DIFFERENTIATION BETWEEN CAREX ARENARIA L. POPULATIONS AT THE EASTERN RANGE MARGIN BASED ON FEMALE AND MALE GLUMES VARIATION

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ABSTRACT

480 spikes from 16 populations of Carex arenaria L. planted in an experimental garden were collected and analysed for 4 female and 4 male glumes each. The characteristic of the interpopulational differentiation on the area of Poland was based on multivariate analysis, Student t-test and the coefficients of variation. The separateness of three populations from the isolated inland stations - 3 (Góra), 11 (Tuczno), 15 (Poznań) and individual character of - 2 (Wiselka), 6 (Sobieszewo) from the coast and 9 (Ołobok) from Lower Silesia is shown. The lowest level of variation and in consequence a particular usefulness for taxonomic considerations have two characters - a and a' (length of female and male glumes). The obtained pattern of interpopulational differentiation may be caused by various factors – migration routes on the Polish territory; selection pressures associated with different ecological conditions present in fixed dunes along the Baltic Sea coast and in isolated inland stations, occupied by C. arenaria; reduction of an extensive primary populations to markedly smaller isolated sub-populations.

KEY WORDS: Carex arenaria L., differentiation, glumes, range margin.

INTRODUCTION

The continuous range of C. arenaria spreads over the Atlantic and Baltic coasts of Europe from Portugal up to the Botnicka Gulf. It occurs also on the coasts of British Isles and Ireland and on the southern coast of Norway and Sweden. On the other hand, the distribution in the mainland of Central Europe is scattered (Meusel et al. 1965).

C. arenaria L., the sand sedge, reaches the eastern margin of its inland range on the territory of Poland. Many populations occur in the coastal area, mostly on the fixed and white dunes, creating the consistent formations with a character of the continuous range. Further on the inland area, this species occurs on many isolated stations, creating rather small populations (Szafer et al. 1967; Szafer and Zarzycki 1972). On the basis of phenolic compounds analysis in C. arenaria population from the area of Poland, five groups correlated with their geographical origin were distinguished (Urbaniak 1984).

C. arenaria propagates itself in both ways, by clonal growth as well as by sexual reproduction (Harper 1977; Noble et al. 1979).

A significant selecting pressure that can occur among small isolated populations, on the margin of the range, mostly under extreme environmental conditions, might lead to the process of differentiation within genetic structure of the species (Mayr 1963; Barrett and Kohn 1991; Nevo et al. 1997). This phenomenon has been observed among different plant species, e.g. Veronica peregrina (Keeler 1978) and Hordeum jubatum (Shumaker and Babble 1980). Also the populations of Carex arenaria, that originate from the area of continuous range, from the coastal area, differ in the frequency of phenolic compounds as compared to populations from isolated stations (Urbaniak 1984). However, the data obtained from the morphological analysis of the spikes, collected from many populations located in different regions of Poland, did not confirm this differentiation (Szweykowski and Mendelak 1969; Urbaniak 1984). This fact was a main trigger to start the plant culture under the similar conditions of the experimental garden, which resulted in the elimination of the differentiating environmental factors, as well as in the exposition of the genetical variation (Clausen et al. 1940; Stebbins 1950; Clausen and Hiesey 1958; Via 1987).

The main concern of this study lies in presenting the interpopulational differentiation of C. arenaria, based on the analysis of morphological characters of female and male glumes after the common garden experiment.

Other questions refer to the comparison between the populations originated from the area of the continuous range and the populations from the isolated inland stations.

MATERIALS AND METHODS

30 rhizomes, from each of 16 investigated populations, were randomly digged up from different locations of C. arenaria on the area of Poland (Fig. 1 and Tab. 1). Parallel tran-
were done, with the use of zoom 17.5 x, for the purpose of measurements of 8 characters – 4 characters of female and 4 of male glumes (length of female (a) and male (a') glumes; maximum width of female (b) and male (b') glumes; distance between the maximum width of female (c) and male (c') glumes and its base; width of the of female (d) and male (d') glumes in one third of its length), (Fig. 2).

