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Variation within *Lotus corniculatus* L. s. l. from Switzerland
III. Microdifferentiation in *L. alpinus* (DC) Schleicher above the timberline

by

Krystyna URBANSKA-WORYTKIEWICZ and Othmar SCHWANK

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1. Introduction

In the first paper of this series, a preliminary report on chromosome numbers and cyanogenesis in *Lotus corniculatus* L.s.l. from Switzerland was presented (URBANSKA-WORYTKIEWICZ and WILDI 1975). Variation patterns described then in *L. alpinus* from subalpine and alpine vegetation zone suggested an influence of altitude above sea level upon the microdifferentiation of this taxon; they also pointed out to the importance of substrate. It was therefore decided to study these aspects. The present paper deals with *Lotus alpinus* from above the timberline, the studied altitude bracket being 2200 - 3100 m a.s.l. A possible influence of substrate was studied in acidic silicate,

carbonate as well as serpentine; on the one hand, the restricted yet geologically heterogenous area from Davos (Grisons) was studied in more detail, on the other hand, various geologically different localities in Northern and Central Swiss Alps were taken into consideration.

Acknowledgements

We wish to express our thanks to Ms. B. Egger (Geobotanical Institute) for information on annual nitrogen accumulation on alpine soils from the region of Davos and comments on water conditions within the serpentine. Our thanks are also due to Mr. H.-R. Oberholzer (Swiss Federal Research Station for Agronomy, Zürich) for preliminary observations on root nodules in *L. alpinus* as well as isolation of the *Rhizobium* strains. We are most grateful to Dr. W. Wildi (Geological Institute SFIT Zürich) for advice on geological nomenclature, to Mr. A. Grünig (Geobotanical Institute) for the translation of the summary into German and to Ms. E. Wohlmann-Bräm who made the drawings. The information of Ms. A. Rueggli-Walser on *Lotus alpinus* in the region of Schesaplana, Grisons, is greatly appreciated.

2. Material and methods

The present report summarizes the data collected in 1975-1979; the junior author (O.S.) participated in the programme during his Diploma Thesis (1976-1977). On the whole, 3394 plants were examined as to their chromosome number and cyanogenesis; the best represented were materials from acidic silicate (1746 individuals), whereas the samples from carbonate comprised 1139 plants and only 509 individuals were studied from serpentine.

Chromosome numbers were examined in stem apex smears stained with lacto-propionic orcein; the method proved to be quite satisfactory for a fast cytological control. Cyanogenesis was studied in the standard picrate paper test with a sulphur-free toluene as organic dissolvent; only adult plants were tested, both the reproducing as well as non-reproducing ones being used. Most frequently, two uppermost well-developed leaves were taken. For the time being, only two gross phenotypes were distinguished; the term "cyanogenic" used in the report refers accordingly to plants carrying both glucoside and enzyme.

For the classification of rocky substratum, the Geological Atlas of Switzerland was used as the reference; the denomination of the three substrate

groups is, however, arbitrary. The samples respectively coded as Si 12 and Si 24 i.e. those from acidic silicate, originated from various types of acidic crystalline and sedimentary rocks (e.g. gneiss, quartzites, paraschists, radiolarite). As far as the material from carbonate is concerned, the sample codes Ca 12 and Ca 24 refer to plants from the dolomite, calciferous schists and other carbonate-bearing rocks. The serpentine group coded Se 24 comprises, in addition to the true serpentine substratum, plants from other basic crystalline rocks e.g. ophicalcite.

3. Results

3.1. Cytological variation

Lotus alpinus is differentiated into two chromosomal races viz. diploid ($2n=12$) and tetraploid ($2n=24$); detailed references in this subject were given in a previous publication (URBANSKA-WORYTKIEWICZ and WILDI 1975). The present results corroborate our preliminary data on the general distribution of *L. alpinus* in Switzerland, diploids being found most frequently in Central Swiss Alps and only occasionally recorded in northern parts of the Alpine ridge. The precise distribution of diploids and tetraploids above the timberline is apparently influenced by altitude, but still more so by type of substrate; the resulting trends are sometimes amazingly accurate. As far as the three studied alpine substrates are concerned, the study is still in progress and some points are open to verification, but general patterns have emerged from the obtained results (Fig.1). They can be commented upon in the following way:

I. Acidic silicate. This type of substrate combined with higher altitudes within the alpine zone seems to be representative of the diploid *Lotus alpinus*. The diploids occurred most frequently between 2300-2900 m a.s.l., the upper altitude limit being found so far at about 3100 m a.s.l. (Gornergrat near Zermatt, Wallis). It is interesting to note that even at the highest altitudes, the diploids completed their reproductive cycle, flowering as well as fruit-setting being observed.

