatgestein (Ca).

Small as it was, the group of glucoside carriers was mostly represented by the cyanogenic phenotype *AcLi*; 71 plants with both dominant alleles corresponded to 79.8%, only 18 acyanogenic glucosidic plants *Acli* being found (Fig. 5).

Carbonate (Table 15). Glucosidic plants represented the majority in all samples studied and their frequencies exceeded sometimes 90%. Out of the 1099 plants studied, as much as 848 viz. 77.2% were glucosidic (Fig. 5). The group of glucosidic plants from carbonate consisted of 615 cyanogenic individuals *AcLi* (72.5%), 233 acyanogenic types *Acli* representing the remainder (Fig. 5).

The present study revealed thus that populations of *Lotus alpinus* from acidic silicate and carbonate are essentially different as to the very occurrence of glucosidic plants. On the other hand, relative frequencies of cyanogenic and acyanogenic glucoside carriers are rather similar in both substrata, the *AcLi/Acli* proportion being 72.5/27.5 per cent in silicate and 79.8/20.2 per cent in carbonate.

3.2.4. *Enzymatic plants*

Acidic silicate (Table 16). Frequency of enzymatic plants in samples was rather variable, mean frequency being of 44.0%. In the whole material studied, 423 plants viz. 42.3% were identified as enzyme carriers (Fig. 6). The enzymatic group consisted largely of acyanogenic plants *acLi*,

Table 16. Frequencies (%) of enzymatic plants AcLi and acLi in samples from acidic silicate

Häufigkeit (%) der enzymatischen Pflanzen AcLi und acLi in Proben von saurem Silikatgestein

Sample code	Frequency (%)
19/82	17.9
2/82	32.4
14/82	32.4
16/82	36.0
18/82	48.6
6/82	49.3
13/82	50.0
15/82	52.0
20/82	63.4
17/82	63.6

Table 17. Frequencies (%) of enzymatic plants AcLi and acLi in samples from carbonate

Häufigkeit (%) der enzymatischen Pflanzen AcLi und acLi in Proben von Karbonatgestein

Sample code	Frequency (%)
3/82	37.7
4/82	48.5
10/82	50.5
12/82	58.0
9/82	63.4
8/82	63.8
VS/82	70.7
7/82	71.3
5/82	77.6
11/82	80.6

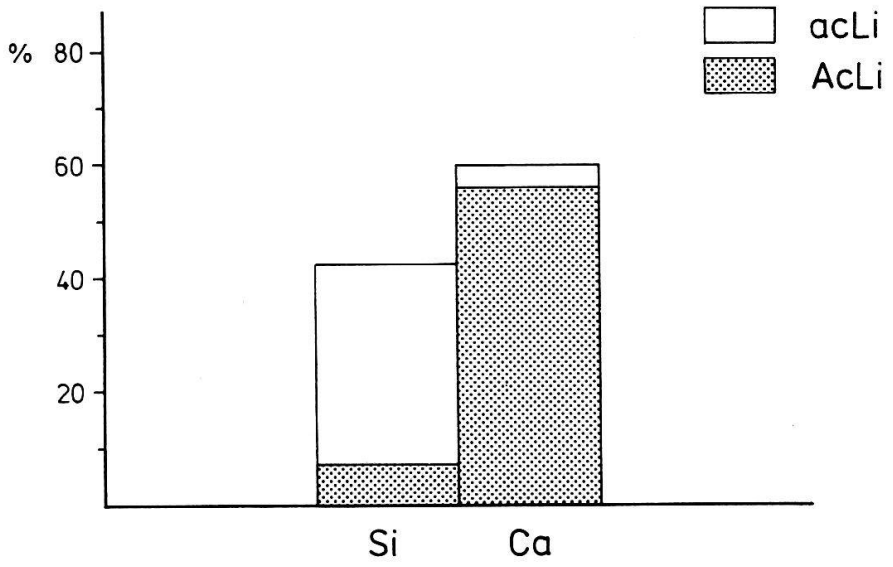

Fig. 6. Global frequencies (%) and allelic configurations of enzymatic plants in the material from acidic silicate (Si) and carbonate (Ca)

Häufigkeit (%) und Allel-Konfigurationen bei enzymatischen Pflanzen von saurem Silikat- (Si) und Karbonatgestein

352 individuals corresponding to 83.2% being found (Fig. 6). Only 71 plants represented the cyanogenic configuration *AcLi*.