![Diagram of the glume showing the method of measurements](image)

**Fig. 2. Diagram of the glume showing the method of measurements (a (a')-d (d') denoted particular characters).**

Results of measurements served to calculate the coefficients of variation; Mahalanobis distances with Hotelling's T² statistics and minimum spanning tree, constructed on the basis of the shortest Mahalanobis distances, with boundary value defined by the average plus two standard deviation (Caliński and Kaczmarek 1973), and dendrograms using agglomerative grouping by the method of the nearest neighborhood on the basis of Euclidean distances (Karoński and Caliński 1973). Furthermore, t-Student test was used to examine the significance of differences between the average values of the particular characters. These average values of particular characters, which were examined under the angle of significance in Student t-test, were ordered, successively from the lowest to the highest one (Figs 3.1-3.4 and 6.1-6.4).

**RESULTS.**

**Analysis of coefficients of variation.**

The main aim of this analysis is to point out the characters with the lowest variation, which are the most useful for the

**TABLE 1. List of investigated populations:**

<table>
<thead>
<tr>
<th>No. of Population</th>
<th>Station (City voivodship)</th>
<th>Date of the collection of rhizomes</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Międzyzdroje (Szczecin voivodship)</td>
<td>30th November 1977</td>
<td>fixed dune</td>
</tr>
<tr>
<td>2</td>
<td>Wisłoka (Szczecin voivodship)</td>
<td>30th November 1977</td>
<td>margin of pine forest growing on fixed dune</td>
</tr>
<tr>
<td>3</td>
<td>Góra (Poznań voivodship)</td>
<td>5th June 1977</td>
<td>margin of pine forest</td>
</tr>
<tr>
<td>4</td>
<td>Chłupy (Gdańsk voivodship)</td>
<td>15th July 1978</td>
<td>margin of pine forest growing on fixed dune</td>
</tr>
<tr>
<td>5</td>
<td>Dąbki (Słupsk voivodship)</td>
<td>14th July 1978</td>
<td>fixed dune</td>
</tr>
<tr>
<td>6</td>
<td>Sobieszewo (Gdańsk voivodship)</td>
<td>29th November 1977</td>
<td>margin of pine forest growing on fixed dune</td>
</tr>
<tr>
<td>7</td>
<td>Ustka (Słupsk voivodship)</td>
<td>14th July 1978</td>
<td>fixed dune</td>
</tr>
<tr>
<td>8</td>
<td>Chłopy (Koszalin voivodship)</td>
<td>4th June 1973</td>
<td>fixed dune</td>
</tr>
<tr>
<td>9</td>
<td>Ołobok (Jelenia Góra voivodship)</td>
<td>13th April 1973</td>
<td>young pine stand</td>
</tr>
<tr>
<td>10</td>
<td>Piaski (Elblag voivodship)</td>
<td>15th July 1978</td>
<td>fixed dune</td>
</tr>
<tr>
<td>11</td>
<td>Tuczno (Piła voivodship)</td>
<td>1st November 1977</td>
<td>margin of pine forest</td>
</tr>
<tr>
<td>12</td>
<td>Piaseczna (Jelenia Góra voivodship)</td>
<td>13th April 1973</td>
<td>margin of pine forest</td>
</tr>
<tr>
<td>13</td>
<td>Leba (Słupsk voivodship)</td>
<td>4th April 1973</td>
<td>fixed dune</td>
</tr>
<tr>
<td>14</td>
<td>Białogóra (Gdańsk voivodship)</td>
<td>15th July 1978</td>
<td>margin of pine forest growing on fixed dune</td>
</tr>
<tr>
<td>15</td>
<td>Miłostowo (Poznań voivodship)</td>
<td>15th November 1977</td>
<td>margin of pine forest</td>
</tr>
<tr>
<td>16</td>
<td>Rąbka (Słupsk voivodship)</td>
<td>4th April 1973</td>
<td>margin of pine forest growing on fixed dune</td>
</tr>
</tbody>
</table>
taxonomic purposes. This coefficient allows referring to the interpopulational variation as well. The maximal 10% value of the coefficient of variation is regarded as the criterion of homogeneity of the population for the particular characters. Based on the comparison of the coefficients of variation, calculated for 4 characters of male glumes it is observed that the examined populations are homogenic in character a’ (length of male glumes), except the following populations – 4 (Chalupy) – 10.5% and 10 (Piaski) – 11.9%, located in the north-eastern part of the investigated area.

