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**Variation within *Lotus corniculatus* L. s. l. from
Switzerland**
**I. Preliminary report on chromosome numbers
and cyanogenesis**

by

KRYSTYNA URBANSKA-WORYTKIEWICZ and OTTO WILDI

Studies of intraspecific variation represent one of the most interesting approaches to the problem of the plant adaptation. Closely related populations that inhabit different environments often display morphological, genetical and physiological differences; comparative investigations carried out with such a material contribute to a better comprehension of selective factors operating in a given ecological niche and, on the other hand, may show specific mechanisms that have modified the adaptation trends within a group. The type of sampling technique used is of the utmost importance for the kind of study and the samples taken from the limited areas, along rather regular gradients of soil or altitude are of a special interest.

The present study was undertaken to determine some aspects of variation occurring within Swiss populations of the *Lotus corniculatus* group, a particular attention being given to materials from the Alpine region. *L. corniculatus* s. l. has not hitherto been investigated in detail from Switzerland. According to previous fragmentary data, Swiss representatives of the group are either diploid ($2n=12$) or tetraploid ($2n=24$); they manifest a great deal of variation both in their morphology as well as ecological requirements. It is well-known fact that the *L. corniculatus* group is polymorphic for the production of hydrogen cyanide yet only very few plants from Switzerland have hitherto been tested. Thus, it seemed interesting to study variation within Swiss material and the very first questions were: 1/ is the variation within the group graded or discontinuous and 2/ is it habitat-correlated or not. The present paper

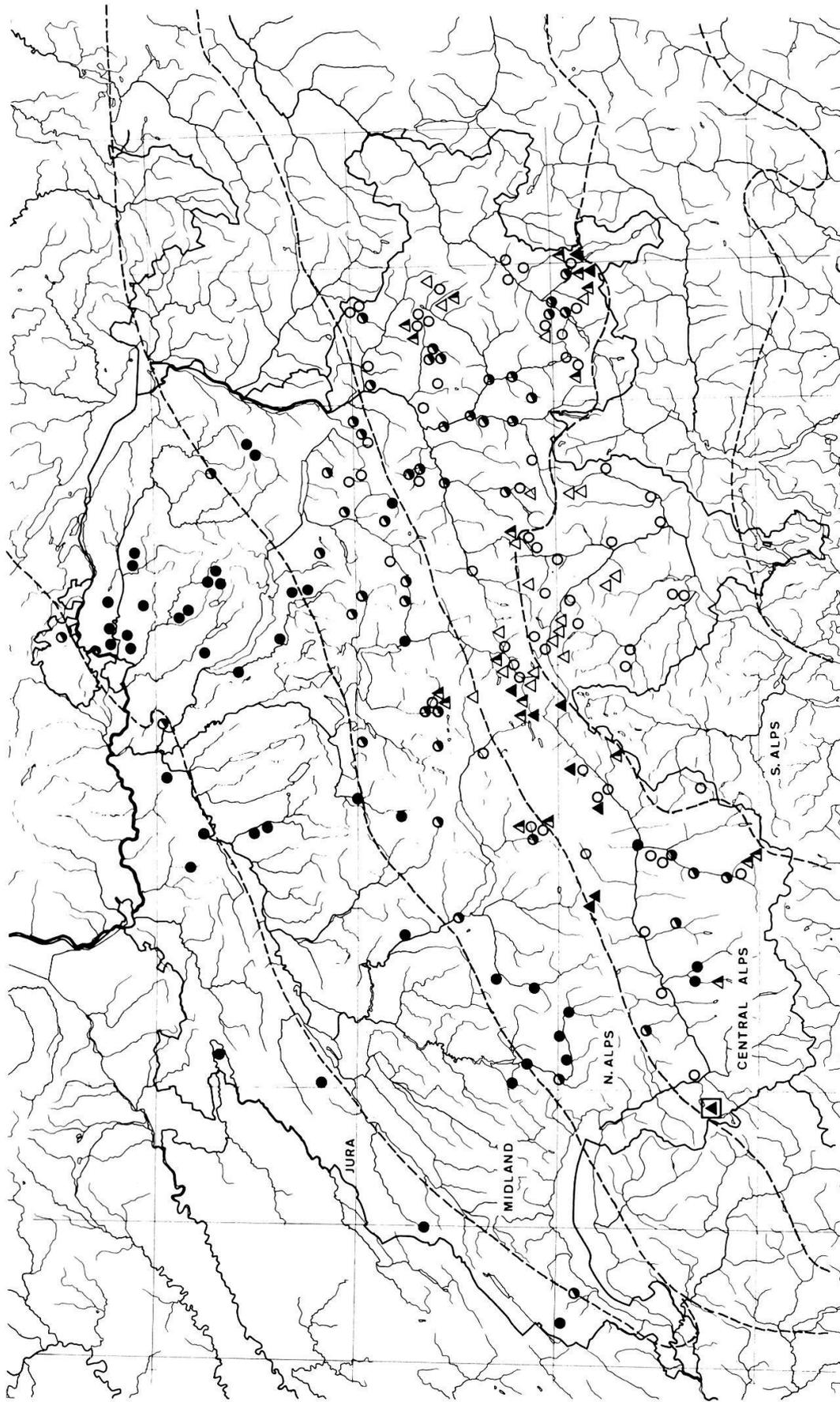


Fig. 1. Distribution of the studied material; not all stations from intensively sampled areas are marked. ▲ 2n=12, only HCN⁺; △ 2n=12, only HCN⁻; ● 2n=12, heterogeneous samples. ○ 2n=24, only HCN⁺; ○ 2n=24, only HCN⁻; ○ 2n=24, heterogeneous samples. ▣ 2n=12, HCN⁺(Favarger 1953, Grant and Sidhu 1967. Boundaries of the respective regions of Switzerland(broken lines) after Hess, Landolt and Hirzel(1970), by permission of the authors.

deals with the first results obtained in the course of our investigations.

Acknowledgements

We acknowledge collectively the many colleagues and friends who provided samples and data; a complete list of contributors will be published later. The valuable technical assistance of Mrs. A. HEGI, Mrs. M. SIEGL, Mr. E. SCHAEFER and Mr. H. SIGG is gratefully recognized. Drawings and diagrams were precisely made by Miss E. BRÄM to whom we present our thanks. Constructive comments of Prof. Dr. E. LANDOLT are greatly appreciated.

Materials and methods

Material for the present study comprised samples from 258 populations (1858 plants), mainly from the Alpine region (Fig. 1); for comparison, some lowland populations were as well scored. A few populations studied from Italian Alps and a single one from the region of Innsbruck have not been included into the present paper, the stations being situated too far off the investigated area. Two methods of sampling were used: 1/ the first one involved populations distributed in various parts of Swiss Alps; they inhabited stations situated at various altitudes, most frequently within subalpine and alpine zone. 2/ The second group of samples consisted of material collected within limited areas, along a more or less regular altitude gradient; for instance, samples in the region of Zermatt were taken at possibly regular intervals from about 1650 m a. s. l. up to 2940 m a. s. l. (Fig. 8). Similar collections were carried out in the Engadine, in the Bernese Oberland etc.

8 - 12 plants were usually taken from a given population, except for some lowland stations that were sampled in a very fragmentary way. Individuals were most frequently collected within a distance of about 3 m from each other. Brief notes on altitude, exposition, type of soil and a general aspect of vegetation were taken during the field work. Some part of the material was transferred to the experimental garden of the Geobotanical Institute where the plants have been kept under uniform conditions for further observations.

The attention of the authors was principally given to chromosome numbers as well as cyanogenesis. Somatic chromosome numbers were studied on squashes made from not pre-treated young leaves or shoots, stained with lacto-propionic orcein. Each of the studied plants was tested for the production of hydrogen cyanide according to the standard sodium picrate method (DAWSON 1941)

and the plants were subsequently rated as cyanogenic or acyanogenic. The phenotypic expression being of first importance for the present study, the terms "cyanogenic" and "acyanogenic" used in further part of our paper refer in fact to gross phenotypes and a detailed genotypic structure of the tested plants has not been further investigated.

