VARIABILITY CHARACTERISTICS AND COMPARISON OF *CAREX ARENARIA* L. AND *CAREX LIGERICA* GAY POPULATIONS BASED ON RHIZOME CHARACTERS

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(Received: July 6, 1993. Accepted: May 14, 1994)

ABSTRACT

The studies included 9 populations of *Carex arenaria* L. and 7 populations of *Carex ligerica* Gay, compared with each other on grounds of variability analysis, related to rhizome characters. The sedges reach in the area of Poland their eastern range limits, with isolated populations spread along the range margins. The studied plants were placed in a greenhouse in homogenous conditions, which made possible an analysis of genetic variability in the populations. The obtained results point to the absence of gene flow between the studied species and, thus, to their clearly distinct character. Genetic drift was postulated as one of the causes of the obtained variability pattern.

KEY WORDS: *Carex arenaria*, *Carex ligerica*, variation, populations, genetic drift, rhizome characters

INTRODUCTION

Populations growing along range limits of a given species, frequently isolated ones, represent important objects of studies, both from the evolutionary and taxonomic point of view. A detailed account of the problem has been published by Lewontin (1957, 1974). The author accentuates, above all, the instability of peripheral habitats, resulting in variable effects of selection, acting on different genotypes in different time. Moreover, the genetic structure of such a population was significantly affected by inbreeding effect, low number of population members and by geographic isolation. The factors contribute to a low level of heterozygosity in the isolated populations (Ford and Ball 1991). The effect on genetic structure of a population is particularly significant if the factors act on vegetatively propagating plant species. In such cases, the local population may consist of few members (Urbaniak 1984, Horak and Holt 1986). The studies performed till now on variability of *Carex arenaria* L. and *Carex ligerica* Gay populations were based on biochemical or morphological-anatomical characters (Szweykowski and Mendelak 1969, Szweykowski and Wagner 1975, Szweykowski and Chwilkowska 1976, Krzakowa et al. 1978, Urbaniak 1984, 1988a, 1988b, 1990, 1992a, 1992b). The results of the above studies were based, most frequently, on work performed with plants which grew in homogenous conditions of a greenhouse for at least a year. This allowed to assume that the obtained variability pattern reflected the genetic structure of a population. Phenolic compounds demonstrated a similar composition in both species and only some of them could qualitatively differentiate *Carex arenaria* L. and *Carex ligerica* Gay populations. The analysis of leaf characters showed also a distinct character of populations of the two species.

Within *Carex ligerica* a more pronounced interpopulational variability was detected, as compared to *Carex arenaria*. The two sedge species most frequently inhabit margins of pine forests or mid-forest clearings. On the other hand, within the continuous range at the seacoast, the most frequent habitat involves grey dunes. In such sites *Carex arenaria* forms vast populations, consisting most frequently of a few hundreds of plants.

Occasionally, populations of the two species grow next to each other, as e.g. in Kopanica near Wolsztyn and in Tychnowy near Kwidzyn. In Kopanica near Wolsztyn large populations were also observed with intermixed plants of *Carex arenaria* and *Carex ligerica*. In other cases, the two species are separated from each other, as e.g. in Złotoria near Toruń, where *Carex ligerica* grows at a distance of approximately 20 km from *Carex arenaria* stands. The studied sedges belong to anemophilous plants forming diaspores with great numbers of individuals – 14,800 diaspores per m² in the population from Hvaler in Norway (Lye 1993). In this respect, sexual propagation seems to constitute a factor of high significance. On the other hand, it should be stressed that capacity for a very intense vegetative propagation was noted in *Carex arenaria* and *Carex ligerica*. The property makes the populations of *Carex arenaria* and *Carex ligerica* very mobile, particularly during spring and summer when stimulated vegetative growth of rhizomes is observed. The penetration of new areas by freshly outgrowing rhizomes takes place not only by elongation of older rhizome parts but also by numerous side outgrowths (observed by the author upon multiple occasions in 1976-1993). At microgeographic scale, such a process may release the effect of genetic drift. The parallel operation of selection which secures adjustment, and of genetic drift which opens chances for testing new genetic

pools, seems to provide conditions for suitable development of *Carex arenaria* and *Carex ligerica* populations. The influence of these factors on sedge populations have been suggested by Ford and Ball (1991).

The above quoted data on *Carex arenaria* and *Carex ligerica*, as well as our own results obtained till now, have induced us to pose a few questions. First of all, considering that hybridization is postulated to represent the causative factor for development of multiple taxons of the *Carex* genus, particular attention has been paid to the potential of gene flow between the studied taxons. Two respective questions have been advanced: 1. can traces of gene flow between the studied species be detected?, 2. does gene flow take place between populations within a given species? Moreover, presenting the results based on rhizome characters, an attempt has been made to correlate the obtained variability pattern with patterns obtained earlier. The study has also aimed at comparing the *Carex ligerica* population from Tychnowy and Kadyny with the remaining populations of the *Carex ligerica* group and at relating them to *Carex arenaria* populations. The populations, growing at stands positioned on easternmost limits of the species range, seem to be exceptionally predisposed to illustrate intense evolutionary processes.