Character b’ (maximal width of male glumes) and c’ (distance between the maximal width of male glumes and its base) are stable as well, showing the variation not higher than 18%.

The highest variation, exceeding 20% to 34.3% – 1 (Międzyzdroje), is characteristic for d’ (width of male glume in one third of its length).

The coefficients of variation calculated for female glumes are a little different. The variation for the character a (length of female glumes) is similar to the one calculated for male.
glumes and it is not higher than 10% in most of the populations. In one case — population 9 (Ołobok) it reaches 20%. The variation of the character b (maximal width of female glumes) is much higher and oscillates between 14.6% to 26.3%. The same situation is observed for character c (distance between the maximal width of the female glumes and its base) where the variation ranges from 9.3% to 25.9%. The highest variation, from 14.0% — 9 (Ołobok) to 30.2% — 1 (Miedzyzdroje) is observed for character d (width of female glumes in one third of its length) as well as in case of male glumes.

**Female glumes**

The results obtained in Student t-test for 4 particular characters of female glumes, emphasizing the significance of differences in 16 populations of *Carex arenaria*, are shown on Figs 3.1-3.4.

Character a (length of female glumes) distinguishes two populations — 11 (Tuczno) originates from the isolated station, located in the centre of West Pomerania, and population 6 (Sobieszowo), from the west part of the coast. Other populations form two groups, which include populations originating from the different geographical regions of Poland (Fig. 3.1).

Based on character b (maximal width of female glumes) it is possible to distinguish only one population — 2 (Wiselka), located in the west part of the Polish coast (Fig. 3.2).

However, a tendency towards separateness, without any geographical correlation, is characteristic of two groups of populations, among which the most individual is population 12 (Piaseczna) from Lower Silesia (Fig. 3.2).

Character c (distance between the maximal width of female glumes and its base) does not show any individual characters of any of the populations (Fig. 3.3).

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**TABLE 2. Mahalanobis distances (D_{calc}) between 16 Polish populations of Carex arenaria calculated on the basis of 4 female glume characters with Hotelling T^2 statistics (T^2 calc). Significant Mahalanobis distances: ** at the level 0.01, * at the level 0.05. T^2 critical value: at the level 0.01 = 99.23, at the level 0.05 = 97.56.**
Character d (width of the female glumes in one third of its length) indicates the tendency to separation of two populations – 2 (Wiselka) and 12 (Piaseczna), (Fig. 3,4).

Some of the populations are distinguished by critical Mahalanobis distances, which are included in Tab. 2, together with Hotelling's T^2 statistics.

Population 2 (Wiselka) originating from the west part of the coast, from Wolin Island, is worthy of notice since it is different from the rest of the coastal populations, except 10 (Pisaki), which is the most distant from it. The aforementioned population 2 (Wiselka), is similar to the geographically distant populations located in Lower Silesia 9 (Ołobok) and 12 (Piaseczna), as well as to population 15 (Poznań), originates from the isolated station (Tab. 2).

Dendrite shows that population 11 (Tuczno), originating from the central part of West Pomerania, and population 2 (Wiselka) from the west part of the Baltic coast, are distinguished by Mahalanobis distances with the highest value, which are, respectively – 1.33 and 1.34. These values significantly differ from the average value – 0.81, and are close to the boundary value – 1.38 (Fig. 4).

