

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

**Herausgeber:** Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel

**Band:** 42 (1972-1973)

**Artikel:** Biosystematic investigations in *Cardamine pratensis* L.s.l : 1. Diploid taxa from Central Europe and their fertility relationships

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**Kapitel:** 10: Discussion

**DOI:** <https://doi.org/10.5169/seals-377678>

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seasonal barriers; seed incompatibility seems to be as well a rather important mechanism preventing spontaneous hybridization. Similar patterns appeared in relation between *C. Matthioli* and *C. nemorosa* as well as *C. udicola* and *C. nemorosa*. However, the crossing behaviour of *C. udicola* remains still to be investigated in detail.

It can be concluded that isolation barriers occurring between diploid taxa of the *C. pratensis* group are very variable in their nature and strength. They apparently act in cooperation: the most of diploid taxa remain distinct over their range partly because of differences in geographical distribution, partly because where they occur together their habitats differ and they have different times of flowering. But in some places they meet and flower together; given that the pollen is carried by insect vectors from one species to another, seed incompatibility is likely to represent a further barrier to successful hybridization. This internal mechanism acts at various post-mating stages, not only affecting development of embryo and endosperm, but also seems to influence the strongly reduced potential of germination of the hybrid seeds.

## 10. Discussion

The results of the present investigations contribute to the knowledge of evolutionary mechanisms that have played rôle in the speciation at homoploid level within the *Cardamine pratensis* group.

Some aspects of the problem i.e. types of variation and isolation barriers should be characterized in a general way. One might say that interpopulational variation within the *C. pratensis* complex is to a large extent camouflaged by the intrapopulational one. Alloamy that is a predominating type of the breeding system in all studied diploid taxa, undoubtedly represents an important factor in the creation of new genotypes. On the other hand, vegetative reproduction, strongly marked within the group of *C. pratensis*, seems to neutralize in some part the effects of selection; this means that the plants which have a characteristic genotype can be preserved in population even if they are sometimes unbalanced.

Isolation barriers occurring within the *C. pratensis* group are strongly diversified. The particular taxa are not separated by a single mechanism,

yet by a combination of different ones acting in cooperation. In this way, a joint effect of several incomplete isolation factors may bring about more or less effective separation of the respective species from its congeners.

The spatial isolation is rather pronounced at diploid level within the group of *C. pratensis* and rarely more than two 16chromosomic taxa occur within the same geographical area. Most of them are further separated by ecological and (or) seasonal barriers. The effects of the external barriers are more or less reinforced by internal mechanisms of isolation: in particular, seed incompatibility appearing at various post-mating stages prevents partly or totally the gene exchange between some diploid representatives of the *C. pratensis* group. A similar pattern of isolation was recently observed by GUSTAFSSON (1973, 1973a) within the group of *Atriplex triangularis* from Scandinavia. It should be pointed out that the isolation barriers occurring between diploid taxa of the *C. pratensis* complex are greatly variable as to their strength: some diploids are apparently well-separated from certain representatives of the group, whereas a different combination gives either a slight or a good chance for hybridization. The observations performed in nature are in agreement with the results of interspecific crosses.

It might be assumed that the events of speciation that marked an evolutionary divergence of *C. granulosa*, *C. Matthioli*, *C. nemorosa* and *C. rivularis* must have occurred relatively early in the phylogeny of the group. The present results concerning karyology of these diploids show small yet rather definite differences both in total amount of chromatine as well as in structural arrangement of the chromosomes. Each of these four taxa displays rather a stable set of morphological characters that permit to recognize it without difficulties. It seems probable that morphological and karyological differentiation of this sort might have gradually been achieved in rather a long time.