Carbonate (Table 17). Enzymatic plants represented more than fifty per cent in most of the samples examined. On the whole, 657 enzyme-carrying individuals were found, the corresponding global frequency being of 59.8% (Fig. 6). The enzymatic group from carbonate was represented by 615 cyanogenic individuals *AcLi* (93.6%, Fig. 6), the acyanogenic configuration *acLi* being found solely in 42 plants.

When the two alpine substrata were compared to each other, global frequencies of enzymatic plants did not offer as drastic differences as those of the glucosidic plants (Fig. 6). On the other hand, opposite tendencies in the distribution of allelic configurations were unmistakable (Fig. 6); in this respect, the enzymatic groups differed completely from the glucosidic ones that represented comparable trends in distribution of allelic configurations within both substrata studied (Fig. 5).

3.3. *Frequencies of Ac/ac and Li/li alleles*

3.3.1. *Variation in samples and global evaluations*

Acidic silicate (Table 18). The frequencies of the dominant allele *Ac* varied in the samples studied from 2.8% to 22.6%; on the other hand, the recessive form *ac* always occurred in high frequencies (77.4% - 97.2%). Variation ranges of the *Li/li* alleles partly overlapped, the dominant form varying between 17.9% and 63.7% and the recessive one between 36.7% and 82.1%.

Carbonate (Table 19). Frequencies of the dominant allele *Ac* were consistently high (57.4% - 99.0%), whereas those of the recessive form *ac* always represented lower values (1.0% - 42.6%). As far as the *Li/li* alleles are concerned, the dominant form varied in frequency between 37.8% and 80.6%, the variation range of the recessive allelomorph being 19.4%-62.2% (Table 19).

An exceedingly interesting pattern emerged when the samples from acidic silicate were compared to those from carbonate. The dominant alleles and the recessive ones did occur in inverse proportions in either of the two alpine substrata. The *Ac/ac* alleles formed the two distinct classes of

Table 18. Allelic frequencies (%) in samples from acidic silicate
Häufigkeit (%) von Allelen in Proben von saurem Silikat

Sample code	Ac	ac	Li	li
14/82	2.8	97.2	32.4	67.6
19/82	3.8	96.2	17.9	82.1
6/82	4.0	96.0	49.4	50.6
13/82	5.8	94.2	50.0	50.0
16/82	6.0	94.0	36.0	64.0
17/82	8.0	92.0	63.7	36.3
18/82	8.4	91.6	48.6	51.4
2/82	12.0	88.0	26.6	73.4
20/82	16.8	83.2	63.3	36.7
15/82	22.6	77.4	52.0	48.0

Table 19. Allelic frequencies (%) in samples from carbonate

Häufigkeit (%) von Allelen in Proben von Karbonatgestein

Sample code	Ac	ac	Li	li
3/82	57.4	42.6	37.8	62.2
4/82	64.8	35.2	48.4	51.6
7/82	73.2	26.8	71.2	28.8
VS/82	73.2	26.8	70.8	29.2
8/82	76.6	23.4	63.8	36.2
9/82	79.2	20.8	63.4	36.6
5/82	79.6	20.4	77.6	22.4
12/82	93.0	7.0	58.0	42.0
11/82	98.0	2.0	80.6	19.4
10/82	99.0	1.0	50.6	49.4

Table 20. Global allelic frequencies (%) in the material from acidic silicate (Si) and carbonate (Ca)

Häufigkeit (%) von Allelen bei Material von saurem Silikat- (Si) und Karbonatgestein (Ca)

Substratum	Ac	ac	Li	li
Si	8.8	91.2	42.2	57.8
Ca	77.2	22.8	59.8	40.2

frequency within either substratum; however, the actual variation range in the samples from silicate was rather narrow and corresponded to 19.8% (2.8 - 22.6/77.4 - 97.2 per cent), whereas the samples from carbonate varied over 41.6% (57.4 - 99.0/1.0 - 42.6 per cent). The *Li/li* alleles, on the other hand, had very similar ranges of frequency variation within both substrata studied; it corresponded to 45.8% in samples from silicate (17.9 - 63.7/36.3 - 82.1 per cent) and to 42.8% in samples from carbonate (37.8 - 80.6/19.4 . 62.2 per cent).

Global evaluations (Table 20, Fig. 7) generally reflected the intriguing differences in allelic frequencies, but the variation related to *Ac/ac* alleles was shown to a lesser degree.