Two populations: 6 (Sobieszewo), from the east part of the Baltic coast, and 11 (Tuczno), distinguish themselves on the dendrogram (Fig. 5). The rest of populations form three groups having no geographical connection.

**Male glumes**

Based on Student t-test for character a' (length of the male glumes) it is possible to distinguish two groups of populations (Fig. 6,1). The first group consists of two populations – 11 (Tuczno) and 15 (Poznań), both coming from the isolated stations.

Fig. 4. Dendrite of 16 Carex arenaria L. populations for 4 female glumes characters constructed on the basis of the shorter Mahalanobis distances. Each distance of two populations is described additionally by Hotelling T^2 statistics (figures to the left or below). T^2 0.05 denotes critical value of Hotelling T^2 statistics.

Fig. 5. Dendrogram describing the final groups by means of Euclidean distances for 4 female glumes characters.

The second group is represented by 12 populations originating from two different areas, in which C. arenaria is very frequent, viz. from the coast and Lower Silesia. Moreover, there are two separate populations: 3 (Góra) from the isolated station and 6 (Sobieszewo), from the east part of the coast. Groups of populations mentioned above were plotted on the map of Poland (Fig. 7).

Character b' (maximal width of male glume) does not affect the interpopulational differentiation of C. arenaria (Fig. 6,2).

J judging by Student t-test for character c' (distance between the maximal width of male glumes and its base), it is possible to observe the tendency towards separation for three populations – 6 (Sobieszewo), 11 (Tuczno) and 3 (Góra), (Fig. 6,3).

Character d' (width of male glumes in one third of its length) shows the individual character of population 9 (Ołobok) and 13 (Leba), (Fig. 6,4).

A table with Mahalanobis distances, completed with Hotelling's T^2 statistics, indicates that a part of the observed distances between the pairs of populations is statistically significant (Tab. 3). A particularly individual character distinguishes population 11 (Tuczno), which differs from 8 in the total number of 16 populations.

None of the distances connecting the populations in the dendrite were statistically significant (Fig. 8). However, populations from the isolated stations – 15 (Poznań), 11 (Tuczno), 3 (Góra) and 9 (Ołobok) from Lower Silesia are distinguished by the highest Mahalanobis distances, which significantly exceed the average (0.94), and in case of population 9 (Ołobok) is equal to the boundary value, which is 1.66 (Fig. 8).

In the dendrogram one cut, illustrating the groups of populations, was done (Fig. 9). It is important to notice the repeated separateness of the populations from the isolated stations – 3 (Góra), 11 (Tuczno) and 15 (Poznań), as well as the individual character of population 9 (Ołobok), from Lower Silesia Fig. 6a). These particular groups were plotted on the map (Fig. 9).

**DISCUSSION**

Preliminary results regarding C. arenaria showed that the isolated inland population was less variable than the populations growing on the territory of continuous distribution (Szweykowski and Wagner 1975). Still, it would be rather inappropriate to consider this conclusion as reliable since it was based only on the comparison of one population from the iso-
Figs 6.1-6.4. Results of Student t-test for all investigated populations to individual characters of male glumes. Arabic numbers denotes particular populations, (x – differences significant at the level 0.05, xx – differences significant at the level 0.01).

The comparison presented in this work, between the coefficients of variation for 11 populations from the coastal area and for 2 populations from Lower Silesia, plus 3 populations from the isolated inland stations seems to prove this point. Each of these populations has its own individual profile, based on slightly different combinations of the coefficients of variation for the particular characters. It is impossible then, to distinguish any groups of populations on the basis of higher or lower levels of variation.

An increase or decrease of the level of variation in the peripheral populations is not a rule. It is proved by the allozyme studies of *Picea abies* (Tigerstedt 1973) and *Pitlox drummondii* (Levin 1977).