Remarks on taxonomical treatment of the studied material

Lotus corniculatus L. s. l. undoubtedly is one of the most variable species within the genus. Numerous taxa have been described within this group; their taxonomic rank varies greatly, for the particular authors differ in their concept of a given unit. A precise assessment of relationships occurring between taxa of *L. corniculatus* s. l. requires long-termed, detailed biosystematic studies; for the time being, we have followed the taxonomical treatment of the group recently proposed by HESS, LANDOLT and HIRZEL (1970). Morphological characters given by the Swiss authors in descriptions of the respective taxa (Table I) were checked and plants corresponding to a given species were provisionally given its binomial. Individuals that apparently represented morphological transitions between *Lotus corniculatus* and *L. alpinus* have not been included into the present paper.

According to their morphological affinities, five taxa were thus distinguished within the studied material: *Lotus uliginosus* Schkhr., *L. corniculatus* L., *L. pilosus* Jordan, *L. alpinus* (DC) Schleicher and *L. tenuis* Waldst. et Kit. They will be separately discussed below.

Table I. Morphological characters given for particular taxa of the
L. corniculatus group by HESS, LANDOLT and HIRZEL (1970)

Taxon	Stem	Leaflets	N of flowers per inflorescence
<i>L. uliginosus</i>	upright or ascending, usually glabrous, 30-80 cm tall	up to 2.5 cm long, 1.5-3 times as long as broad, ciliate at the leaf margin (hairs about 1 mm long) otherwise glabrous or sparsely hairy	8 - 14
<i>L. corniculatus</i>	curved and ascending or erect, nearly glabrous, 10-40 cm tall	up to 2 cm long 1-3 times as long as broad, glabrous or ciliate at the leaf margin	4 - 8
<i>L. pilosus</i>	decumbent or curved and ascending, sparsely hairy, 5-15 cm tall	up to 1.2cm long, 1.5-2.5 times as long as broad, sparsely hairy on both leaf surfaces	2 - 5
<i>L. alpinus</i>	decumbent, at the uppermost part ascending, usually glabrous, 5-10 cm tall	up to 0.8cm long, 1-1.5 times as long as broad, glabrous or ciliate at the leaf margin	1 - 3
<i>L. tenuis</i>	decumbent, curved and ascending or upright, usually glabrous, 15-35 cm tall	up to 1.5 cm long, 3-10 times as long as broad, glabrous	1 - 5

Calyx	Hairs at the calyx tip	Corolla	Keel tip colour
6-7 mm long, nearly glabrous, tips ciliate, usually somewhat longer than the calyx tube, prior to flowering curved and spreading	about 1 mm long	12-14 mm long, in overblown flowers yellow	pale yellow
5-7 mm long, usually glabrous, tips glabrous or ciliate, usually a little shorter than the calyx tube, prior to flowering convergent	0.5-1 mm long if present	10-16 mm long, in overblown flowers mostly yellow	pale (yellow or reddish)
5-7mm long, sparsely hairy, tips sparsely hairy, often longer than the calyx tube, prior to flowering convergent	about 1 mm long	8-15 mm long, in overblown flowers mostly yellow	pale (usually yellow or reddish)
6-7 mm long, nearly glabrous, tips ciliate, prior to flowering convergent	0.5-1 mm long	12-18 mm long, in overblown flowers orange	dark purple
4-5 mm long, nearly glabrous, tips sometimes ciliate (but then hairs single), prior to flowering convergent	0.2 mm long if present	7-11 mm long, in overblown flowers orange	pale yellow

Results

Lotus uliginosus Schkhur $2n=12; HCN^-$

L. uliginosus occurs rather infrequently in Switzerland, within colline and montane zone; as the only Swiss representative of the *L. corniculatus* group, it shows a positive preference for wet stations (HESS, LANDOLT and HIRZEL 1970).

L. uliginosus was investigated only from four localities in Switzerland (two stations from the region of Zurich, one from surroundingd of Geneva and one from the canton of Lucerne). All 14 studied plants proved to be diploid ($2n=12$). Our results corroborate thus the data of most previous authors (TSCHECHOV and KARTASHOVA 1932, MAUDE 1939, DAWSON 1941, GUINOCHET 1945, LARSEN 1955, LÖVE and LÖVE 1956, GADELLA and KLIPHUIS 1963, 1966, GILOT 1965, GRANT 1965, SKALINSKA et al. 1966, CHRTKOVA-ZERTOVA 1967, ZANDSTRA and GRANT 1968). Tetraploid chromosome number $2n=24$ was reported only twice, by

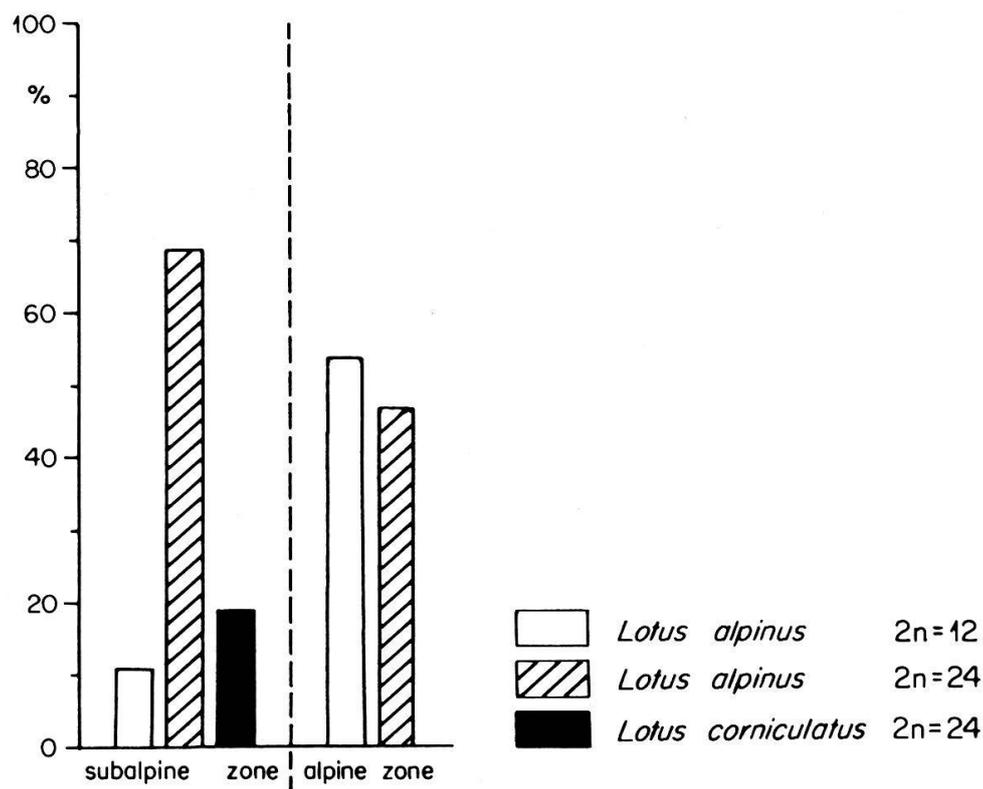
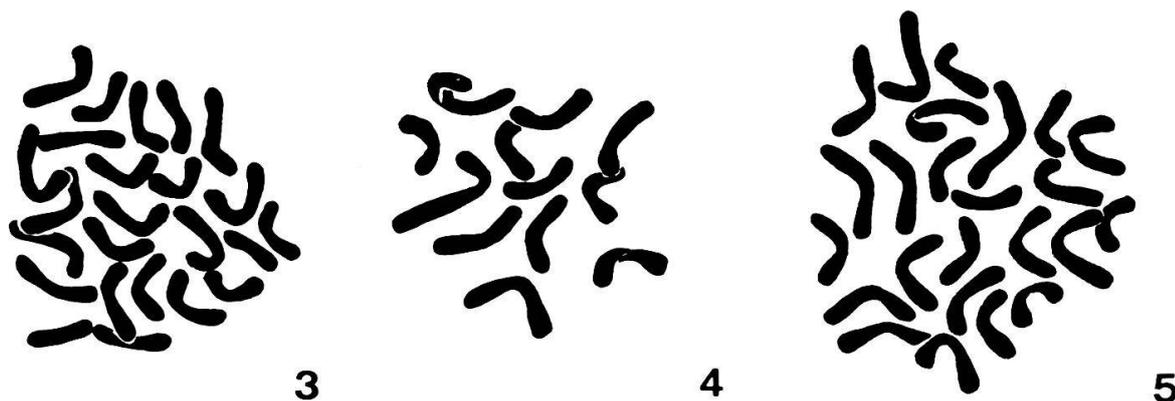


Fig. 2. Frequency (%) of *Lotus alpinus* ($2n=12$, $2n=24$) and *L. corniculatus* in the material studied from subalpine and alpine zone of Swiss Alps.