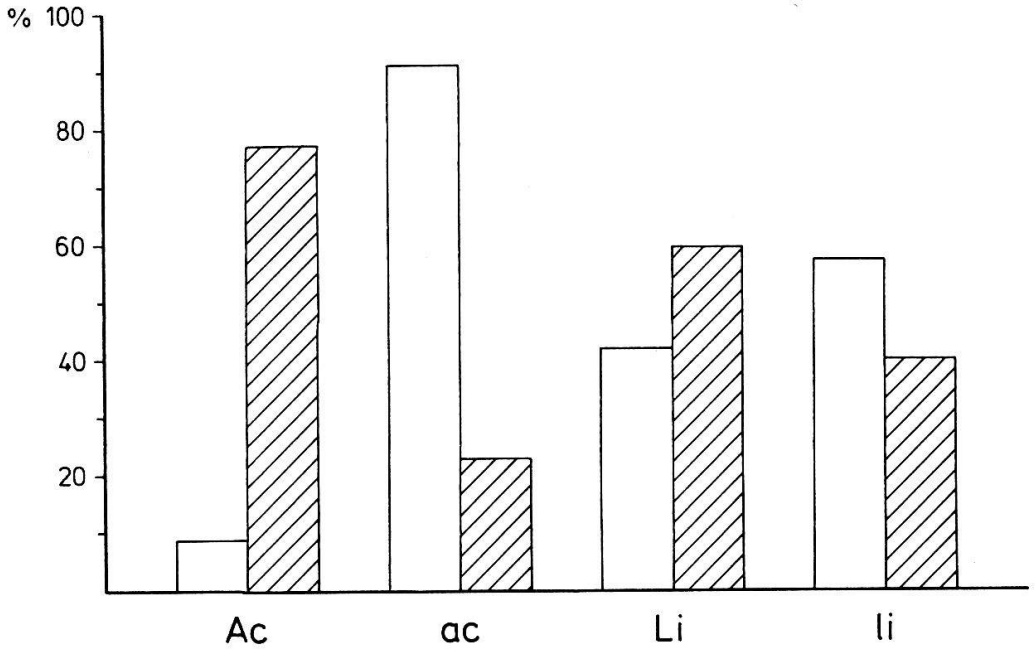

Fig. 7. Global allelic frequencies (%) in the material from acidic silicate and carbonate

Häufigkeit (%) von Allelen bei Material von saurem Silikat- und Karbonatgestein.

3.3.2. *Allelic frequencies in the acyanogenic material*

Acidic silicate (Table 21). The *Ac/ac* alleles formed small, radically distinct frequency classes, the dominant form varying from 0.0% - 6.5%, whereas the recessive one was represented by a well-defined group of high frequencies (93.5% - 100.0%). The *Li/li* alleles varied within partly overlapping ranges of 44.9% (16.4 - 61.3/38.7 - 83.6 per cent).

Carbonate (Table 22). The distribution of allelic frequencies in the samples from carbonate clearly represented an opposite tendency as compared to the silicate. The partly overlapping variation ranges of the *Ac/ac* alleles corresponded to as much as 79.3% (18.5 - 97.8/2.2 - 81.5 per cent). On the other hand, frequencies of the *Li/li* alleles represented two distinct classes; the dominant form varied in frequency from 0.0% - 22.9%, whereas the recessive one consistently occurred in high frequencies (77.1% - 100.0%).

Table 21. Allelic frequencies (%) in acyanogenic samples from acidic silicate

Häufigkeit (%) von Allelen in Proben von saurem Silikatgestein

Sample code	Ac	ac	Li	li
18/82	0.0	100.0	43.9	56.1
14/82	0.9	99.1	31.2	68.8
16/82	1.1	98.9	32.6	67.4
2/82	1.4	98.6	17.7	82.3
6/82	1.4	98.6	47.9	52.1
19/82	1.9	98.1	16.4	83.6
17/82	2.1	97.9	61.3	38.7
20/82	2.3	97.7	57.0	43.0
13/82	3.0	97.0	48.5	51.5
15/82	6.5	93.5	41.9	58.1