The range of interpopulational differentiation of *C. arenaria* is shown in the tables containing the values of Mahalanobis distances and Hotelling's $T^2$ statistics (Tabs. 2 and 3).
The individual character of population 2 (Wisłoka) – originating from the furthest part of the western coast, attracts the most attention, since it differs from all of the populations from the coastal area in the characters of female glumes, with the exception of the most distant geographically – population 10 (Piaski), (Tab. 2).

On the other hand, the individual character of population 11 (Tuczno) is indicated by the comparison of Mahalanobis distances for the characters of male glumes (Tab. 3).

It is important to know if this individual picture of the variations, characteristic of the particular populations and revealed on the basis of the coefficients of variation, connected by some common characters that would allow to distinguish their groups. The answer is positive, since the dendrogram of the grouping analysis for 4 characters of male glumes shows the separateness of three of the populations from the isolated stations: 3 (Góra), 11 (Tuczno) and 15 (Poznań), as well as the individual character of population 9 (Ołobok), located in the south-west part of the range (Fig. 9).

In the light of the current state of knowledge about the interpopulational differentiation of C. arenaria in the area of Poland (Urbanik 1984), in particular, about the individual character of the populations from the isolated inland stations, the obtained result is just the complement that shows similar tendencies.

Interesting, as well, is the comparison between populations with the use of Student t-test, which examines the significance of the differences among average values of the particular characters. After applying the character a’ (length of male glumes), the obtained range of variability seems most valuable (Fig. 3.1 and 7). It confirmed the convergence with the grouping analysis (Fig. 9), indicating again the individual character of the populations from the isolated stations – 3 (Góra), 11 (Tuczno) and 15 (Poznań). Such a result indicates

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</tr>
</tbody>
</table>

Table 3. Mahalanobis distances (Dcalc) between 16 Polish populations of C. arenaria calculated on the basis of 4 male glumes characters with Hotelling T**2 statistics (T**2calc). Significant Mahalanobis distances: ** at the level 0.01, * at the level 0.05. T**2 critical value: at the level 0.01 = 99.22, at the level 0.05 = 87.56.
Population 6 (Sobieszowo), from the eastern part of the seashore, distinguishes itself from the whole group of populations with short female and male glumes (Fig. 3.1, 6.1, 7). Its individual character is disclosed by dendrogram of grouping analysis for 4 characters of female glumes (Fig. 5). This result is not accidental. The examination of interpopulational variation of C. arenaria on the basis of the frequencies of phenolic compounds, contributed to the distinction of the group of populations, exactly from that geographical region, which was located in the area of the Gdansk Gulf (Urbaniak 1984). This correlation of the results is very symptomatic and it entitles us to come up with the thesis that from the genetic point of view the populations of C. arenaria from the Polish coastal area do not create one consistent group.

The important problem we are facing while trying to understand the contemporary stage of differentiation of the particular species in the area of Central Europe is contained in the next question: "How much actually has the postglacial migration of the plants affected the current level of differentiation?" The species related to the Atlantic climate migrated to the Polish lowland mainly through two routes: near the sea and along Torun - Eberswald proglacial stream valley (Czubinski 1950; Matuszkiwicz 1991). Another migrating route led from the south part of Sweden, through the islands: Oeland and Gotland, further to the east and then across the south shoreline of the Baltic Sea, towards Pomerania. The Danish Islands, together with Bornholm, create a connection between Southern Sweden and Meklemburg-Pomeranian coast, and that could be another migrating route for the plants, in this geographical region, particularly because of the annual pathway of the birds across the Odra valley, which might be a cause of this process, since the above mentioned islands are the place of the birds' temporary stay (Czubinski 1950; Vanner Wall 1990).

In the southwestern part of Poland, the populations of C. arenaria migrated from the West, across Lusatia (Lausitz), up to the barrier created by Lower Silesian Pine woods (Czeccott 1926).