*) classification of altitude zones after HESS, LANDOLT and HIRZEL (1970)
 **)

MILOVIDOV (1941) and STRID (1971); solely the latter author investigated the plants of a known origin (Albania).

The sodium picrate test carried out with *L. uliginosus* from Switzerland was invariably negative. The present results confirm thus the original data of AMSTRONG et al. (1912, 1913) as well as those of DAWSON (1941) dealing with British plants.



Figs 3-5. Somatic metaphases in *Lotus corniculatus* s.l. (the collection numbers are given in brackets). 3. *L. corniculatus*: $2n=24$, Swiss Midland (213/2). 4. *L. alpinus*: $2n=12$, Southern Alps (210/3). 5. *L. alpinus*: $2n=24$, Central Alps (220/6). c. 2750 X.

Lotus corniculatus L. $2n=24$; HCN^- , HCN^+

543 plants collected from 89 stations were studied: most of them have been found at lower altitudes and only 7 samples originated from subalpine zone where *L. alpinus* was frequently observed yet *L. corniculatus* seemed to be rather scarce (Fig. 2). No stations of *L. corniculatus* were found within subalpine zone of Southern Swiss Alps.

All the studied plants represented a tetraploid level ($2n=24$, Fig. 3). The present results are in agreement with ample previous records (for detailed references see FEOROV et al. ed. 1969). The only chromosome number other than tetraploid i. e. $2n=32$, reported by KODAMA (1967) from Japan, has not been confirmed hitherto. The chromosomes within the set of *L. corniculatus* manifested some degree of differentiation; however, no sharp differences in length were noted, apparently intermediate types occurring between the

longest and the shortest chromosomes of the complement. Our preliminary observations correspond in a general way to the results of CHENG and GRANT (1973) concerning *L. corniculatus* from the Balkans; however, detailed karyotype analysis of Swiss material is required.

The study on cyanogenesis brought about some interesting results. The majority of samples tested for the production of hydrogen cyanide proved to be homogenous (68 out of 89); they were either acyanogenic or cyanogenic, the latter type apparently dominating within the studied material (45 samples versus 23). Mixed samples were rather rare, especially in the material from Swiss Midland. On the whole, 320 tested plants were cyanogenic whereas 223 others gave no reaction.

Table II

Lotus corniculatus (2n=24) in colline, montane and subalpine zone of Swiss Alps as well as north of the Alpine ridge

Region	N of investigated plants			Zone
	HCN ⁻	HCN ⁺	Total	
Northern Alps and north of the Alpine ridge	-	12	12	subalpine
	8	111	119	montane
	22	108	130	colline
Central Alps	45	26	71	subalpine
	37	42	79	montane
	39	21	60	colline
Southern Alps	-	-	-	subalpine
	27	-	27	montane
	45	-	45	colline

A general pattern of frequency of cyanogenic/acyanogenic variants, apparently influenced by geographical distribution of the studied population samples, is the dominating peculiarity found in the course of the present work (Tables II, VI, Figs. 6, 9). Out of 51 samples from Northern Swiss Alps, northern Alpine foot-hills, Swiss Midland and Jura, 42 consisted exclusively of cyanogenic plants (191 individuals) whereas only 2 acyanogenic samples (5 plants) were observed. Mixed samples were rare in the studied material (7);

they comprised on the whole 40 cyanogenic plants and 25 acyanogenic ones. Total number of plants studied from Northern Swiss Alps as well as north of the Alpine ridge comported 261, cyanogenic variants apparently representing the majority (231).

Frequency of cyanogenic plants of *Lotus corniculatus* decreased rapidly within the material from Central Swiss Alps. Out of 27 studied samples, only three comprised solely cyanogenic individuals; 10 samples were exclusively acyanogenic and mixed samples occurred rather frequently (14). In general, 121 acyanogenic plants and 89 cyanogenic ones were found within the material studied from this area.

Southern Swiss Alps were solely represented by acyanogenic plants; all 72 studied individuals originating from 11 stations invariable belonged to this category.

Thus, on the whole, cyanogenic variants of *L. corniculatus* in Switzerland seem to occur in their maximal frequency within regions situated north of the Alpine ridge and in Northern Swiss Alps. On the other hand, Central Alps might be considered as a transition area where cyanogenic and acyanogenic variants remain in a certain balance. Southern Swiss Alps were so far exclusively represented by acyanogenic plants of *L. corniculatus*; further investigations are indispensable to explain this amazing situation, for cyanogenic variants seem, at their best, to be exceedingly rare in this area. The above described pattern appears rather distinctly both in the distribution of the respective stations (Fig. 1) as well as in frequencies of cyanogenic and acyanogenic plants calculated for each of the discussed regions (Figs 6, 9, Tables II, VI).

An interesting point arises when distribution of cyanogenic/acyanogenic variants is being considered in relation to the type of station. Cyanogenic plants of *L. corniculatus* were particularly frequent in stations remaining under human influence (verges of roads, fertilized meadows); on the other hand, acyanogenic individuals appeared within open pastures, ancient clearing as well as in rocky, dry sites, being frequently observed on loose, not much developed soils. Another detail appears when altitude zones are being considered (Table II, Fig. 6): it seems likely that frequency of cyanogenic variants decreases together with increasing altitude a. s. l., this trend being apparently superimposed on the geographical pattern of distribution. Our present data do not