Table 22. Allelic frequencies (%) in acyanogenic samples from carbonate

Häufigkeit (%) von Allelen in Proben von Karbonatgestein

Sample code	Ac	ac	Li	li
VS/82	18.5	81.5	11.1	88.9
7/82	25.0	75.0	19.4	80.6
5/82	25.9	74.1	18.5	81.5
3/82	31.7	68.3	0.0	100.0
8/82	40.5	59.5	8.1	91.9
4/82	40.8	59.2	13.3	86.7
9/82	56.3	43.7	22.9	77.1
12/82	83.3	16.7	0.0	100.0
11/82	89.5	10.5	0.0	100.0
10/82	97.8	2.2	0.0	100.0

Table 23. Global allelic frequencies (%) in the acyanogenic material from acidic silicate (Si) and carbonate (Ca)

Häufigkeit (%) von Allelen im cyanogenen Material von saurem Silikat- (Si) und Karbonatgestein (Ca)

Substratum	Ac	ac	Li	li
Si	2.0	98.0	37.8	62.2
Ca	48.2	51.8	8.6	91.4

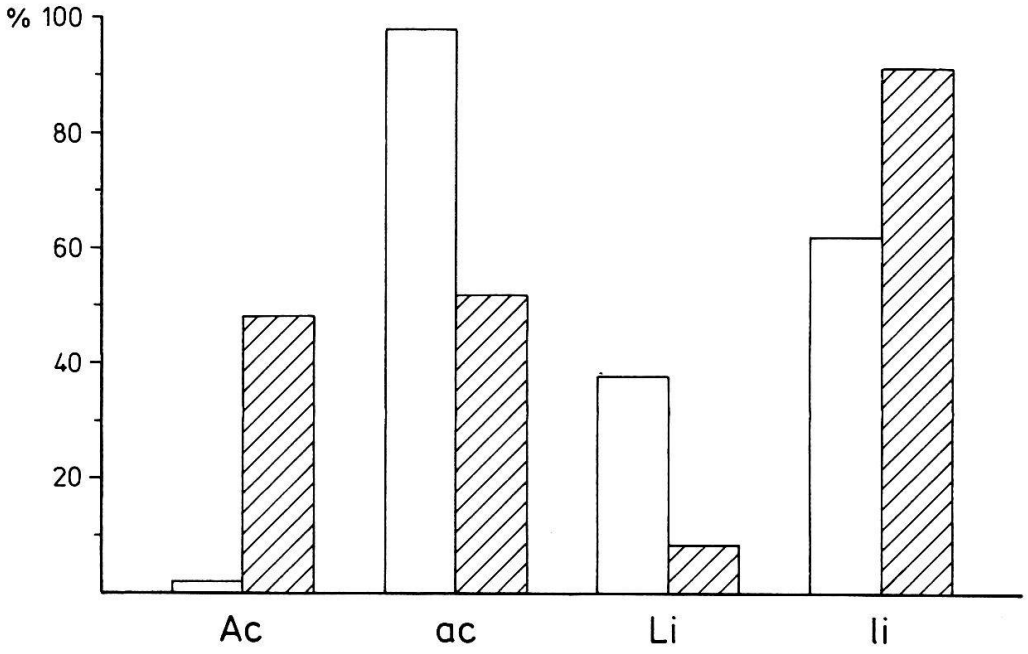

Fig. 8. Global allelic frequencies (%) in the acyanogenic material from acidic silicate and carbonate

Häufigkeit (%) von Allelen bei acyanogenem Material von saurem Silikat- und Karbonatgestein

acidic silicate
saures Silikatgestein

carbonate
Karbonatgestein

Global evaluations (Table 23, Fig. 8) clearly showed the differences between particular allelic frequencies for the material from acidic silicate and carbonate.

4. Discussion

Antithetical patterns in distribution of phenotypic and allelic frequencies observed in *Lotus alpinus* from acidic silicate and carbonate suggest distinct selective pressures operating in either of the two alpine substrata.

Influence of edaphic factors upon the cyanogenesis in plants is apparent-

ly rather complex. For instance, some reports indicate a relationship between drought and distribution of gross phenotypes (e.g. CORKILL 1952, FOULDS and GRIME 1972, ABBOTT 1977, BAND et al. 1981). It seems that the soil moisture stress may also act indirectly e.g. by lessening the availability of phosphorus in soil (BOYD et al. 1938) or limiting the soil nitrogen (DEMENT and MOONEY 1974). Not only physical soil properties but also its actual ionic composition seem to play an important rôle in the polymorphism of cyanogenesis. Data of KEYMER and ELLIS (1978) as well as those of FOULDS (1982) indicate an influence of sodium chloride concentration. The results of the present author and the recent study of DICKENMANN (1982) strongly suggest a relationship between cyanogenesis polymorphism and the bound nitrogen form in alpine soils.