At lower altitudes within the alpine vegetation zone, acidic silicate was most frequently inhabited by tetraploid populations of *L. alpinus*. Depending

on the region, the 24chromosomal plants reached about 2300-2400 m a.s.l. but usually disappeared above this limit giving way to the diploids. The contact zone between diploids and tetraploids was narrow (60-70 m of a vertical difference) and heteroploid populations were but exceptional; no triploids were ever found. In these respects, the present results confirm our previous data (URBANSKA-WORYTKIEWICZ and WILDI 1975).

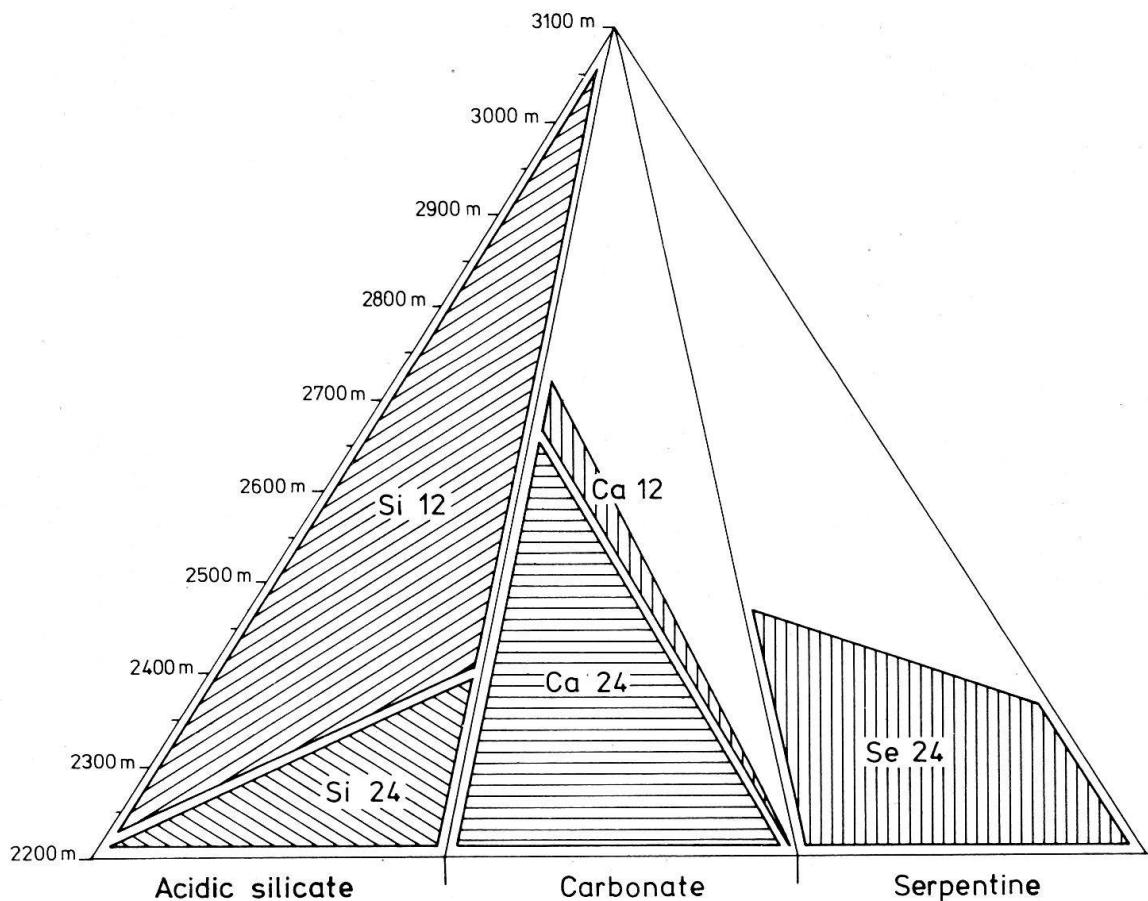


Fig. 1. Distribution patterns of diploid and tetraploid *Lotus alpinus* within the three studied types of substrate above the timberline.