*Cardamine granulosa* is rather isolated from other diploids. It represents not only a taxon that is morphologically extreme within the group, but also has the lowest amount of the chromatine. As far as its geographical distribution is concerned, *C. granulosa* occurs within a limited area

in western Piedmont, between Turin and eastern foothills of the Cotian Alps, in a few isolated stations. Only a single station of *C. granulosa* was recorded outside this area in the region of Guastalla (Emilia). It is impossible to decide whether the distribution range of *C. granulosa* was originally wider, for no data are available. However, at least part of the original area of *C. granulosa* has been destroyed by construction sites in the surroundings of Turin. This was probably the reason why LÖVKVIST (1956) has been unable to get any living plants for his investigations and wrote: "It is not certain whether this species is still among the living plants in the present flora". In the recent edition of the Flora Europaea, *C. granulosa* is also quoted as "now possibly extinct". In spite of these prognostics, *C. granulosa* has actually been found in two stations and it cannot be excluded that there are some further chances to find this taxon in some other places.

It might be assumed that *C. granulosa* was originally a forest plant growing in rather moist, humic soils; it might later colonize some shadowy meadows that got mown late in summer. Apparently *C. granulosa* does not stand well a competition in normal fertilized meadows, its flowering time being rather late. Natural or nearly natural forests within the Plain of the Po River have practically disappeared at times, being replaced by agricultural fields and the poplar plantations. It seems probable that *C. granulosa* has therefore only a limited opportunity to find a convenient type of station.

*Cardamine Matthioli* can usually be distinguished from other diploid taxa of the group by its very narrow and rather long siliques. As far as the cytological characters of this taxon are concerned, it stays near *C. granulosa*; however, it seems to be genetically isolated from *C. granulosa*, *C. rivularis* and *C. nemorosa*. This area of geographical distribution of *C. Matthioli* spreads from Transsylvania to Piedmont. Two races of *C. Matthioli* were found within the investigated area: a/ plants that inhabit fertilized meadows and b/ individuals found in wet sites, rich in nutrients. It should be noted that the stations of *C. Matthioli*, situated south of the Alps appear to be destroyed for the most part. Only local,

isolated and fairly small populations were found; it is likely that they are remnants of a formerly wider and more continuous range. It is rather difficult to precise an exact type of station that might have originally been inhabited by *C. Matthioli*. The authors observed it mostly in the habitats remaining under human influence: fertilized meadows, drain ditches, open swamp vegetations in sites rich in nutrients. Only a single population of *C. Matthioli* was found in a poplar forest near Pavia (Lombardy). On the other hand, SOÛ (1968) has reported this taxon from the *Alnion*-forests in Hungary.

It might be assumed that *C. Matthioli* has arrived from the East to the West at post-glacial period and colonized in the first place the *Alnion*-forest, very frequent then and widespread in the Plain of the Po River. An alternative hypothesis might be that *C. Matthioli* migrated westwards later, after the Plain of the Po River has been cleared of forests; the spreading of *C. Matthioli* could be then influenced by human activities. However, it is impossible to decide which of these two interpretations would be correct, for too few data stay at our disposal. The *Alnion*-forest became exceedingly rare in the Plain of the Po River and only very few records of *C. Matthioli* are known from these relictic stations. The chance of surviving of *C. Matthioli* in the Plain of the Po River got still diminished during the last hundred years; meadows that were not replaced by cultivation fields are systematically ploughed and intensively grazed so that the conditions there do not seem suitable anymore for *C. Matthioli*. It seems probable that actual stations of this taxon in the Plain of the Po River are mostly confined to a few wet sites rich in nutrients, such as the localities Nos 568, 569, 570 and 698 found by the present authors (Table 2 ). The management of the meadows has apparently not been altered, only in the Alpine foothills situated in some marginal parts of the Plain of the Po River; it can be assumed that a frequent occurrence of *C. Matthioli* in fertilized meadows near Pinerolo (western Piedmont) is conditioned by this particular ecological factor.