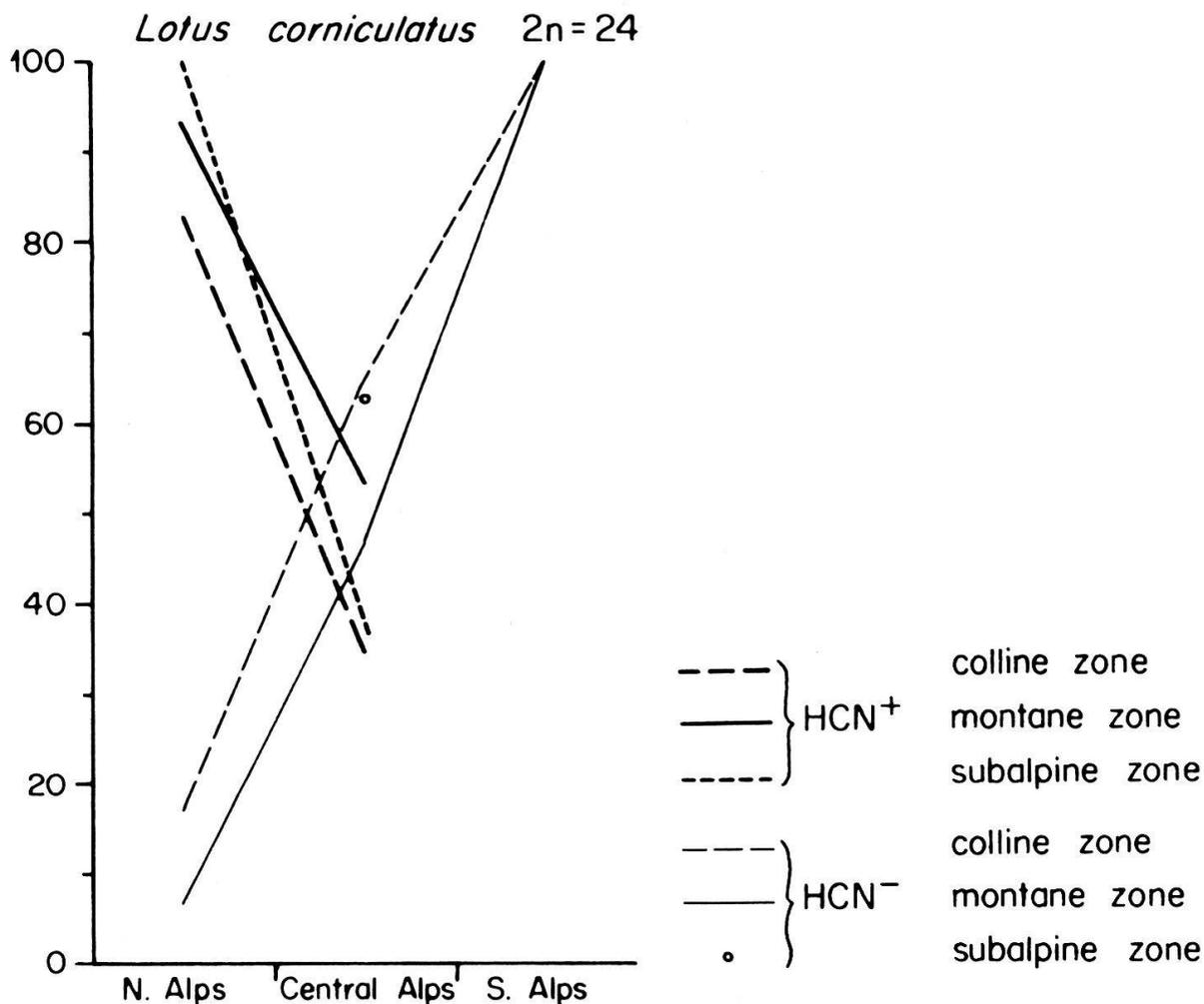


Fig. 6: *Lotus corniculatus* (2n=24); frequency (%) of cyanogenic and acyanogenic plants in relation to geographical distribution and altitude zones within the studied area.

allow, however, an accurate evaluation as a great many more samples are required; further studies are being continued in this subject.

Cyanogenesis in *L. corniculatus* from Switzerland has not been studied hitherto. More general aspects of this problem will be dealt with in discussion.

Lotus pilosus Jordan 2n=24; HCN⁻

Only three plants belonging to this taxon were studied from the region of Airolo (Ri d'Albinasca, 1490 m a. s. l.). All they were tetraploid (2n=24); our results confirm the previous data of GUINOCHET (1945) as well as those of LARSEN (1954). Cyanogenesis in *L. pilosus* has not hitherto been investigated; the plants studied in the course of the present work were invariably acyanogenic.

L. alpinus represented the majority of our material: 1277 plants originating from 161 populations were investigated. They represented two chromosomal races i. e. a diploid ($2n=12$, Fig. 4) as well as a tetraploid one ($2n=24$, Fig. 5) distributed within subalpine and alpine zone of Swiss Alps (Fig. 2).

Diploid plants of *L. alpinus* were found in 65 populations (549 plants). It is interesting to note that diploid cytotype seems to occur rather infrequently in Northern Swiss Alps, its main area of distribution in Switzerland corresponding to Central Alps and centrally situated ridges of Southern Alps. Diploid populations inhabited principally the alpine zone and some of them reached fairly high altitudes (e. g. 3105 m a.s.l. at Gornergrat near Zermatt, according to BECHERER 1956). 12chromosomic *Lotus alpinus* has been discovered by FAVARGER (1953) who studied material from a single Swiss stations; FAVARGER noted then differences in chromosome length occurring within the diploid set. Later on, diploid *L. alpinus* was recorded from other Alpine regions (LARSEN 1954, ŽERTOVA 1964, FAVARGER 1969, GADELLA and KLIPHUIS 1970) as well as from the Pyrenees (FAVARGER and HUYNH in LÖVE and SÖLBRIG 1964, KÜPFER 1974). Differences in chromosome length observed in the course of the present work corroborate the characteristic given by FAVARGER as well as the results obtained by CHENG and GRANT (1973). Our results contribute to a better knowledge of distribution of the diploid *L. alpinus* within Swiss Alps.

As far as the tetraploid cytotype of *L. alpinus* is concerned, 728 plants from 96 populations were studied. The material was collected within subalpine and alpine zone (Fig. 2), the highest station of tetraploids being found so far at 2650 m a.s.l. (Arosler Weissshorn).

Preliminary observations on chromosome morphology led to reveal some differences in the length of chromosomes occurring within the tetraploid set. Some chromosomes appeared distinctly longer than others (Fig. 5); in this respect, tetraploid *L. alpinus* is similar to the diploid cytotype rather than to *L. corniculatus* where an apparently graded length differentiation of chromosomes was observed (CHENG and GRANT 1973). It should be emphasized, however, that this problem requires a great deal of more detailed studies that have not

yet been completed.

Tetraploid cytotype of *L. alpinus* has previously been reported from Austrian Alps by ŽERTOVA (1964) who provided a drawing of somatic metaphase but unfortunately gave no description of chromosomes. It should be mentioned, however, that already FAVARGER (1953) found some tetraploid plants at 2000 m a.s.l. in a station near Creusaz, Wallis. FAVARGER studied solely the meiotic chromosomes; his material being not suitable for a detailed determination, was provisionally assigned to *L. corniculatus* var. *hirsutus* f. *minor*. However, BECHERER determined later these plants as *L. alpinus*. Some Swiss tetraploids were studied by LARSEN (1954a, b) but this author has not given an exact origin of this material and in his second paper, dealing with several Alpine plants from higher altitudes, drawings are missing altogether. LARSEN assigned his material to various forms of the var. *arvensis* of *L. corniculatus*. Given these uncomplete data concerning morphological affinities of the Alpine tetraploids, detailed cytotaxonomical and ecological investigations on both chromosomic races of *L. alpinus* would be advisable.

A brief mention is due to the distribution of the respective cytotypes within populations of *Lotus alpinus*. For the most part, the studied samples proved to be homoploid, either diploid or tetraploid plants being the sole representatives; only 7 heteroploid samples were found (Table V). Distribution of diploid and tetraploid populations of *L. alpinus* seems to be strongly influenced by altitude above sea level; stations situated at very high altitudes are most frequently inhabited by diploid plants: out of 26 samples collected between 2400 - 3000 m a. s. l. that were studied in course of the present work, 21 consisted of diploids, a single one was heteroploid and 4 comprised exclusively tetraploid individuals. It is interesting to note that all four tetraploid samples originated from the region of Arosler Weisshorn (2650 m a. s. l.) where no diploids whatsoever have been found.

Limits of the zone inhabited by diploid *L. alpinus* often corresponded to an ancient or an actual timberline, absolute values of altitude a. s. l. fluctuating in various parts of Swiss Alps. However, one of the most peculiar features of vertical distribution of the two chromosomic races appeared in the regions where tetraploids reached well above the timberline up to a certain altitude, but then disappeared without any apparent change of gradient

and higher up were replaced by diploids; it should be noted that vertical distance between the last observed tetraploid population and the first diploid one was often remarkably limited e. g. 60 - 70 m. Further investigation on this interesting problem are to be continued and ecological factors should be studied in detail.

As far as cyanogenesis in *Lotus alpinus* is concerned, a few diploid individuals apparently originating from the station recorded by FAVARGER (1953) were previously studied by GRANT and SIDHU (1967). The plants tested by the Canadian authors were cyanogenic; in spite of these results, JONES (1972) positively characterized *L. alpinus* as acyanogenic but produced no references as to the source of this information.