II. Carbonate. This type of substrate was most frequently inhabited by the tetraploids. It should be stressed that the 24chromosomal carbonate populations of *L. alpinus* reached much higher altitudes than the tetraploids grow-

ing upon acidic silicate or serpentine (Fig. 1); the highest altitude observed so far for tetraploids was 2650 m a.s.l. (Aroser Weissfluh, Grisons). Another interesting feature was that in some carbonate regions (e.g. Schiahorn, 2708 m, Schesaplana, 2964 m, both Grisons), tetraploids disappeared at about 2500 m a.s.l., in spite of no appreciable change of gradient and/or vegetation type.

The calciferous substratum in Swiss Alps seems to be only exceptionally inhabited by the diploid *Lotus alpinus*; in spite of repeated search, the 12chromosomal populations were found only twice upon carbonate, both times within high mountain massifs containing numerous glaciers. The station in the Diable-rets had locally well-developed soil with the corresponding pH-readings of about 5.0. On the other hand, plants found between Point de la Plaine Morte and Tubang and in particular those occurring in Tubang, were growing in steep scree slopes, the pH values being 7.5-8.0. It should be noted that the diploids in Tubang occurred within narrow stripes of an open vegetation only between 2700-2600 m a.s.l. and disappeared already at about 2600 m a.s.l. to be replaced by tetraploids without any particular change in the environment. An exact borderline between diploids and tetraploids remains to be determined in Tubang, but an intermediate zone, if actually existing, must be exceedingly narrow.

III. Serpentine. This type of substrate was found so far inhabited solely by tetraploid populations of *Lotus alpinus*. The 24chromosomal plants were locally abundant and apparently well adapted to the difficult edaphic conditions; however, their altitude limit did not exceed some 2450 m a.s.l. in spite of fact that a rather well-developed vegetation was sometimes observed above this limit.

3.2. Cyanogenesis

Lotus alpinus is polymorphic for cyanogenesis (URBANSKA-WORYTKIEWICZ and WILDI 1975). The variation in frequencies of cyanogenic/acyanogenic phenotypes occurring within Swiss populations is rather complex; at the present stage of investigations, it is difficult to be conclusive about the importance of particular factors because of the marked relationships between them. There is some evidence of a regional variation within Swiss Alps; in addition, local

Table 1. Cyanogenesis in *Lotus alpinus* in three alpine substrate types.

Substrate	Sample code	2n	Number of studied plants HCN ⁻	HCN ⁺	Total
Acidic silicate	Si	12	948	255	1203
Acidic silicate	Si	24	504	39	543
Carbonate	Ca	12	96	240	336
Carbonate	Ca	24	577	226	803
Serpentine	Se	24	487	22	509

differences not related to small variations in altitude were sometimes noted. Both these aspects will need to be considered in future. The hitherto obtained results do, however, indicate a strong influence of substrate upon the phenotypic frequencies and suggest as well a relationship between degree of polyploidy and cyanogenesis (Table 1, Figs 2-4).

A global evaluation of the HCN-tests revealed an exceedingly interesting general pattern of microdifferentiation occurring within alpine populations (Fig. 2). The highest frequencies of cyanogenic phenotypes occurred invariably in populations growing upon carbonate. It should be noted, however, that there was a pronounced difference between diploids and tetraploids, the former ones comprising as much as 71.4 %, the latter ones - only 28.1 % of cyanogenic adults. All the tested populations from carbonate were polymorphic for cyanogenesis. As far as the samples from acidic silicate are concerned, diploid populations had 21.2 % of cyanogenic phenotypes; on the other hand, there was a marked drop in frequencies of HCN-positive plants within the tetraploid material, the corresponding percentage being only 7.2 %. The distribution of cyanogenic phenotypes within populations growing upon acidic silicate was rather erratic, some populations being uniformly acyanogenic both on the diploid as well as the tetraploid level. The material from serpentine was characterized by a well-defined trend towards acyanogenic status, remarkably low frequencies of cyanogenic plants viz. 4.3 % being found. It should be added that the rare cyanogenic individuals originated all but one from a single large population.