Human influence apparently played an important rôle in destruction of the habitats in which *C. Matthioli* could have grown previously. On the other hand, it seems probable that *C. Matthioli* might have been eliminated

from some of its former stations through competition from recently introduced, white-flowering *Cardaminopsis arenosa* (L.) Hayek. This problem requires further investigations; however, *C. arenosa* that occurs at present frequently in meadows situated south of the Alps, has not been known there in the last century. The data of *C. arenosa* given by COMOLLI in 1847 refer probably to *Cardaminopsis Borbasii* (Zapal.) Hess et Landolt, a taxon that has pink flowers. Still in 1910 CHENEVARD has not reported any stations of *Cardaminopsis arenosa* from Ticino. Actually it is very common in this region. In Valsesia, the authors could not find any *C. Matthioli*, yet *Cardaminopsis arenosa* occurred frequently in the meadows. In Grigna, near Ballabio, notably reduced population of *C. Matthioli* was confined to a wet station, but adjoining meadows were populated by *Cardaminopsis arenosa*.

*Cardamine rivularis* represents an opposite extreme within the *C. pratensis* group both as to morphological characters as well as to the chromatine content. The results of experimental crosses point to a complete isolation of *C. rivularis* from *C. granulosa* and to rather a pronounced interspecific incompatibility with *C. Matthioli*; on the other hand, numerous reciprocal hybrids, easily obtained from crosses between *C. rivularis* and *C. nemorosa*, suggest a close relationship between these two taxa.

*C. rivularis* has the widest range of geographical distribution as compared to all other diploid taxa of the group: it spreads from Eastern Carpathians to Western Alps and the Massif Central. The area of *C. rivularis* is particularly discontinuous. This might be explained to some extent by ecological requirements of this mountain taxon that grows in wet stations rather poor in nutrients. On the other hand, some gaps in the distribution range of *C. rivularis* are rather obscure: in spite of apparently suitable ecological conditions, it does not occur in SW Alps as well as in some parts of Central and Southern Alps. It remains an open question whether the absence of *C. rivularis* in these regions is due to some particular migration trends, or it is merely incidental. However, it should be mentioned that some of the areas where diploid *C. rivularis* is actually missing, are being inhabited by polyploid types of the *C. pra-*

*tensis* group ( $2n=32$ ,  $2n=40$ ) that might have proved themselves more efficient competitors.

The stations of *C. rivularis* are situated below potential timberline and distributed within the area that has been covered by the ice sheet during the glaciation period. One might suppose that *C. rivularis* has survived the glaciation in some lowland stations which were not glaciated and its area might still have been continuous at that time. After the retreat of the glaciers, *C. rivularis* might have migrated along the Alpine valleys and has maintained itself in the mountain stations while its lower situated habitats have been destroyed by growing forests. It is also possible that the disappearance of *C. rivularis* in lower stations might have been caused by competition from some other taxa of the *C. pratensis* group which were better adapted to new conditions.

*C. rivularis* occurs most frequently in the natural stations such as open flat shores of lakes or around creeks where the soil is turfy, base-poor and contains rather a low amount of nitrogen. Only rarely it was found in very slightly manured, humid meadows and pastures i.e. in the stations influenced by human activities.

An interesting detail should be mentioned: among the studied diploid taxa, *C. rivularis* is the only one that manifests a tendency to produce unreduced pollen grains (up to 32%). This particular character has apparently contributed to the formation of the triploid ( $2n=24$ ) and hexaploid ( $2n=48$ ) natural hybrids between *C. rivularis* and *C. amara* (URBANSKA-WORYTKIEWICZ and LANDOLT 1972, URBANSKA-WORYTKIEWICZ and LANDOLT unpubl.); it can also be of an evolutionary value for *C. rivularis* itself. Further investigations will be carried out on this interesting problem.

*Cardamine nemorosa* can be distinguished from *C. rivularis*, *C. Matthioli*, and *C. granulosa* for some of its morphological characters are rather easily recognizable (type of hairs, thickness of the style, large terminal leaflets in basal leaves). The relationship between *C. nemorosa* and *C. rivularis* manifests itself to some extent in a similar chromatine content of the two taxa as well as in their breeding behaviour; it is still more definitely marked in their fairly good crossability. By contrast, *C. nemo-*

*rosa* is completely isolated from *C. granulosa* and *C. Matthioli*.