Differencies in frequencies of gross phenotypes represent an important aspect of the cyanogenesis polymorphism in *Lotus alpinus*. The results of the present study generally confirm the author's previous data (e.g. URBANSKA 1982, URBANSKA and DICKENMANN 1981, URBANSKA and SCHWANK 1980). Very pronounced differences in distribution of cyanogenic and acyanogenic plants upon acidic silicate and carbonate corroborate prima facie the opinion of JONES (1970, 1972) that the phenotype of cyanogenesis itself is selected directly. The data of DICKENMANN (1982) on *Ranunculus montanus* s.l. from high altitude sites in the Swiss Alps also suggest a gross phenotype selection.

The present study indicates, however, that the polymorphism of cyanogenesis in *Lotus alpinus* is related not only to gross phenotypes but also the actual allelic configurations. We don't think that the distinct patterns observed upon silicate and carbonate are due to the sampling technique. As justly pointed out by JONES (1973), recessive alleles could easily be overlooked when population samples are not sufficiently large; however, in case of *Lotus alpinus* the dominant alleles *Ac* and *Li* are involved and the variation pattern is rather consistent.

Our investigations revealed that glucosidic plants *AcLi* represented nearly a half of the whole acyanogenic material from carbonate but corresponded to only 1.9% of the material from acidic silicate. An inverse tendency occurred in frequencies of acyanogenic enzymatic plants *acLi* that apparently were favourized upon silicate but definitely not upon

carbonate, zero frequencies being found in four out of the ten samples studied.

Details concerning the substratum and the ionic composition of the soil were rather seldom given in papers dealing with *Lotus corniculatus* and *Trifolium repens*. The excellent study of FOULDS and GRIME (1972) is, to the author's best knowledge, the only one where the site selection was actually based on the degree of rock exposition. The glucosidic acyanogenic plants *Acli* were very well represented in samples studied by the British authors from dry limestone outcrops; on the other hand, the enzymatic plants *acLi* were conspicuously rare with zero frequencies in three out of the four samples studied. It is exceedingly interesting that these patterns correspond rather exactly to the trends found in *Lotus alpinus* from carbonate. Also DE ARAUJO (1976) observed in some samples of *Trifolium repens* low or zero frequencies in *acLi* plants parallelly to very high frequencies of glucosidic individuals *AcLi* and *Acli*. Unfortunately, no data on edaphic conditions were given in his paper. It should be very interesting to have more information on his subject, especially from sites where soil development is not advanced. Differential performance of plants representing various allelic configurations was previously observed in *Trifolium repens* by DADAY (1965); he supposed that the locus concerned with cyanoglucoside might be linked to genes influencing fitness. FOULDS and GRIME (1972a) found that glucosidic plants of *T. repens* showed higher mortality than the corresponding types of *L. corniculatus* when subjected to severe drought; however, they observed no differences possibly related to the locus controlling the biosynthesis of enzyme. On the other hand, DOMMEE et al. (1980) found that individuals of *T. repens* carrying the dominant allele *Li* developed better in vitro than the plants carrying the recessive allelomorph, the root growth being particularly concerned. Recent studies of TILL (1983) also suggest that differences in allelic configurations might influence differential responses of *T. repens* towards some environmental factors.

Cyanogenesis was frequently considered as a protective mechanism against herbivores (for detailed information on the subject see e.g. JONES 1972, 1973, JONES et al. 1978). There is both a direct and a circumstantial evidence of a preferential eating of the acyanogenic plants of *Lotus*

corniculatus and *T. repens* by some herbivores (CRAWFORD-SIDEBOTHAM 1972, ANGSEESING and ANGSEESING 1973, WHITMAN 1973, ELLIS et al. 1977); however, no data are available on plants carrying only one dominant allele. Curiously enough, KEYMER and ELLIS (1978) found that a non-selective grazing of *Lotus corniculatus* caused the most reduction in glucosidic individuals representing both cyanogenic and acyanogenic types. It should be most interesting to know whether some herbivores are not only able to distinguish between the gross phenotypes but also to recognize the particular acyanogenic individuals, especially by the glucosidic ones *Acli*: it is known that the cyanoglucoside itself may be deterrent to potential consuments (e.g. NAYER and FRAENKEL 1963).