MATERIAL AND METHODS

To compare *Carex arenaria* and *Carex ligerica* populations, plants from the following stands were collected:

I. *Carex arenaria* – 1. Międzyzdroje, grey dune, 28 plants, collected in 1977; 2. Ustka, grey dune, 30, 1978; 3. Rabka, border of pine forest growing on grey dune, 1978; 4. Białogóra, border of pine forest growing on grey dune, 30, 1978; 5.

Lulkowo, border of pine forest, 29, 1977; 6. Witnica, young pine stand, 30, 1978; 7. Konotop, border of pine forest, 30, 1978; 8. Ołobok, young pine stand, 30, 1973; 9. Zielonka, border of pine forest, 30, 1978.

II. *Carex ligerica* – 10. Kadyny, border of pine forest, 27, 1977; 11. Szumilowo, young pine stand, 27, 1976; 12. Kopanica, border of pine forest, 27, 1977; 13. Złotoryja, inter forest dune, 27, 1976; 14. Toruń-Wrzosy, border of pine forest, 27, 1976; 15. Toruń-Wrzosy, border of pine forest, 27, 1976; 16. Tychnowy, border of pine forest, 27, 1977. Sites of collection of the 16 studied populations, including nine *Carex arenaria* and seven *Carex ligerica* populations, were marked on the map of Poland (Fig. 1). In the field rhizomes were collected at random, digging out individuals every 1 m, in a few parallel rows. Subsequently, the sedges were planted in a mixture of soil, sand and peat (1:2:1, v/v). The pots with planted sedges were transferred to a greenhouse, creating in this manner homogenous developmental conditions and eliminating differential environmental influences. The culture was continued for one year. Subsequently, rhizomes were collected for studies. From each pot three uppermost fragments of rhizomes were taken. The collected material was stored in 70% ethanol. A transverse slice was taken in the middle of the internode between the third and fourth nodes, counted downwards from top of the rhizome. Three cross-section slices, representing three branches of the rhizome and originating from the same plant were placed on a microscopical glass and embedded in polyvinyl alcohol. Characters a, b, c, d, e, f were measured under light microscope, at 40 x magnification (Fig. 2). The characters measured corresponded to those examined in the study of Szwejkowski, Chwiłkowska 1976. In order to detect the interpopulational variation as revealed by anatomical characters of the rhizome, the following

Fig. 1. Location of the studied populations (*C. arenaria* – full circles, *C. ligerica* – empty circles)

Fig. 2. Diagram of the rhizome cross-section showing the characters measured: a – large rhizome diameter, b – small rhizome diameter, c – large stele diameter, d – small stele diameter, e – number of air chambers in the cortex, f – number of vascular bundles

statistical analysis was used, discriminating variables analysis – the procedure aims at maximum intergroup spanning and dendrite technique based on Mahalanobis shortest distances.

RESULTS AND DISCUSSION

In the presented study we attempted to relate the findings to earlier obtained results. Therefore, the material for investigations, in this case rhizomes, were taken from the same population samples, earlier examined in respect to leaf character variability and in respect to phenolic compounds.

The applied in this study method of discriminant variables tends to maximize taxonomic distances between individual populations, stressing clearly the distinct character of the compared species (Figs 3-5). In earlier studies pertaining the same problem (Urbaniak 1992a, 1992b) the notably greater interpopulational variability of *Carex ligerica* has been stressed, as compared to the variability pattern noted for *Carex arenaria* populations. No such conclusions could have been drawn on grounds of the variability pattern of rhizome anatomical characters. In principle, the two species formed two separate, uniform groups. Within *Carex ligerica*, only

two populations from Toruń, marked by numbers 14 and 15, could be distinguished. In the field they grew next to each other. In a close neighborhood of them grew *Carex arenaria*. In order to supplement the discriminant analysis, the shortest dendrite based on Mahalanobis distance has been drawn (Fig. 3). Once more the clear separation of the two species has been evident. As already mentioned, the two *Carex ligerica* populations of Toruń-Wrzosy, i.e. populations 14 and 15, have shown a distinct character. At this stage it should be mentioned that timing of florescence is similar for the two sedges: they bloom in May and June. The obtained till now results of studies comparing *Carex arenaria* and *Carex ligerica* unequivocally point to distinct taxonomic entities, to which the two species belong. In none of the character groups analyzed, i.e. in groups of biochemical traits, phenolic compounds, anatomical traits of leaves and of rhizomes, data indicating gene flow have been found.

Populations of the two analyzed species present examples of plants reaching in the area of Poland the eastern limits of their range, growing frequently in small, isolated groups.