In an attempt to consider the relationships between cyanogenesis and type of substrate notwithstanding the cytological differentiation, the data contained

in Table 1 were transformed into percentages. Fig. 3 presents the issue, frequencies of cyanogenic phenotypes being quite distinct in each of the three studied types of substrate: carbonate samples are globally characterized by 40.9 %, acidic silicate samples comprising 16.9 % and samples from serpentine being predominantly acyanogenic (4.3 %).

The second approach adopted in the present report was to consider frequencies of cyanogenic phenotypes solely in relation to the degree of polyploidy, not paying attention to the substrate (Fig. 4). The results suggest different ways of adaptation in either of the two chromosomal races of *Lotus alpinus*, the percentage of cyanogenic diploid individuals being about twice as high

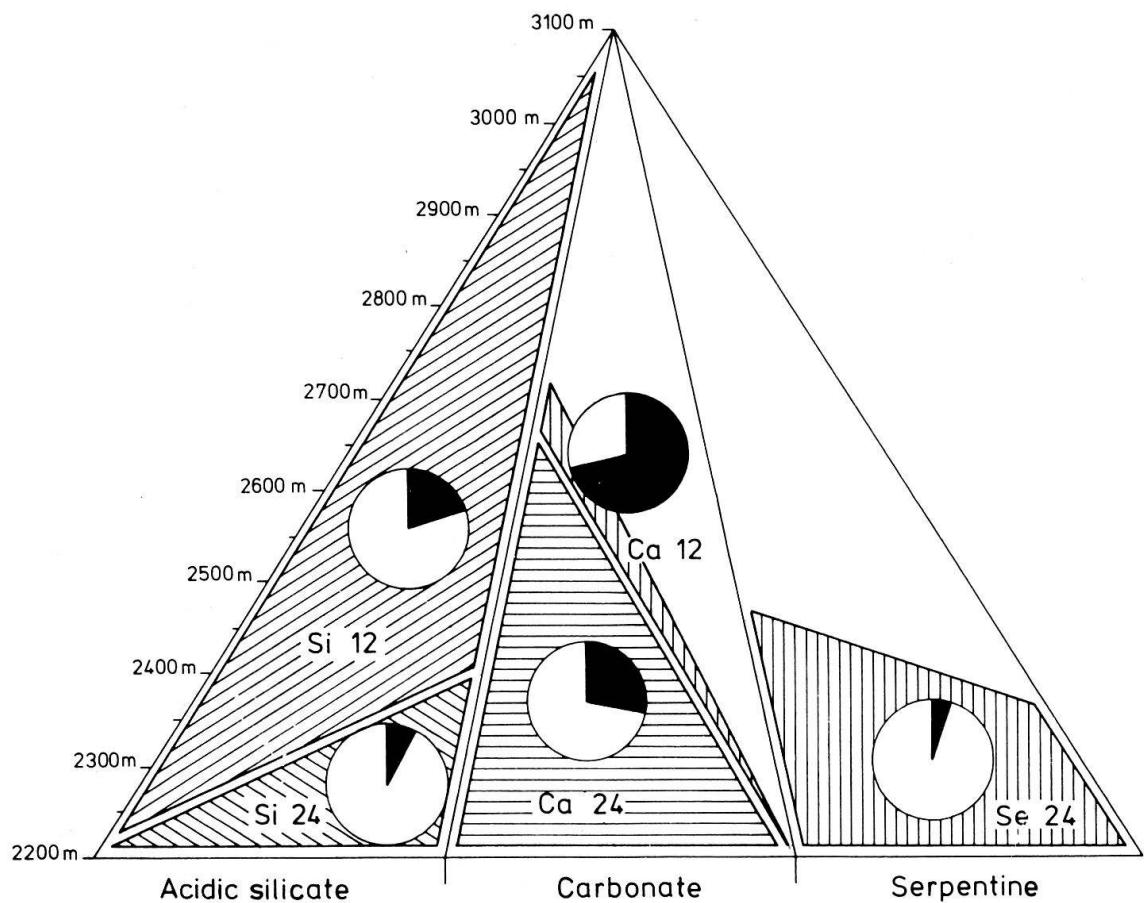


Fig. 2. Cyanogenesis in *Lotus alpinus* from the three alpine substrates; black sections (pies) refer to frequencies (%) of cyanogenic phenotypes.