Cyanoglucosides seem to be not only useful in some antiherbivore strategies but also relevant for nitrogen economy, especially in plants living in difficult environments. DEMENT and MOONEY (1974) suppose that cyanoglucosides in *Heteromeles arbutifolius* are produced early in season when climatic conditions are favourable to a rapid N-cycling in the chapparal soil; later on, when nitrogen becomes limiting and predator pressure diminishes, glucosides could be metabolized and the nitrogen used by plants. Distinct translocation of cyanoglucosides from rosette leaves to reproductive structures observed by the present author in *Eschscholzia mexicana* (URBANSKA, in press) suggest as well both a protective function and a rôle in the nitrogen economy of the annual desert taxon. It is quite possible that cyanogenic compounds might play a part in the complex nitrogen budget of legumes as indicated e.g. by data of ABROL and CONN (1966) or those of BLUMENTHAL et al. (1968).

Apart from their possible importance as a source of nitrogen, cyanogenic compounds seem to be concerned with some essential aspects of plant life, endogenous HCN acting as a possible regulator in several enzymatic processes. As yet the available data are very fragmentary, but it seems that various physiological functions might be involved. Influence of cyanide upon cytochrome oxidase has since long been known (see e.g. MARSH and GODDARD 1939, LUNDEGARDH 1966). Studies of FOULDS and YOUNG (1977) reveal that the effect of HCN in plants may be greater on enzymes involved in photosynthesis than those controlling respiration. Data of ECK and HAGEMANN (1974) as well as the results of SOLOMONSON and SPEHAR

(1977) suggest that endogenous cyanide might operate as agent in the nitrate reductase regulation. The physiological importance of rapid inactivation or turn-over of the nitrate reductase may permit a rapid adjustment of activity in response to changes in external nitrogen supply or alterations in the plant requirements for reduced nitrogen (see e.g. LEE and STEWART 1978); it could accordingly represent an important adaptive feature.

Fitness in plants comprises various facets, not only the very survival but also metabolic processes, vegetative performance as well as reproduction being involved. Plant life strategies are finely balanced, allelic structure of particular individuals obviously contributing to differences observable within and between populations. It could be that balanced polymorphism for cyanogenesis in some taxa might reflect these various aspects.

In his interesting concept of a cyclical selection, JONES (1970) assumed a "physiological superiority" of cyanogenic plants. As far as *Lotus alpinus* is concerned, not only the cyanogenic phenotypes but *glucosidic* plants in general apparently are at advantage upon carbonate (global frequency of 77.2%). The production of cyanoglucoside appears therefore to be a rather important element in the resource allocation pattern in plants inhabiting carboniferous alpine soils and using NO_3-N. It is conceivable that a differential fitness of plants carrying the dominant allele *Ac* might be partly due e.g. to an efficient nitrate assimilation and a subsequent storage of nitrogen in form of cyanoglucosides that are less costly to produce and metabolize than biopolymeres. Glucosidic individuals or at least the cyanogenic ones might also be protected against some alpine herbivores. On the other hand, the *acli* plants carrying recessive alleles in both loci might be able to allocate more of their resources to growth and reproduction.

Acidic siliceous soils in the Alps supposedly contain ammonium as a prevailing form of the bound nitrogen in high altitude sites. Strategies of uptake and assimilation of NH_4-N obviously are different from those involved in feeding on nitrate and may require regulators others than cyanide. The accumulation of cyanoglucosides and other nitrogen compounds is possibly achieved at the expense of plant growth and reproduction; the

absolute predominance of *aglucosidic* individuals of *Lotus alpinus* upon acidic silicate (global frequency of 91.1%) strongly suggests that plants in extreme ecosystems live in a strict budget and can afford only indispensable expenses.

It goes without saying that the considerations presented above are open to verification, experimental studies in *Lotus alpinus* being imperative. Of a special interest should be an experimental program involving the four allelic configurations, not only the productivity but also the sexual phase being studied e.g. under various supply conditions of NO_3-N and NH_4-N.

Some available data do suggest that differential growth and reproduction may represent key factors in the maintenance of the balanced polymorphism for cyanogenesis (e.g. DAWSON 1942, JONES 1962, URBANSKA et al. 1979). The previous studies in reproduction of taxa that are polymorphic for cyanogenesis rather infrequently dealt with precise allelic configurations. It should be most important to know more about general performance, seed output as well as germination and seedling establishment in glucosidic, aglucosidic and/or enzymatic individuals representing both cyanogenic and acyanogenic phenotypes. Further reports are awaited with interest.