The whole area of geographical distribution of *C. nemorosa* is rather difficult to trace. It is notably discontinuous and spreads at least from Niedersachsen to the southern part of the Jura. It can be assumed that *C. nemorosa* might have migrated into the studied area from two opposite directions: it might have arrived to SW Jura from the West whereas northern Jura and its surroundings might become inhabited by plants that arrived from the North. These putative migration paths have apparently stayed off the Black Forest and the Vosges; that would have accounted for the absence of *C. nemorosa* in the middle part of the Jura.

The actual stations of *C. nemorosa* are very local and most frequently isolated from each other. In spite of its apparently relic character, *C. nemorosa* does not seem to be endangered by extinction as it occurs nearly always in rather natural forest stations.

As shown above, various phenomena of *primary speciation* were involved in the evolution of the *C. pratensis* group. We are using this term as proposed recently by GRANT (1971), to include the speciation phenomena involved in primary evolutionary divergence and to exclude the hybrid speciation. However, it seems possible that *re-fusion* has also contributed to the formation of some diploid taxa within the *C. pratensis* complex: *C. udicola* and *C. pratensis* seem to be of a hybrid origin.

*C. udicola* is of rather an intermediate character within the group of *C. pratensis*. As to the morphology, it stays between *C. Matthioli* and *C. rivularis*, the range of variability being rather wide. The chromosome set of this taxon can be characterized in a general way as approaching that of *C. Matthioli*. On the other hand, ecological preferences of *C. udicola* are very similar to those of *C. rivularis* (wet, poor soils).

The actual geographical distribution of *C. udicola* represents rather an obscure pattern. This taxon occurs very locally in two areas, fairly separated from each other; one of them is situated in northern part of the Alps (surroundings of the Lake of Thun), the other - in southern Ticino. It is interesting to note that the populations of *C. udicola* from northern Alps comprise both the plants with white and pink petals whereas in sou-



thern Ticino only white-flowering individuals were found. According to the herbarium data, the former area of diploid *C. udicola* was wider than the actual one: numerous stations were recorded from Ticino, the Swiss Midland, Bavaria, Upper Austria, Tchechoslovakia and southern Poland. At present, diploid *C. udicola* seems to be on a verge of extinction due to human interference (draining of the reed-meadows, construction sites on the lake shores, pollution); it should be added that in numerous stations the diploids have apparently been replaced by plants representing various polyploid levels.

Only a limited material of *C. udicola* was used in the experimental crosses the present paper is dealing with. Solely the plants from Ticino were investigated; it should be pointed out that they fall outside the normal scheme of crossability. The seed setting after selfings appeared to be normal. In spite of rather a good seed output, *C. udicola* from Ticino was seed-sterile: no germination whatsoever has been observed either in selfings, or in cross-experiments of any kind. The only three hybrid plants were obtained from crosses with *C. nemorosa* where *C. udicola* has been used as male parent. It is impossible to say at present which factor has influenced an apparent seed sterility occurring in the plants described above. Only a few individuals of *C. udicola* from Ticino were investigated, so the phenomenon might be merely incidental. Further investigations are required on this subject.

Only general conclusions concerning the origin of *C. udicola* can be presented, for the study on this taxon has not yet been completed. One can assume that *C. udicola* might have arisen either through a racial differentiation from *C. Matthioli* or through hybridization between *C. Matthioli* and *C. rivularis*.

It cannot be excluded that *C. udicola* represents a specialised, isolated race of *C. Matthioli* that got stabilized through genetic drift; the cytological characters of *C. udicola* would rather support this assumption. On the other hand, the seed sterility observed in crosses between *C. udicola* and *C. Matthioli* point to rather an accentuated incompatibility between the two taxa. *C. udicola* does not fit so well within the range of morphological variation of *C. Matthioli*. Intermediate morphological and ecologi-

cal characters of *C. udicola* seem to be in favour of its putative hybrid origin. This taxon might have arisen from crosses between *C. Matthioli* and *C. rivularis*; it is possible that these taxa were wider distributed at the post-glacial time and they could incidentally get into contact with each other through a random migration. It should be noted, however, that a possibility of a successful hybridization between *C. Matthioli* and *C. rivularis* is actually very difficult to verify as both taxa show a mutual incompatibility, at least in the experimental conditions. Further investigations, including *C. Matthioli* and *C. rivularis* from various parts of their distribution range, would be advisable.