Table III. Diploid *Lotus alpinus* (2n=12) in subalpine and alpine zone of Swiss Alps

Region	N of investigated plants			Zone
	HCN ⁻	HCN ⁺	Total	
Northern Alps	17	25	42	alpine
	-	-	-	subalpine
Central Alps	205	177	382	alpine
	34	5	39	subalpine
Southern Alps	77	-	77	alpine
	9	-	9	subalpine

Table IV. Tetraploid *Lotus alpinus* (2n=24) in subalpine and alpine zone of Swiss Alps

Region	N of investigated plants			Zone
	HCN ⁻	HCN ⁺	Total	
Northern Alps	73	41	114	alpine
	35	48	83	subalpine
Central Alps	239	61	300	alpine
	161	24	185	subalpine
Southern Alps	20	-	20	alpine
	26	-	26	subalpine

The present investigations led to reveal both cyanogenic as well as acyanogenic plants within each of the two studied chromosomal races of *L. alpinus*. Frequency of cyanogenic/acyanogenic variants within populations not only seems to be generally correlated with geographical distribution of *L. alpinus* within the Alpine area of Switzerland and altitude a. s. l., but also is apparently influenced by the respective chromosome numbers (Tables III, IV, V, VI, Figs 7, 9).

Out of 549 plants of the diploid *L. alpinus*, 207 proved to be cyanogenic and 342 were acyanogenic. Solely mixed samples were found in Northern Swiss Alps where cyanogenic plants slightly dominated (25 versus 17 acyanogenic ones). The major part of the studied material originated from Central Alps where diploid *L. alpinus* seems to have its main distribution area in Switzerland. 46 samples were investigated from this region; mixed samples were found in nearly the same frequency as the homogenous ones (24 : 22), but the latter category was mostly represented by acyanogenic samples (14). Plants from Southern Alps were exclusively acyanogenic.

Distribution of the respective variants in relation to altitude zones presented a remarkable pattern (Figs 7, 8, Table III). No diploid plants of *L. alpinus* were found within subalpine zone of Northern Swiss Alps yet in the material from alpine zone of this region cyanogenic plants were rather dominating (59,5%, Fig. 7). Only a limited material was investigated but it should be kept in mind that a diploid *L. alpinus* appears to be rare in Northern Alps. Relative frequency of cyanogenic plants seems to increase as well in alpine zone of Central Alps as compared to subalpine zone of this region (12,8% in subalpine zone, 43,7% in alpine zone) although, according to the general geographic pattern, acyanogenic plants are dominating. As to Southern Alps, plants from both altitude zones were exclusively acyanogenic and in this respect diploid *L. alpinus* behaved like *L. corniculatus*.

Comparative investigations carried out with tetraploid plants of *L. alpinus* revealed some differences in their distribution trend (Table IV, Fig. 7). Firstly, tetraploids seem to occur much more frequently in the Alps than the diploids (Fig. 2); on the whole, 96 populations were found, 41 within subalpine zone and 55 at higher altitudes (altogether 728 plants). Secondly, tetraploids apparently have a wider area of distribution, Northern Alps being

accordingly rather well represented in our collections (32 samples). It should be added parenthetically that some tetraploid plants morphologically corresponding to *L. alpinus* were recently found also in Swiss Jura; they have to be investigated in detail. Samples from Northern Alps were most frequently heterogenous as to cyanogenesis (20); in addition, 7 acyanogenic samples and 5 cyanogenic ones occurred in the studied material. On the whole, 197 plants were investigated from this region (Table IV, Fig. 7); 108 were acyanogenic and 89 proved to be cyanogenic. On the other hand, materials from Central Alps mostly consisted of homogenous samples (35 out of 58), acyanogenic individuals indisputably dominating (400 versus 85 cyanogenic ones). As in *L. corniculatus* or in the diploid *L. alpinus*, tetraploids studied from Southern Alps were exclusively acyanogenic (Tables IV, VI, Fig. 7, 9).

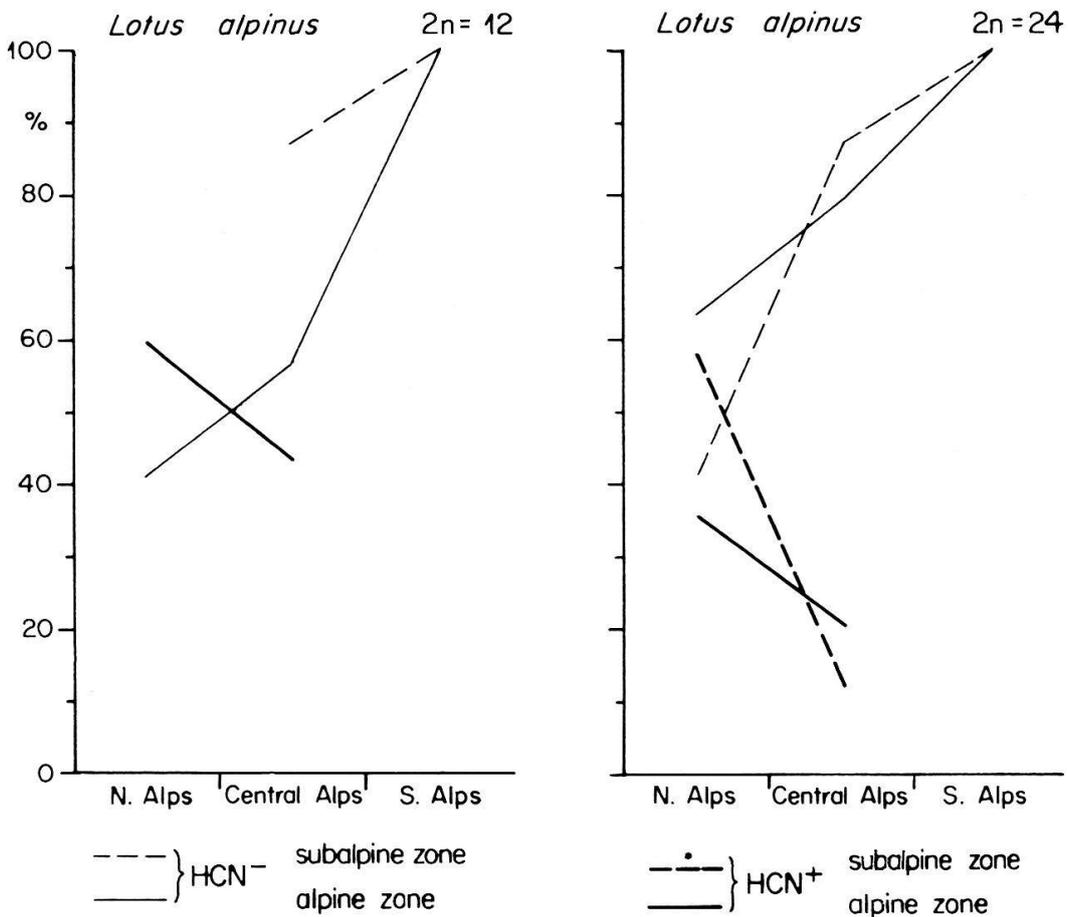


Fig. 7: *Lotus alpinus* (2n=12, 24); frequency of cyanogenic and acyanogenic plants in relation to geographical distribution and altitude zones within the studied area

Another aspect of the distribution pattern that is different in tetraploid *L. alpinus* as compared with the diploid race, is frequency of cyanogenic/acyanogenic variants in relation to altitude zones (Table. IV, Fig. 7). As described above, frequency of cyanogenic diploid variants seems to increase with an increasing altitude a. s. l. A definitely inverse trend occurs within the tetraploid race; it seems to be reinforced by geographical distribution within the Alpin ridge (Table VI) but manifests itself rather clearly. In subalpine zone of Northern Swiss Alps, HCN-positive variants were slightly dominating (57,8%, Fig. 7); on the other hand, there occurs a sharp fall in their frequency (down to 13%) in Central Alps and no cyanogenic plants were found so far in Southern Alps. As far as higher altitude are concerned, cyanogenic tetraploid plants were still less frequent; in alpine zone of Northern Alps their frequency was recorded as 36%, in Central Alps it was still less pronounced (20,3%) and appeared reduced to zero in Southern Alps.