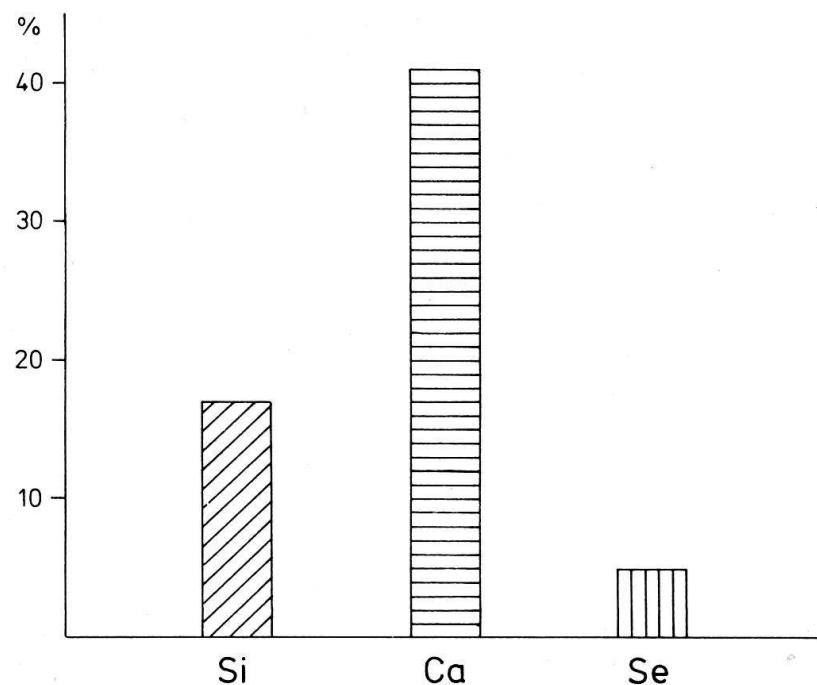


Fig. 3. Global frequencies (%) of cyanogenic phenotypes in three alpine substrates, evaluated with no regard to the degree of polypliody.
 Si = acidic silicate, Ca = carbonate, Se = serpentine.

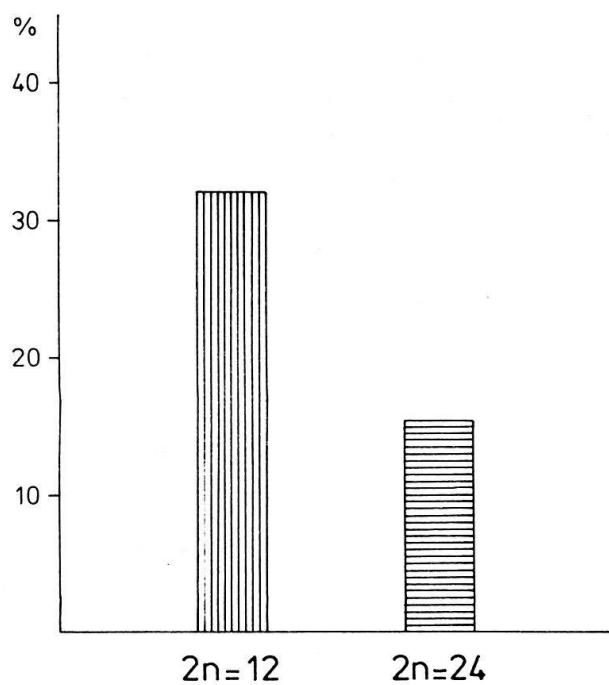


Fig. 4. Frequencies (%) of cyanogenic phenotypes in two chromosome races of *Lotus alpinus* from above the timberline, with no regard to the type of substrate.

Table 2. Frequencies (%) of cyanogenic phenotypes in the two chromosomal races of *Lotus alpinus* within subalpine and alpine vegetation zone. Previous data of URBANSKA-WORYTKIEWICZ and WILDI (1975) are marked with an asterisk (*).

Vegetation zone	Frequencies (%) of cyanogenic phenotypes	
	2n=12	2n=24
alpine	40.3*	23.5*
	32.2	15.5
subalpine	10.4*	24.5*

as that of the tetraploids (32.3 % vs. 15.5 %). It is not excluded that some shift toward a higher frequency on the diploid level is due to the peculiar occurrence of highly cyanogenic diploid populations upon carbonate, but a general tendency remains rather distinct.