Summary

Antithetical patterns in distribution of phenotypic and allelic frequencies observed in *Lotus alpinus* from acidic silicate and carbonate suggest distinct selective factors operating in either of the two alpine substrata.

The material from silicate was largely acyanogenic (92.9%) whereas cyanogenic plants prevailed in the material from carbonate (56.0%). The polymorphism of cyanogenesis in *L. alpinus* is related not only to gross phenotypes, but also the actual allelic configurations, differences in the acyanogenic material from silicate and carbonate being particularly pronounced.

Opposite tendencies in distribution of cyanoglucoside allele *Ac* upon silicate and carbonate were clearly recognizable in global evaluations, the respective frequencies being 8.8 vs. 77.2 per cent. The most characteristic differences observed in acyanogenic material related to both dominant alleles *Ac* and *Li*: the glucoside allele occurred only in 2.0%

upon silicate but in 48.2% upon carbonate, an inverse tendency being found in the enzyme allele frequencies (37.8 vs. 8.6 per cent).

Some metabolic processes, vegetative development and reproduction are considered as possible aspects of a differential fitness in plants representing various allelic configurations.

Zusammenfassung

Bei *Lotus alpinus* von saurem Silikat- und Karbonatgestein wurden verschiedenartige Verbreitungsmuster von Phänotypen und Allelen beobachtet, die vermuten lassen, dass unterschiedliche Selektionsfaktoren auf den beiden Unterlagen wirken.

Das Material von der Silikatunterlage war weitgehend acyanogen (92.9%), während auf der Karbonatunterlage cyanogene Pflanzen vorherrschten (56.0%). Der Polymorphismus der Cyanogenese zeigt sich nicht nur in den hauptsächlichen Phänotypen, sondern auch in der Allel-Zusammensetzung, wobei die Unterschiede innerhalb der acyanogenen Pflanzen von Silikat- und Karbonatgestein besonders ausgeprägt sind.

Sehr charakteristisch erwiesen sich gegensätzliche Tendenzen in der Verbreitung der Cyanoglucosid-Allele *Ac* auf dem Silikat und auf dem Karbonat bei der Gesamtauswertung; die entsprechenden Häufigkeiten waren 8.8 bzw. 77.2%. Die deutlichsten Unterschiede bei den acyanogenen Pflanzen wurden in bezug auf die dominanten Allele *Ac* und *Li* beobachtet: das Glucosid-Allel trat auf Silikat nur in 2% auf, gegenüber 48.2% auf Karbonat. Umgekehrte Verhältnisse werden für das Enzym-Allel angetroffen (37.8 bzw. 8.6%).

Physiologische Vorgänge, vegetative Entwicklung und Fortpflanzung tragen in unterschiedlicher Weise zur Lebenstüchtigkeit von Pflanzen verschiedener Allel-Zusammensetzung bei.

Résumé

Les tendances antithétiques reconnues dans la distribution des phénotypes et allèles chez *Lotus alpinus* sur silice et sur carbonate laissent supposer des facteurs sélectifs différents opérant sur chacun des deux substrats alpins.

Le matériel en provenance de substrat siliceux s'est révélé largement acyanogénique (92.9%); en revanche, les plantes cyanogéniques ont été majoritaires sur substrats carbonatés (56.0%). Le polymorphisme de la cyanogénèse chez *L. alpinus* est lié non seulement aux phénotypes principaux mais aussi aux configurations alléliques différentes, ce qui se voit en premier lieu dans le matériel acyanogénique.

Les tendances opposées dans la distribution de l'allèle *Ac* sur silice et sur carbonate ont été observées dans les évaluations globales, les fré-

quences respectives étant 8.8 contre 77.2 pour cent. Les différences les plus caractéristiques trouvées dans le matériel acyanogénique se rapportaient aux deux allèles dominants *Ac* et *Li*: l'un ne représentait que 2.0% sur silice mais il était présent à 48.2% sur carbonate, l'autre au contraire étant plus fréquent sur silice que sur carbonate (37.8 contre 8.6 pour cent).

Certains processus métaboliques, le développement végétatif ainsi que la reproduction sont considérés comme des aspects possibles d'une "fitness" différentielle des plantes portant des configurations alléliques différentes.

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