Considerable differences occurring between diploid and tetraploid *Lotus alpinus* as to the distribution of cyanogenic/acyanogenic variants within populations, are particularly distinct when a set of samples taken along an altitude gradient is being analysed (Fig. 8). It seems also worth mentioning that 24chromosomic plants from heteroploid populations were most frequently acyanogenic whereas diploid HCN-positive plants were often quite well represented in the respective samples (Table V).

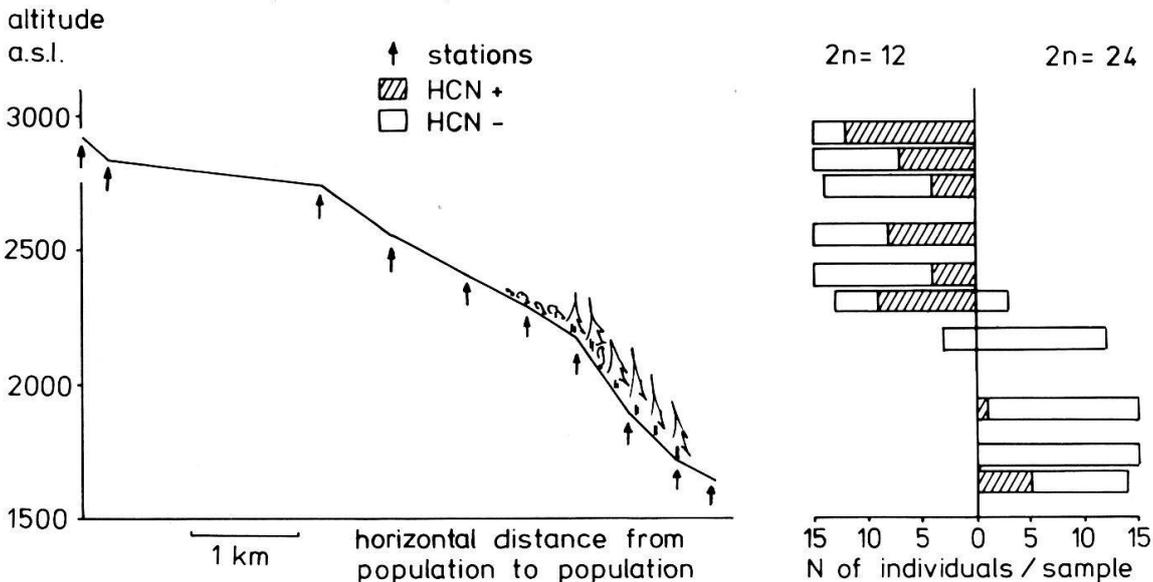


Fig. 8. Chromosome numbers and cyanogenic/acyanogenic variants within samples of *Lotus alpinus* collected along an altitude gradient in the region of Zermatt, Wallis

L. tenuis occurs in rather dispersed stations in Switzerland; it appears in lowland sites (sheep pastures) that can generally be characterized by a variable soil humidity (HESS, LANDOLT and HIRZEL 1970). 22 plants from three neighbouring populations near Zurich were investigated by the present authors. They were invariably diploid and our results confirm the recent data of LANDOLT (op. cit.) from the same region as well as numerous previous records (for detailed references see FEDOROV et al. ed., 1969).

All the studied plants of *L. tenuis* proved to be cyanogenic. The present observations corroborate thus the data of ARMSTRONG et al. (1912, 1913) and those of DAWSON (1941). On the other hand, GRANT and SIDHU (1967) reported *L. tenuis* from Canada as being polymorphic for the production of hydrogen cyanide; numerous acyanogenic plants of *L. tenuis* were also observed by ZANDSTRA and GRANT (1968).

Discussion

Investigations on polymorphic variation in plants show that the extent of the polymorphism is often geographically variable and remains under a strong influence of ecological factors. Search for limits of any particular zone and studies on factors controlling various distribution trends may contribute to a better understanding of biologically important problem of the plant adaptation.

The present paper deals with two interesting aspects of polymorphic variation within the *Lotus corniculatus* group i. e. chromosome numbers as well as cyanogenesis. Our discussion is mostly confined to *L. alpinus*, for the other taxa of the group have not sufficiently been investigated. *L. alpinus* from Switzerland proved to be cytologically differentiated into two chromosomal races; their respective distribution is strongly influenced by the altitude above sea level, the stations situated at very high altitudes being usually inhabited by the diploids. The first author who pointed out these differences was FAVARGER (1964, 1967) who considered a diploid *Lotus alpinus* as an oreophytic taxon and a tetraploid *L. corniculatus* as a species of lower altitudes. The present results suggest that the trend discussed by FAVARGER corresponds to the two chromosomal races of *L. alpinus* rather than

to two different taxa of the *L. corniculatus* group; it seems also likely that apparent limits of the respective distribution zones of diploid and tetraploid *L. alpinus* occur within alpine zone itself or around the timberline, thus within altitudes higher than those assumed by FAVARGER. Another interesting point presents an apparently limited gene-flow between neighbouring diploid and tetraploid populations of *L. alpinus*. This problem remains to be investigated in detail as it do, on the whole, fertility relationships occurring between the two chromosomic races; none the less, some general remarks can be presented. As mentioned before, diploid and tetraploid populations of *L. alpinus* within alpine zone were often separated by a remarkably narrow vertical distance and no apparent changes of gradient accompanied limits of the respective areas. In spite of that, heteroploid populations were found only exceptionally. It should be added that nearly all mixed populations inhabited stations disturbed in some or other way (an avalanche track; upper stations of ski-lifts; a sliding slope of a machine-prepared ski-run; a cleared forest at timberline; a pasture where the vegetation surface was broken up, partly as a result of trampling). It is likely that heteroploid populations of *L. alpinus* appear mainly in disturbed environmental conditions.

Table V. Distribution of cyanogenic and acyanogenic variants within heteroploid populations of *Lotus alpinus*

Region	Place of origin	Altitude a. s. l.	2n=12		2n=24	
			HCN ⁻	HCN ⁺	HCN ⁻	HCN ⁺
CA	Corviglia	2550 m	2	-	12	3
CA	Riffelalp I	2305 m	4	9	3	-
CA	Piz Lagalb	2300 m	-	13	1	-
NA	Jochpass	2300 m	1	2	1	2
CA	Riederalp	2200 m	-	1	11	-
CA	Riffelalp II	2180 m	3	-	12	-
CA	Hospental	1500 m	2	-	4	-

CA: Central Alps, NA: Northern Alps

Further detail that seems worth mentioning is that the tetraploid *Lotus alpinus* does sometimes appear at high altitudes; in the course of the present work four populations were found between 2500 - 2650 m a.s.l. It should be noted, however, that all these stations occurred within the region of Arosler Weisshorn, including its summit, and no diploids were found so far in this area. Speculations on competitive abilities of diploid and tetraploid race of

L. alpinus are obviously rather hazardous, but one wonders whether the presence of diploids prevents tetraploid plants from getting into higher situated stations.

Intermediate morphological types between *L. alpinus* and *L. corniculatus* were noted by some authors (see HESS, LANDOLT and HIRZEL 1970); it might be assumed that they partly result from a gene exchange at tetraploid level, populations of 24-chromosomal *L. alpinus* and those of *L. corniculatus* both occurring within subalpine zone of Swiss Alps. However, the problem of inter-fertility relationships occurring between these two taxa is not sufficiently known. According to the previous data, experimental hybridization between some *Lotus* species has been achieved with considerable difficulty and the embryo-culture was a pre-requisite in numerous cases (GRANT et al. 1962, BENT 1958, 1962). On the other hand, some hybrids were produced with relative ease (SOMAROO and GRANT 1971). As far as the Alpine populations are concerned, a positive evidence of the natural hybridization has not hitherto been produced and further detailed studies are indispensable.

Thus, on the whole, the present results permit to characterize the cytological variation occurring within Swiss materials of *L. alpinus* as representing discontinuous pattern of an euploid differentiation. A more precise evaluation of factors controlling distribution of the respective chromosome races of *L. alpinus* requires further investigations; especially interesting would be to study the type of soil (carbonate and silicate soils, respectively).