*Cardamine pratensis* is of rather intermediate character within the studied group. Its origin could be alternatively explained in two ways: 1/ through a racial differentiation or 2/ through hybridization.

It might be assumed that *C. pratensis* has originally derived, through a racial differentiation from an ancient stock that has also given rise to *C. nemorosa*; only later it might have acquired genes from *C. rivularis* or, perhaps, from *C. udicola* and its competitive abilities became improved in this way. Morphological and cytological characters of *C. pratensis* do not exclude such a hypothesis. However, a limited, apparently unilateral intercompatibility of *C. pratensis* and *C. nemorosa* as well as the data concerning geographical distribution of *C. pratensis* and its particular vigour, are rather in favour of its hybrid origin.

*C. pratensis* presents a somewhat complicated problem as far as one of its putative parent form is concerned. The relationship between this taxon and *C. nemorosa* is clearly evident; on the other hand, it is a little difficult to decide about the other parent.

Most likely, *C. pratensis* could be placed as an intermediate taxon between *C. rivularis* and *C. nemorosa*. The latter taxon apparently has more influence upon the characters of *C. pratensis*; this affinity appears not only in morphology but also in structural differentiation of the chromosome set. As to its ecology, *C. pratensis* occurs in stations that are intermediate between those of *C. nemorosa* and *C. rivularis*, the altitude zone and type of soil resembling rather *C. nemorosa*, yet the type of vegetation (meadows and pastures) showing more affinities with *C. rivularis*.

As far as the geographical distribution is concerned, *C. pratensis* is the only diploid taxon within the group which has a well-defined and rather a compact area; it stays between discontinuous areas of *C. nemorosa* and those of *C. rivularis*. In some regions *C. pratensis* comes into contact with *C. nemorosa* and was observed flowering simultaneously with the latter taxon. Only exceptionally was *C. pratensis* entering the area inhabited by *C. rivularis*, but then flowering time of these two taxa overlapped, at least partly.

The results of interspecific crosses bring an interesting information about the fertility relationships occurring between *C. nemorosa*, *C. rivularis* and *C. pratensis*. In spite of their geographical, ecological and seasonal isolation, *C. nemorosa* and *C. rivularis* appear to be intercompatible and rather easily produce reciprocal hybrids in experimental conditions. On the other hand, *C. pratensis* shows certain compatibility with *C. nemorosa* and *C. rivularis*, but solely when these two taxa are used as male parents. An opposite cross-direction revealed a pronounced seed-incompatibility that manifested itself mostly in very low percentage of germinating seeds.

It could be assumed that *C. pratensis* has arisen from spontaneous crosses between *C. nemorosa* and *C. rivularis*, at times when these two taxa were still in contact; subsequently, repeated backcrosses with *C. nemorosa* might have affected both visible traits and structural arrangement of the chromosomes of *C. pratensis*. Similar cases were reported by GRANT and GRANT (1960) in *Gilia cana* and *G. ochroleuca vivida*, both representing diploid taxa within the sect. *Arachnoides* of the genus *Gilia*.

The pattern of the geographical distribution of *C. nemorosa* does not permit to postulate that this taxon might have formerly occurred in the Alps. More probable would be the assumption that *C. rivularis* has maintained itself for a longer time at the post-glacial period in some suitable stations north of the Alps. e.g. in the region between the Lake of Constance and the valley of the Danube. Such distribution might have given an opportunity for some crosses between *C. nemorosa* and *C. rivularis*.