To compare our preliminary results (URBANSKA-WORYTKIEWICZ and WILDI 1975) with the present ones, we reworked some of the previous data using phenotype frequencies and not numbers of examined plants. They were compared globally no regional groups being distinguished and the sole attention being paid to the level of polyploidy (Table 2).

The comparison shows a marked increase in frequencies of cyanogenic diploid phenotypes when passing from subalpine to alpine vegetation zone. On the other hand, the previous data do not suggest any substantial differences in the corresponding frequencies of tetraploids revealed in the present study. It should be noted, however, that the predominantly acyanogenic alpine tetraploids from serpentine were not yet examined at that time. Curiously enough, both the previous and the present data show nearly the same difference in frequencies of cyanogenic diploids and tetraploids within the alpine zone (16.8 % vs. 16.7 %).

4. Discussion

Data obtained on relative frequencies of cyanogenic and acyanogenic phenotypes within populations polymorphic for cyanogenesis indicate that numerous

ecological components are involved, abiotic as well as biotic factors playing a selective rôle. However, contradictory findings being reported on several occasions, JONES (1977) argued that interpretations should be confined to the plants and areas actually studied; his opinion is fully supported by the results of the present investigations.

Amongst the abiotic factors considered as being of importance for genotypic frequencies, temperature should be mentioned. DADAY (1954a) found that cyanogenic forms of *Trifolium repens* in lowland stations of Europe and the Near East apparently were at a selective disadvantage in low winter mean temperatures; later on, he demonstrated a corresponding behaviour of *T. repens* in Australia (DADAY 1965). DADAY suggested that the mechanism of selection against cyanogenic phenotypes in cold temperatures was an irreversible inhibition of respiration by HCN released by the activated enzyme. The data of DADAY concerning the European material were based on samples originating from localities separated by large distances; on the other hand, results of JONES (1968) suggest no important temperature effect over short distances. It should be noted, however, that the two reports are hardly comparable, not only the sampling technique but also the material being different: DADAY was dealing with plants derived from seed samples, whereas JONES studied adults actually growing within British populations.

Cyanogenesis in *Lotus corniculatus* was studied in lowland European stations mostly by JONES and his collaborators (e.g. JONES 1962, 1968, 1970, 1971, 1972a,b, 1973a,b, 1977; JONES et al. 1978; CRAWFORD-SIDEBOTHAM 1972; ELLIS, KEYMER and JONES 1977a,b; KEYMER 1978); hitherto obtained results seem inconclusive as far as relationships between winter temperatures and phenotypic frequencies are concerned. On the other hand, our preliminary studies in *L. corniculatus* from Switzerland (URBANSKA-WORYTKIEWICZ and WILDI 1975) revealed that plants from Southern Swiss Alps were acyanogenic, whereas populations from valleys of Central Swiss Alps manifested a balanced polymorphism and those from Northern Swiss Alps as well as Swiss Midland were predominantly cyanogenic. Interestingly enough, areas situated south from the Gotthard Pass enjoy mild winter temperatures, whereas Central Swiss Alps (e.g. Wallis) have a continental type of climate. The regional variation observed in *L. corniculatus* from Switzerland shows thus tendencies inverse to those reported in *Trifolium repens* by DADAY. A precise comparison, however, must be postponed

until a more detailed study on *L. corniculatus* from Switzerland is completed; it should also be most advisable to study cyanogenesis within Swiss populations of *Trifolium repens*, as no data on plants actually growing in the wild are available.

The problem of a possible influence of temperature upon cyanogenesis is closely related to the question of the influence of altitude, particularly relevant in Alpine countries. DADAY (1954b) was the first to study this aspect. Plants examined by the British author were obtained in greenhouse from six wild seed samples of *Trifolium repens*; five Swiss samples originated from various altitudes within montane and subalpine vegetation zone, up to 1860 m a.s.l. The only Austrian sample was taken in lower alpine zone at 2130 m a.s.l. In the material studied by DADAY, both dominant glucoside and enzyme allele frequencies decreased with increasing altitude, the gene frequency clines showing a corresponding gradation with the January mean temperature. The general tendency observed by DADAY in plants from the Alpine region was confirmed by DE ARAUJO (1976) who observed a significant decrease in frequency of cyanogenic plants of *T. repens* accompanying small variations in altitude within a restricted area from North Wales. As far as *Lotus corniculatus* is concerned, our preliminary results (URBANSKA-WORYTKIEWICZ and WILDI 1975) are rather ambiguous, a regional variation apparently influencing the whole trend; it should be mentioned, however, that a tendency towards increasing frequencies of cyanogenic plants with increasing altitude occurred within northern parts of the Alpine ridge.