A polymorphism for cyanogenesis occurring within *L. corniculatus* was investigated by numerous authors, at the time being particularly in Canada by W. F. GRANT and his collaborators as well as in Great Britain (JONES et al.). Various aspects of this problem were studied and some interesting results are known. However, the data are far from being complete and informations concerning the distribution of cyanogenic and/or acyanogenic variants within the genus *Lotus* L. are sometimes rather confusing (JONES 1972).

The present investigations led to reveal a geographically variable polymorphism for cyanogenesis occurring within Swiss populations of *L. corniculatus* (Table II, VI, Figs 6, 9). Cyanogenic variants occur in their highest frequency within lowland populations north of the Alpine ridge, but this

Table VI. Average frequency (%) of cyanogenic and acyanogenic plants in the studied material in relation to its geographical distribution

A: acyanogenic plants

%

Taxon	2n	N. Alps	Central Alps	S. Alps
<i>Lotus corniculatus</i>	24	11.8	58.4	100
<i>Lotus alpinus</i>	12	40.5	71.7	100
<i>Lotus alpinus</i>	24	53.1	83.3	100

B: cyanogenic plants

%

Taxon	2n	N. Alps	Central Alps	S. Alps
<i>Lotus corniculatus</i>	24	92.1	41.6	nil
<i>Lotus alpinus</i>	12	59.5	27.7	nil
<i>Lotus alpinus</i>	24	47.9	16.7	nil

frequency decreases in Northern Alps, appears still more reduced in Central Alps and Southern Alps are exclusively represented by acyanogenic individuals. In more general terms, this pattern of distribution might be described as a ratio-cline across the Swiss Midland and the Alps with the frequency of cyanogenic individuals decreasing from north to south. Our investigations being not completed, no definite interpretation of the results is offered; however, some details observed in field deserve a brief comment.

Cyanogenic plants of *L. corniculatus* occurred most frequently in stations that were strongly influenced by human activities as verges of roads, apparently made and sown by Man and also in fertilized meadows of Swiss Midland. On the other hand, samples from natural rocky roadsides or pastured, meagre slopes in northern Alpine foot-hills and also those from the Alpine valleys comprised numerous acyanogenic individuals. The above observations seem to be in favour of the hypothesis advanced by MELVILLE and DOAK (1940), further developed by FOULDS and GRIME (1971, 1971a) and supported by the recent data of MATILE (1975). According to this hypothesis, the enzyme and glucoside are compartmentalized in a normal leaf cell of a cyanogenic plant, their multiple locations being not excluded. They would be brought into a full contact when a damage occurs to internal membranes of the cell, either as a result of disturbed foliar water balance or after destruction of the leaf tissues (eating, treatment with organic solvents). Consequently, one might consider frost or desiccation as selective factors operating against cyanogenic individuals.

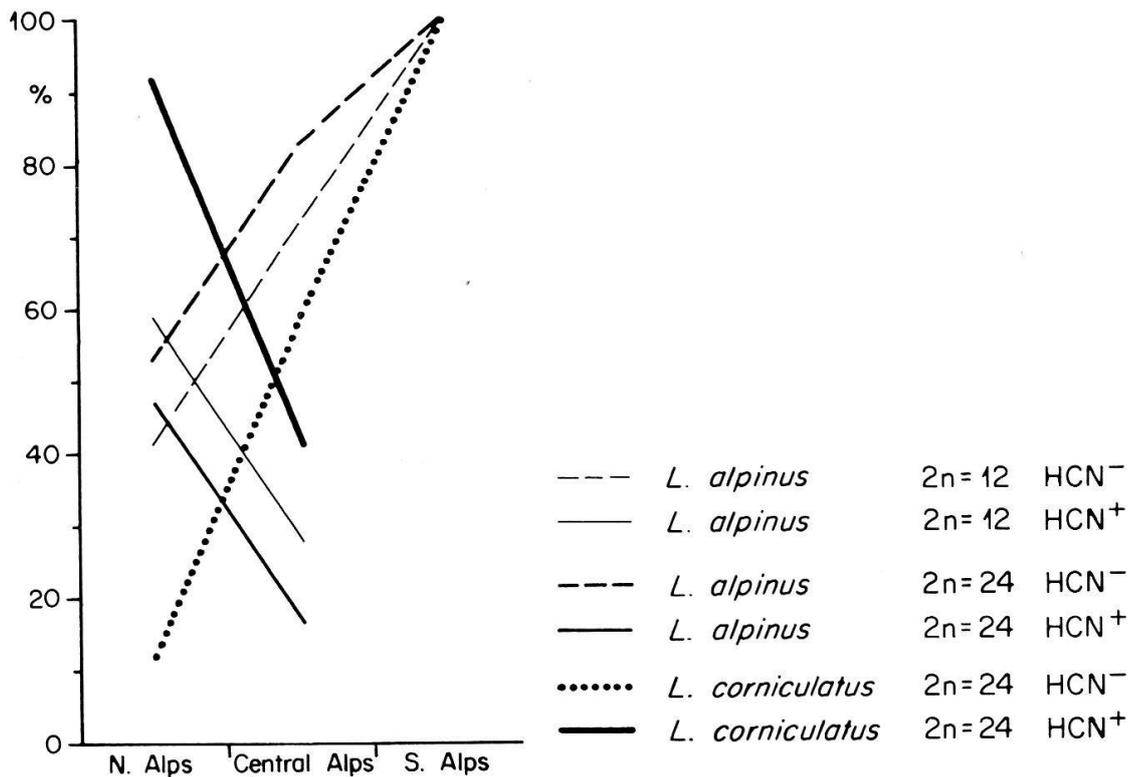


Fig. 9: Average frequency (%) of cyanogenic and acyanogenic plants in relation to geographical distribution of the studied material

This hypothesis would also confirm the opinion of DADAY (1954) that cold winter temperatures stay in relation to a low frequency of cyanogenic plants in populations. FOULDS and GRIME (1971, 1971a) obtained an experimental evidence that soil water stress indeed reduced frequencies of cyanogenic plants in *Trifolium repens* and *Lotus corniculatus*, each of the two species responding in a different way to the same selection. Recent data of JONES (1973) suggest that a size of a draughted area might be important for the aspect of the population; small draughted areas in Great Britain do not seem to be strongly influenced unless the selection is of an extreme type.

High frequencies of cyanogenic plants observed by the present authors in lowland populations of *L. corniculatus* within intensively managed Swiss Midland stay in agreement with the data of JONES (1973) concerning the occurrence of cyanogenic variants in the grass seed used in commerce. On the other hand, selection in agronomic strains of *L. corniculatus* recently studied by the British author in West Germany seemed to be stronger for morphological characters than against cyanogenesis; this might also be the case in some

parts of Switzerland. Selective predation of acyanogenic plants by various animals, recently discussed at length by JONES (1972, 1973) appears to play an important role in lowland populations of *L. corniculatus*; unfortunately, no details are known about the biotic environment of *L. corniculatus* in Switzerland and it would be very advisable to study animals associated with this species.

Our results concerning the cyanogenesis in *Lotus alpinus* show that this species conforms to the geographical trend described above for *L. corniculatus* (Tables III, IV, VI, Figs 7, 9). Still more intriguing, however, is the peculiar pattern of vertical distribution of the two respective variants within each of the two studied chromosomic races of *L. alpinus*. Here again a ratio-cline was revealed within the tetraploid race, a positively decreasing frequency of cyanogenic individuals occurring with increasing altitude above sea level. In this respect, the present results correspond to the classical observations of DADAY (1954b) on *Trifolium repens*. By contrast, diploid *Lotus alpinus* that usually occurs at still higher altitudes than the tetraploids does seem to maintain either a well-balanced polymorphism for cyanogenesis or sometimes even a prevalence of HCN-positive variants in populations. These remarkable differences are particularly distinct when a set of samples taken within a limited area, along a possibly regular altitude gradient is being considered (Fig. 8); apparently different adaptation norms that occur within the diploid and the tetraploid race of *Lotus alpinus* manifest themselves sometimes not even in different frequencies of the respective variants but in mere terms of presence/absence. For instance in the region of Davos, the only HCN-positive plants that were found within an ample material from a variety of stations, were diploid.