The results of experimental crosses as well as the observations on meiosis in  $F_1$  hybrids represent the arguments in favour of the opinion that

*C. rivularis* was the second parent of *C. pratensis*. On the other hand, morphological, ecological and geographical data do not exclude a possibility that *C. udicola* might have been an alternative ancestor for this taxon. The herbarium data point to a rather wide original distribution of *C. udicola*; northern part of its former range (Bavaria) overlaps partly the actual area of *C. pratensis*. Furthermore, *C. udicola* is a low-land taxon; its incidental contact with *C. nemorosa* might have resulted in a hybridization between these two taxa. We must emphasize, however, that exact relationships between *C. udicola* and other diploid taxa of the *C. pratensis* group have not yet been sufficiently verified and further experiments are being continued.

*C. pratensis* has not only a distinct and continuous area of distribution but also occurs very frequently within its stations and apparently is well-adapted to the environmental conditions occurring there. This particular vigour stays rather in a sharp contrast with *C. nemorosa* and *C. rivularis* which appear to be in defensive. The differences in vigour occurring between *C. pratensis* and *C. udicola* are still more conspicuous.

Environmental isolation operates to suppress hybridization between intercompatible species in a stable, closed community; hybrid zygotes formed from time to time are eliminated by stabilizing selection almost as soon as they arise. By contrast, if natural community has been broken and new open habitats are accessible, the hybrids can and do become established because interspecific competition and stabilizing selection are more or less inefficient at that moment. This explanation of a correlation occurring between hybridization and habitat disturbance is an extension of the hypothesis of KERNER (1891) stressed by numerous authors (e.g. STEBBINS 1950, 1959, 1969, 1971, GRANT 1963, 1971, GILLET 1966, 1972, KRUCKEBERG 1969, LEWIN 1970).

It seems probable that the creation and stabilization of the diploid *C. pratensis* might be primarily due to a human influence; new habitats could serve as breeding grounds for a new-born hybrid. The pattern of geographical and ecological distribution of *C. pratensis* studied in the course of the present work, supports this opinion. As pointed out by ANDERSON (1948, 1949), the environmental control carries beyond the  $F_1$

to the second and later hybrid generations. ANDERSON emphasized that the first hybrid generation is more or less intermediate and rather uniform in its ecological preferences; however, in later generations a great diversity of recombination types appear and they might manifest various physiological traits. Accordingly, they would require numerous ecological niches. Introgression would further complicate the differentiation pattern of the hybrids. ANDERSON concluded that an intermediate habitat would enable the  $F_1$  generation to survive but a varied number of ecological niches i.e. "hybridization of the habitat" must exist if any significant amount of  $F_2$  generation is to get established (ANDERSON 1948). Such hybridized habitats are actually produced mainly under human influence. As shown above, *C. pratensis* occurs in preference within fertilized meadows that are cut or grazed; sometimes, it can also be found in forest roads or at the borders of forests. It seems possible that establishment of this hybridogene taxon might coincide with intensive development of live stock-farming.

Characteristic types of geographical distribution of *C. pratensis* might be partly due to some edaphic factors: moraine soils of the glacier of the Rhine are less differentiated and accordingly base-richer than those of non-glaciated areas NW of the Schwäbische Jura. On the other hand, limestone soils in the Jura itself seem to be rather too dry for *C. pratensis*. It should be added that a competition from polyploid taxa of the *C. pratensis* group might confine the diploid to its actual area.

One of the factors limiting the present discussion is the not yet sufficiently known relationship occurring between the diploid taxa of the *C. pratensis* group and higher polyploids of this complex. Another important problem constitutes a balance between sexual reproduction and vegetative propagation in *C. pratensis* s.l. The outbreeding, strongly marked within the group, provides undoubtedly some flexibility, i.e. high rate of variation output to be tested by selection; on the other hand, vegetative propagation may assure certain stability, i.e. gives possibilities for fixation and multiplication of successful biotypes. As far as the diploid *C. pratensis* is concerned, the potential propagation may be of adaptive value in prevailing biotope for this species: the production of small daughter plants

that easily root, is apparently an effective mode of reproduction, especially in cut or grazed meadows where the plants may have considerably less chance to set seeds. A special attention is to be given to these problems in the further course of our investigations.