At higher altitudes *Lotus corniculatus* disappears giving way to *L. alpinus*. Our preliminary studies (URBANSKA-WORYTKIEWICZ and WILDI 1975) brought about an evidence of a relationship between cyanogenesis and the cytological differentiation occurring in *L. alpinus*; it was further confirmed in course of the present study. For this reason, factors influencing the distribution of the two chromosomal races of *L. alpinus* above the timberline should be commented upon before any discussion on cyanogenesis in the alpine taxon is continued.

Within a given area, diploid populations of *L. alpinus* occurred usually at higher altitudes than tetraploid ones and their altitude limits within the upper alpine zone were also higher than those of tetraploids; an influence of altitude upon the distribution of the two chromosomal races was thus notice-

able. However, the edaphic component to the microdifferentiation occurring within *L. alpinus* was much stronger than altitude; the first indications obtained in this respect in our preliminary study were positively confirmed by the present results.

Each of the three studied types of alpine substrate was characterized by a different pattern of distribution of *L. alpinus*, not only upper altitude limits but also zones inhabited respectively by diploids and tetraploids being distinct (Fig. 1). Growth type differences as well as details of the reproductive behaviour suggested a racial edaphic differentiation (URBANSKA-WORYTKIEWICZ and SCHWANK, in press; URBANSKA-WORYTKIEWICZ, SCHWANK and FOSSATI 1979).

Cyanogenesis in *Lotus alpinus* is related in a general way to the cytological differentiation: diploids can be on the whole characterized by a well-marked presence of cyanogenic phenotypes, the resp. frequencies being about twice as high as those in tetraploids. It should be emphasized, however, that the influence of substrate upon phenotypic frequencies was clearly recognizable within each chromosomal race (Fig. 2).

Data on substrate type contained in reports on cyanogenesis in *Trifolium repens* and *Lotus corniculatus* are, unfortunately, rather fragmentary. On the other hand, some attention was paid to the soil moisture as a possible selective factor maintaining polymorphism for cyanogenesis. FOULDS and GRIME (1972a, b) found soil moisture stress acting against cyanogenic phenotypes of *T. repens* and *L. corniculatus*, the response to the selection being, however, different in either of the two species. In some cases, soil moisture seemed to be of no influence (JONES 1973, ELLIS et al. 1977), whereas ABBOTT (1977) found a highly positive association between soil moisture and frequency of cyanogenic phenotypes of *L. corniculatus*.

A possible influence of water stress upon cyanogenesis in *L. alpinus* remains equivocal. The conditions within the alpine zone are greatly varying as far as the water supply is concerned, depending on substrate as well as the development of soil and vegetation in given niches; on the whole, however, carbonate alpine substrate and in particular the dolomite are considered as having an unfavourable water régime (GIGON 1971). The serpentine appears still more extreme in this respect (EGGER, personal communication). On the contrary, acidic silicate is generally regarded as a favourable substrate. Frequencies

of cyanogenic phenotypes observed in *L. alpinus* are not consistent with these characteristics, especially as far as the carbonate is concerned.

At the present stage of investigations, we can only speculate about edaphic factors influencing cyanogenesis in *L. alpinus*. However, a possible rôle of the soil nitrogen calls for attention, some intriguing data being since long dispersed in the literature. For instance, RAVENNA and PELI (1907) found that detached leaves of *Sorghum vulgare* formed cyanide, apparently from nitrate, if illuminated or supplied with sugar in the dark. BOYD et al. (1938) argued that the cyanide content in plants is increased by a high nitrogen supply. It should be worthwhile to reinvestigate these aspects using modern methods.