Some further details call for attention. As mentioned before, tetraploid *L. alpinus* was found in the region of Arosler Weisshorn (2500 - 2650 m a.s.l.) where diploids were not observed; it should be added that these tetraploid populations comprised some cyanogenic plants, most unusual at the high altitudes. On the other hand, rare heteroploid population samples found in our material most frequently comprised dominating acyanogenic variants among tetraploids whereas diploids did not seem to manifest any particular dominance (Table V). Only further studies can help to explain apparent coincidences

between presence or absence of diploids and the respective variation in cyanogenesis occurring within tetraploids *L. alpinus*; perhaps are they fortuitous, but the question about competitive abilities of the two chromosomic races comes again to mind.

Some previous authors noted a low performance as to sexual reproduction manifested by cyanogenic plants of *L. corniculatus* both in the field (JONES 1962) as well as in experimental conditions (FOULDS and GRIME 1971). An apparent influence of temperature upon reproductive vigour was also observed by DADAY (1965) in *Trifolium repens*. It should be added that SMIRNOVA-IKONNIKOVA and MUKHINA (1956) presented interesting data as to variation in the HCN-content in *L. corniculatus* during various stages of its life cycle, the highest values being established for flowers (13.1 and 11.5 mg% of green weight); the Russian authors have even suggested that *L. corniculatus* should be used as a green food only before flowering. It would be interesting to know whether attraction of visiting insects-pollinators and the subsequent seed-setting stays in any relation to the cyanogenic or acyanogenic genotypes of *L. corniculatus* s. l.; this factor might play an important evolutionary role in the respective populations, representing another aspect of a biotic selection. As far as predominantly acyanogenic populations of tetraploid *L. alpinus* are concerned, differential predation as that observed by JONES (1962, 1966, 1972, 1973) does not seem to be a preponderant selective element.

Practically all the previous data concerning the production of the group frequency of cyanogenic/acyanogenic variants in populations deal with tetraploid *L. corniculatus*. Our investigations on Swiss populations are being continued; it will be most interesting to carry on study on *L. alpinus*, including comparative physiological ecology and biology of reproduction of both diploid and tetraploid representatives of this taxon.

Summary

Variation in chromosome numbers and the cyanogenesis were studied in Swiss populations of the *Lotus corniculatus* group, in particular within the Alpine material. The following chromosome numbers were found: *L. uliginosus* - $2n=12$; *L. corniculatus* - $2n=24$; *L. pilosus* - $2n=24$; *L. alpinus* - $2n=12, 24$; *L. tenuis* - $2n=12$. The cytological variation within *L. alpinus* is characterized by a discontinuous pattern of an euploid differentiation. Distribution of the respective chromosomic races seems to be strongly influenced by altitude a. s. l., diploid populations usually occurring at higher altitudes than the tetraploid ones. In spite of conditions that apparently are favourable to a potential contact, gene-flow between diploid and tetraploid populations of *L. alpinus* appears rather limited as no intermediate chromosome numbers were found and heteroploid populations were rare, occurring in rather disturbed stations.

Polymorphism for cyanogenesis was observed in *L. corniculatus* and *L. alpinus*. Variation in distribution of cyanogenic/acyanogenic variants of the two taxa might be considered as ratio-cline across the Alps with the frequency of HCN-positive plants decreasing from north to south. Another ratio-cline still occurs within tetraploid *L. alpinus*, frequency of cyanogenic individuals positively decreasing with an increase of altitude a. s. l.; by contrast, diploid cyanogenic plants often occur at very high altitudes. Adaptation norms are apparently different for each of the two chromosomic races of *L. alpinus*.

Factors that might possibly contribute to the variation trends found in the studied material, are briefly discussed.

Résumé

Variation par rapport aux nombres chromosomiques et à la cyanogénèse fut étudiée dans le matériel suisse du *Lotus corniculatus* L. s. l. et notamment dans les populations alpines. Les nombres chromosomiques suivants furent établis pour les taxons respectifs du groupe: *L. uliginosus* - $2n=12$; *L. corniculatus* - $2n=24$; *L. pilosus* - $2n=24$; *L. alpinus* - $2n=12, 24$; *L. tenuis* - $2n=12$. Variation cytologique observée chez *L. alpinus* se caractérise par un aspect discontinu d'une différenciation euploïde. Il paraît bien que la distribution des deux races chromosomiques soit fortement influencée par l'altitude, les populations diploïdes habitant les altitudes plus élevées que les tétraploïdes. Malgré les conditions apparemment favorables pour un contact potentiel, l'échange des gènes entre les populations diploïdes et tétraploïdes du *Lotus alpinus* semble être limité car des nombres chromosomiques intermédiaires ne furent pas trouvés et des rares populations hétéroploïdes s'observent dans les stations plutôt perturbées.

Polymorphisme par rapport à la cyanogénèse fut trouvé chez *L. corniculatus* et *L. alpinus*. La distribution des variantes cyanogéniques/acyanogéniques des deux taxons pourrait être considérée comme un ratio-cline à travers les Alpes suisses, la fréquence des plantes cyanogéniques diminuant du nord au sud. Un autre ratio-cline fut observé dans la distribution verticale du *L. alpinus* tétraploïde, la fréquence des individus cyanogéniques à 24 chro-

mosomes diminuant avec l'altitude croissante; par contre, des variantes cyanogéniques diploides furent bien souvent trouvées aux grandes altitudes. Des normes adaptives paraissent bien différentes chez chacune des deux races chromosomiques du *L. alpinus*.

On a brièvement discuté des facteurs qui auraient pu contribuer à la variation observée dans le matériel suisse.

Zusammenfassung

An schweizerischen Populationen der *Lotus corniculatus* - Gruppe wurde die Variation in der Chromosomenzahl und in der Cyanogenese untersucht, unter besonderer Berücksichtigung von Material aus den Alpen. Die folgenden Chromosomenzahlen wurden vorgefunden: *L. uliginosus*: $2n=12$; *L. corniculatus*: $2n=24$; *L. pilosus*: $2n=24$; *L. alpinus*: $2n=12, 24$; *L. tenuis*: $2n=12$. Die zytologische Variation von *L. alpinus* ist charakterisiert durch ein diskontinuierliches Muster einer euploiden Differenzierung. Die Verteilung der beiden Chromosomenrassen scheint mit verschiedener Höhe ü. M. in Beziehung zu stehen: diploide Populationen kommen meist in grösserer Höhe vor als tetraploide. Trotzdem die Voraussetzungen für einen Kontakt oft gegeben sind, scheint der Genfluss zwischen diploiden und tetraploiden Populationen von *L. alpinus* beschränkt zu sein. Es wurden dann auch keine intermediären Chromosomenzahlen vorgefunden und die wenigen heteroploiden Populationen beschränkten sich auf eher gestörte Standorte.

Polymorphismus für Cyanogenese wurde bei *L. corniculatus* und *L. alpinus* beobachtet. Die Variation in der Verteilung von cyanogenen/acyanogenen Pflanzen der beiden Taxa könnte als Verhältnisklin quer durch die Alpen mit abnehmender Häufigkeit HCN-positiver Varianten von Norden nach Süden interpretiert werden. Ein weiteres Verhältnisklin tritt bei der tetraploiden Rasse von *L. alpinus* auf, deren Anteil HCN-positiver Pflanzen mit zunehmender Höhe über Meer stark abnimmt. Dagegen erscheinen cyanidhaltige diploide Pflanzen auch in sehr grosser Höhe. Die Adaptationsnormen der beiden Chromosomenrassen von *L. alpinus* scheinen offenbar verschieden zu sein.

Faktoren, welche die in den Untersuchungen vorgefundenen Variationsmuster beeinflussen könnten, werden kurz diskutiert.

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