### Summary

Six diploid taxa of the *Cardamine pratensis* group from Central Europe (*C. granulosa*, *C. Matthioli*, *C. udicola*, *C. rivularis*, *C. pratensis* s. str., *C. nemorosa*) are rather closely related. They are partly sympatric and to some extent differentiated in their ecological requirements. A great deal of morphological variation was found; interpopulational variation seems to be camouflaged by intrapopulational one. Allogamy that proved to be a predominating type of breeding system, plays apparently an important rôle in creation of new genotypes; however, its influence is partly counterbalanced by an intensive vegetative propagation: numerous small daughter plants that easily root are produced on leaves and stems.

Cytological variation found within the diploid taxa of the *C. pratensis* group represents diverse aspects. At least three phenomena viz. local migrations, gene flow, and aneusomy contributed to the formation of mixed populations. It seems probable that the populations inhabiting the center of the distribution area of given taxon are subject to the selection pressures which are different from those occurring within the marginal populations.

Isolation barriers that separate the studied diploid taxa are strongly diversified in their nature and strength. The external barriers are more or less reinforced by internal mechanisms of isolation; in particular, seed incompatibility appearing at various post-mating stages prevents partly or totally the gene exchange between some diploid taxa.

Evolution on diploid level within *C. pratensis* s.l. has apparently been influenced by various phenomena of primary speciation that have occurred relatively early in the phylogeny of the group. On the other hand, re-fusion was likely to contribute as well to the formation of some diploid taxa.

Human activities have notably influenced the pattern of geographical distribution of numerous diploids; in former times, creation of new biotopes such as reed-meadows and fertilized meadows apparently has promoted a wider spreading of some taxa (*C. Matthioli*, *C. udicola*, *C. pratensis* s. str.). It seems probable that diploid *C. pratensis* s. str. the taxon of a putative hybrid origin, might have got established only after development of more intensive stock-farming. Recent human influence, however, being most frequently of a destructive effect, results in a rather advanced extinction of some diploid taxa within the studied area. (*C. granulosa*, *C. Matthioli*, *C. udicola*).

## Résumé

Six taxons diploïdes du group de *Cardamine pratensis* que l'on rencontre en Europe centrale (*C. granulosa*, *C. Matthioli*, *C. udicola*, *C. rivularis*, *C. pratensis* s. str. *C. nemorosa*) sont liés par une parenté plutôt étroite. Ils se montrent en partie sympatriques et assez différenciés par rapport à leurs préférences écologiques. La variation morphologique des taxons étudiés est bien prononcée; la variation à l'intérieur des populations paraît camouflager, dans une certaine mesure, celle qui sépare les populations d'un taxon donné. L'allogamie qui est le système reproducteur prédominant chez *C. pratensis* s.l. joue vraisemblablement un rôle important dans la création des génotypes nouveaux; toutefois, son influence est partiellement compensée par la propagation végétative très forte.

La variation cytologique trouvée chez les taxons diploïdes présente des aspects divers. Au moins trois phénomènes : des migrations locales, l'échange des gènes entre les populations voisines ("gene flow") et l'aneusomie, ont contribué à la formation des populations mixtes. Il est probable que les populations vivant au centre de l'aire géographique d'un taxon donné soient soumises à des forces sélectives différentes par rapport à celles qui agissent à l'intérieur des populations marginales.

Les mécanismes d'isolement qui séparent les taxa diploïdes sont fort diversifiés en leur nature et force. L'isolement externe est renforcé par des barrières internes dont la plus significative est l'inviabilité des hybrides ("seed incompatibility"). En se manifestant à divers stades de développement après la fécondation, elle empêche totalement ou presque l'échange des gènes entre certains taxons diploïdes.

L'évolution au niveau diploïde du groupe de *C. pratensis* avait été apparemment marquée par des phénomènes variés de apéciation primaire qui ont dû se présenter assez tôt dans la phylogénie de ce groupe. Il est fort probable que la ré-fusion ait également contribué à la formation de certains taxons diploïdes.