In conclusion, a possible rôle of cyanogenesis in the nitrogen economy of *L. alpinus* should be briefly considered. Each of the three alpine substrates had a different supply of bound nitrogen. In the carbonate, nitrate was largely predominant; acidic silicate soils were usually well-provided with $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, whereas the serpentine contained both nitrogen forms only in limited quantities (EGGER, in preparation). Root nodules containing various strains of *Rhizobium* occurred in *L. alpinus* from all three substrates (OBER-HOLZER, personal communication). *L. alpinus* can thus apparently feed on bound nitrogen as well as assimilate atmospheric nitrogen; however, the question about balancing the nitrogen budget of the alpine taxon remains unanswered. The effects of mineral nitrogen on the symbiosis of legumes occurring in natural vegetation are largely ignored, virtually no work having been done in this subject (PATE 1976). Furthermore, our understanding of the mechanisms of nitrogen fixation is very fragmentary; as recently pointed out by SHANMUGAN et al. (1978), regulation of nitrogenase activity remains to be investigated in detail. The nitrate reductase regulation is also still object to various interpretations; however, it was recently shown that endogenous HCN plays a part in this process (ECK and HAGEMANN 1972, SOLOMONSON and SPEHAR 1977). It should be most exciting to investigate an influence of HCN upon the symbiotic nitrogen fixation, in particular the repression and derepression of *nif* genes.

If a plant uses its HCN for any regulations mechanisms, it should be expected to have a means of detoxifying excess, unless cyanide insensitivity has evolved. Various pathways of the cyanide metabolism were recently reviewed by JONES

(1972a, 1977). We should like to recall that a detoxification of cyanide resulting in the formation of thiocyanate, described in animals by LANG (1933), was supposed to occur also in plants. Thiocyanate was found in plants as early as 1910 by STOECKLIN and CROCHETELLE; GEMEINHARD (1938) not only revealed the presence of thiocyanate in numerous plant species, but also obtained an experimental evidence of its rapid synthesis in plant material setting up the same trial conditions as described by LANG. It should be most interesting to examine in this respect *Lotus alpinus* and other cyanogenic taxa. Further research on cyanogenesis offers indubitably numerous interesting possibilities. Our study is in progress.

Summary

Microdifferentiation occurring in *Lotus alpinus* above the timberline is to some extent influenced by altitude, but still more so by the type of substrate.

Each of the three studied substrates viz. acidic silicate, carbonate and serpentine, was characterized by a different pattern of distribution of *L. alpinus*, not only altitude limits of the taxon, but also zones inhabited respectively by diploids and tetraploids being distinct. Cyanogenesis in *L. alpinus* was related in a general way to the degree of polyploidy: on the whole, frequencies of cyanogenic diploid phenotypes were about twice as high as those occurring on the tetraploid level. The influence of substrate was, however, clearly recognizable within each chromosomal race; the highest frequencies of cyanogenic phenotypes was found upon carbonate, whereas serpentine was mostly inhabited by acyanogenic plants and acidic silicate was intermediary in this respect.

A possible influence of temperature and/or soil water stress upon the phenotypic frequencies in *L. alpinus* is discussed. In conclusion, relationships between the type of substrate, the nitrogen budget balance and cyanogenesis are briefly considered.

Zusammenfassung

Mikrodifferenzierung, wie sie bei *Lotus alpinus* über der Waldgrenze vorkommt, wird bis zu einem gewissen Grade von der Höhe beeinflusst, mehr noch aber durch die Art der Gesteinunterlage.

L. alpinus zeigte bei jedem der drei untersuchten Gesteinstypen (saures Silikat, Karbonat, Serpentin) ein differenziertes Verteilungsmuster: als gesteinsabhängig erwiesen sich sowohl die Höhengrenzen des Taxons als auch die Höhen-

verteilungen seiner beiden Chromosomenrassen. Cyanogenese wird bei *L. alpinus* meist mit dem Polyploidiegrad in Verbindung gebracht; gesamthaft gesehen trat Cyanogenese bei den Diploiden doppelt so häufig auf wie bei den Tetraploiden. Der Einfluss der Gesteinsunterlage machte sich bei jeder Chromosomenrasse klar bemerkbar: der Anteil der cyanogenen Phänotypen war auf Karbonat am höchsten, auf Serpentin am tiefsten; das saure Silikat nahm eine Mittelstellung ein.

Es wird ein möglicher Einfluss von Temperatur und/oder Wassermangel auf die Häufigkeit cyanogener Phänotypen bei *L. alpinus* behandelt. Schliesslich werden noch Ueberlegungen angestellt, welche die Beziehungen zwischen der Art der Gesteinsunterlage, dem Stickstoffhaushalt und der Cyanogenese betreffen.

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