Fig. 7. Results of Student t-test for character a (length of male glumes) transferred to the map of Poland.

that the differentiation of the species on the border area of its range is complex and it regards not only to the biochemical attributes (Urbaniak 1984), but it manifests, as well, in the variation of morphological characters of glumes.

It is interesting that the aforementioned two populations from isolated stations - 3 (Góra) and 11 (Tuczno) differ among themselves extremely in the characters c and c' (distance between the maximum width of female and male glumes and its base), (Figs. 3.3, 6.3) and a' (length of male glumes), (Fig. 6.1). This fact reveals the order of the populations according to the increase of the average values of these characters.

Fig. 8. Dendrite of 16 C. arenaria L. populations for 4 male glume characters on the basis of the shortest Mahalanobis distances. Each distance of two populations is described additionally by Hotelling T² statistics (figures to the left or below). T² 0.05 denotes the critical value of Hotelling T² statistics.
To summarize, there are 6 independent migrating routes, which can possibly have the effect upon the genetic structure of the populations of C. arenaria on the area of Poland.

However, one should consider this idea more as a hypothesis, since for the precise characterization of the migration routes, it would be necessary to analyse the populations of C. arenaria from both, the Polish coast as well as from the areas located further to the east, north, west, and from the islands Öeland, Gotland and Saaremaa or Hiiumaa near Riga Gulf.

Furthermore, differentiation observed at the margin of C. arenaria range may result from the reduction of an extensive primary population to markedly smaller isolated subpopulations (Urbaniak 1994). The other possibility involves the chance that a founders group of individuals or even a single seed initiates formation of a new population. Finally, both processes may lead to genetic differentiation between populations at their range margin (Mayr 1963; Carson 1971; Templeton 1981; Novak et al. 1991). At populational level, selection as a mechanism of adaptive change is often considered as a key factor in shaping the interpopulational differentiation (Bazaz and Sultan 1987). Ecologic conditions of fixed dunes at the Baltic coast, so different from those present deep inland, at isolated stands may be linked to selective pressure, leading to genetic differentiation of C. arenaria.
LITERATURE CITED


ZRÓŻNICOWANIE MIĘDZY POPULACJAMI CAREX ARENARIA L. NA WSCHODNIEJ GRANICY ZASIĘGU

OPARTE NA ZMIENNOŚCI PRZYSADZEK ŻEŃSKICH I MĘSKICH

STRESZCZENIE

Zebracono 480 kłosów z populacji Carex arenaria L. rosnących w ogrodzie eksperymentalnym, w których analizowano 4 cechy przysadzek żeńskich i męskich. Charakterystyka międzypopulacyjnego zróżnicowania na terenie Polski przeprowadzono na podstawie analiz wielocechowych, testu t-Studenta i współczynników zmiennosci. Wskazano na odrębność trzech populacji z izolowanych stanowisk, z głębi lądu — 3 (Góra), 11 (Tuczno), 15 (Poznań); indywidualny charakter — 2 (Wiselka), 6 (Sobieszewo) z wybrzeża i 9 (Ołobok) z Dolnego Śląska. Najniższy poziom zmienności i w konsekwencji szczególną przydatność do rozważań taksonomicznych posiadają dwie cechy — a i a (dlugość mięśni i żeńskich przysadzek). Różne czynniki mogły wpływać na zróżnicowanie w obrębie Carex arenaria — drogi migracji na teren Polski; presja selekcyjna związana z różnymi ekologicznymi warunkami na wydmy szarej, wzdłuż Wybrzeża Bałtyku a izolowanymi stanowiskami w głębi lądu; zmniejszaniem się pierwotnych dużych populacji do znacznie mniejszych izolowanych subpopulacji.

SŁOWA KLUCZOWE: Carex arenaria L., zróżnicowanie, przysadki, kres zasięgu.