L'intervention humaine a fortement influencé la distribution géographique de nombreux taxons diploïdes; autrefois, la création des biotopes nouveaux (prairies marécageuses, prairies fertilisées) avait apparemment promu la répartition assez vaste de plusieurs taxons (*C. Matthioli*, *C. udicola*, *C. pratensis* s.str.). Il semble bien que *C. pratensis* s.str. diploïde, plante des prairies de fauche et des pâturages fertilisés dont le origine est fort probablement hybridogène, n'ait pu s'établir qu'à la suite du développement d'un élevage intensif. Toutefois, l'influence humaine récente, étant le plus fréquemment à effet destructif, aboutit à l'extinction bien avancée de certains taxons diploïdes sur le territoire étudié. (*C. granulosa*, *C. Matthioli*, *C. udicola*).

## Zusammenfassung

Sechs diploide Sippen der Artengruppe der *Cardamine pratensis* aus Zentraleuropa (*C. granulosa*, *C. Matthioli*, *C. udicola*, *C. rivularis*, *C. pratensis* s.str., *C. nemorosa*) wurden zytotaxonomisch untersucht und Kreuzungsexperimente durchgeführt. Die Sippen sind nahe miteinander verwandt, überdecken sich teilweise in ihrer geographischen Verbreitung und zeigen bis zu einem gewissen Grad unterschiedliche ökologische Ansprüche. Die morphologische Variationsbreite der einzelnen Sippen erwies sich recht gross.



Die Variation zwischen den Populationen wird weitgehend überdeckt von der Variation innerhalb der Populationen. Im Fortpflanzungssystem herrscht Fremdbestäubung (Allogamie) vor und scheint eine wichtige Rolle bei der Entstehung neuer Genotypen zu spielen; auf der anderen Seite ist die vegetative Vermehrung durch Sprossung aus Blättern und Stengeln sehr intensiv.

Zytologisch variieren die diploide Sippen von *C. pratensis* s.l. in verschiedener Hinsicht. Zumindest drei Vorgänge tragen zur Bildung von gemischten Populationen bei: lokale Wanderung, Gen-Fluss und Aneusomie. Es ist wahrscheinlich, dass Populationen im Zentrum ihres Sippenareals einem anderen Selektionsdruck ausgesetzt sind als randständige Populationen.

Die Isolationsmechanismen zwischen den einzelnen Sippen sind sehr unterschiedlicher Natur und Wirksamkeit. Externe Isolationsmechanismen werden durch interne verstärkt: „besonders Sameninkompatibilität in verschiedenen Stadien nach der Befruchtung verhindert teilweise oder völlig den Gen-Austausch zwischen einzelnen diploiden Sippen.

Die Evolution auf der diploiden Stufe von *C. pratensis* s.l. wurde offenbar von verschiedenen Vorgängen der primären Artdifferenzierung beeinflusst, welche in der Phylogenie der Artengruppe relativ früh auftraten. Auf der anderen Seite trug wahrscheinlich auch die Bastardierung zur Neubildung von diploiden Sippen bei.

Die Tätigkeit des Menschen hat die geographische Verbreitung der meisten diploiden Sippen deutlich beeinflusst. Früher hat der Mensch durch Neuschaffung von Biotopen (Sumpfwiesen, Fettwiesen) verschiedenen Sippen eine Ausbreitung ermöglicht (besonders *C. Matthioli*, *C. udicola*, *C. pratensis* s.str.). Die diploide *C. pratensis* s.str. konnte sich wahrscheinlich überhaupt erst nach Einführung der intensiven Viehwirtschaft entwickeln; ihre Entstehung dürfte hybridogen sein. In letzter Zeit hat jedoch der Mensch viele notwendige Biotope zerstört; deswegen sind im Untersuchungsgebiet einige diploide Sippen vom Aussterben bedroht (*C. granulosa*, *C. Matthioli*, *C. udicola*).

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