In studies on *Carex saxatilis*, focused on the effect of geographic isolation on genetic structure of population, the isolation factor has been pointed to as the cause of the low

Fig. 3. Dendrite based on shortest taxonomic distances between populations of *C. arenaria* and *C. ligerica* for rhizome characters

heterozygosity level. This prompted the authors to conclude that gene flow between the compared populations has been restrained (Ford and Ball 1991).

In case of the sedges in question the problem seems similar. In the area of Poland *Carex arenaria* populations grow within continuous ranges as well as in numerous isolated stands. Analysing the populations in respect to their content of phenolic compounds, few population groups have been clearly distinguished. Populations within a continuous range differed in their genetic structure from populations of isolated stands (Urbaniak 1984). It should be stressed that in the case of isolated stands the geographic distances between *Carex arenaria* populations exceed 100 km. Therefore, gene flow between populations was relatively improbable. In the case of *Carex ligerica* most results pertained to variability, indicating a decisive interpopulational differentiation (Urbaniak 1988a, 1988b). It should be stressed that in the field, populations of the species are, as a rule, distant from each other by over 100

km (the two discussed stands of Toruń-Wrzosy 14 and 15 and of Złotoria make an exception exceptions). Thus, also in this case gene flow seemed to be relatively improbable. Since even in the case of two *Carex ligerica* populations growing next to each other (at a distance of a few dozen of meters) their distinct character was evidently marked (Fig. 3), the position seemed even more convincing. Moreover, genetic drift seems to represent a factor influencing genetic structure of sedge populations, propagating vegetatively, may be considerable. This may be due both to the mentioned way of propagation, which narrows potential variability, and to conditions in which *Carex arenaria* and *Carex ligerica* grow. Considering the fact that stands in which the discussed species grow are extreme, both in ecologic sense (sandy margins of pine forests, mid-forest clearings, grey dunes of Baltic seacoast) and in geographic sense (in the area of Poland both species reach the eastern limits of their range) and the sedges are exposed to a number of factors specifically affecting the populations.

Fig. 4. Distribution of populations (*C. arenaria* – full circles, *C. ligerica* – empty circles) on a plane of the first and second discriminant variable axes for rhizome characters

Fig. 5. Three-dimensional space diagram (*C. arenaria* – full circles, *C. ligerica* – empty circles) based on the first three discriminant variables for rhizome characters

For example the populations of *Carex arenaria* and *Carex ligerica* from Kopanica near Wolsztyn, which previously inhabited pine forest margins in the form of a 100 m long and 3 m broad belt, have spread in 1976-1980 over an area of approximately 1 ha, forming numerous subpopulations of variable plant density. However, in the following years of 1981-1985, in parallel with growth of young pine forest in the belt, the populations started to divide into increasingly smaller ones, not linked with each other into groups. At present, the original population has become fragmented into multiple groups, each frequently including only few rhizomes, separated by growing pine trees and by the distance of a few to a few dozen of meters (author's observations made in the field in 1976-1985). This type of change, from a relatively small primary population through its marked increase, up to fragmentation into multiple subpopulations seems to create potential conditions for genetic drift, resulting in spatial differentiation of gene frequencies. In the obtained variability pattern, the population of Tychnowy (16), belonging to *Carex ligerica*, occupies an interesting position. It differs relatively extensively from the remaining *Carex ligerica* groups (Figs 3 and 4). A similar variability pattern has been obtained in earlier studies (Urbaniak 1992a, 1992b). In natural conditions, the population encompasses a small area, approximately 20 m away from the outskirts of the pine forest. From the closest stands of the species it is separated by a significant distance of about 100 km. Such a distance effectively prevents gene flow. Taking the above into account, the population should be regarded, in the genetic sense, as distinct from the remaining *Carex ligerica* populations. However, the problem requires further studies to permit the determination of the genetic structure of *Carex arenaria* and *Carex ligerica* populations in greater detail.

ACKNOWLEDGMENTS

I am very grateful to Prof. J. Szweykowski, A. M. University, Poznań, for his comments on the manuscript.

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CHARAKTERYSTYKA ZMIENNOŚCI I PORÓWNANIE POPULACJI *CAREX ARENARIA* L I *CAREX LIGERICA* GAY NA PODSTAWIE CECH KŁĄCZY

STRESZCZENIE

Badaniom poddano 9 populacji *Carex arenaria* i 7 populacji *Carex ligerica*, które porównano na podstawie analizy zmienności cech kłączy. Turzyce te osiągają na terytorium Polski wschodni kres swego zasięgu, z populacjami izolowanymi na obrzeżu. Badane osobniki umieszczono w szklarni w wyrównanych warunkach co stwarza możliwości analizowania zmienności genetycznej populacji. Rezultaty badań wskazują na brak przepływu genów między badanymi gatunkami i w konsekwencji wyraźną odrębność. Jako jeden z mechanizmów sprawczych uzyskanego obrazu zmienności postuluje się dryf genetyczny.

SŁOWA KLUCZOWE: *Carex arenaria*, *Carex ligerica*, zmienność, populacje, dryf genetyczny, cechy kłączy.