COMMENTS ON THE VARIATION OF SPIKE MORPHOLOGY IN SELECTED SPECIES OF *ELYTRIGIA* AND *ELYMUS* (TRITICEAE)

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ABSTRACT

The structure of spikes of *Elytrigia repens*, *E. intermedia* and *Elymus caninus* was investigated. The number of spikelets per spike reveals the weakest correlations with other characters of the spike. The same concerns some character ratios. The correlations provide information about the segmented structure (metamers) of the spike. There is a great difference between matrices of correlation coefficients for *E. repens* and *E. intermedia* related to the development and structure of spike. Characters important for the description of the spike were chosen - in five-character set these are among others: length of glume awn in median spikelet, length of lemma awn in the first floret of the median spikelet, number of spikelets per spike. Length of lemma awn and mean length of the rachis segment were recognized as the best discriminants for species. Ordination of forms along axes of canonical variates does not indicate the subunits within *E. repens*. Intermediate forms between *E. repens* and *Elymus caninus* have not been found. Between *E. repens* and *E. intermedia* there exists some proximity. Heteromorphic individuals were described by means of cluster analysis. They prove the mobility of the genome in ramets of a single genet.

KEY WORDS: *Triticeae*, *Elytrigia repens*, spike morphology, canonical analysis, ramet mutation.

INTRODUCTION

The goal of the present study is to increase our knowledge of the morphological variation existing in some species of the tribe *Triticeae*. Evolution of morphological and e.g. biochemical traits is going on by different ways cf. in *Hordeum murinum* (Giles 1984). There exists also some inconsistency between morphological and biochemical/meiotic data cf. the genus *Hordeum* (Jørgensen 1986). Good morphological characters for e.g. taxonomy purposes have to be found. Distinct changes in plant morphology can be induced by relatively few genetic alterations as morphogenesis in plants is more plastic and less integrative than that in animals (Gottlieb 1984). In plants there exists an iterative pattern of morphogenesis (Gottlieb 1986, Barlow 1989, Bossinger et al. 1991, 1992). The present paper is devoted to this problem by study of trait interrelations within a spike of a quackgrass. *Elytrigia repens* exhibits well known polymorphism and there is a problem of taxonomic subdivision of this species (Petrova 1975, Prokudin 1982), which will be considered here. There occurs a spontaneous hybridization between quackgrass and other wheatgrasses (Heneen 1962, Dewey 1984). It is also noted for populations in Poland (Hansen 1959, Falkowski et al. 1982) where species are geographically overlapped. In three species the studied patterns of variation of spike morphology will be compared by means of multivariate analysis, e.g. CVA, of which the application for study of hybrid populations was discussed by

Adams (1982) and found as especially useful. *Elytrigia repens*, being vegetatively very aggressive, provides special opportunity for research of ramet variation within a single genet (Klekowski 1988). Such an approach is very important with respect to examples of an extreme variability and grass instability (Nielsen and Nath 1961, Heneen and Runemark 1962, Heneen 1963, Richards 1986; Kosina 1994; Kosina and Heslop-Harrison, in press) and this is also the goal of this paper.

Biosystematic studies of wild species of *Triticeae* are also of great value for breeding of forage grasses and for improvement of cereals. Cicin pioneered in the early 50ies the breeding of perennial wheats and utilized for that goal a gene pool of *Elytrigia repens* and *Elytrigia intermedia* (Cicin 1978). Lately an attempt to produce hybrids between wheat and *Elymus caninus* was made by Sharma and Baenziger (1986). Alien species can be, e.g. in wheat breeding, a source of cold hardiness or of salinity tolerance (Fedak 1985). An analysis of spike morphology has a practical implication as this structure determines the grain yield, e.g. in the genus *Triticum* L. (Kosina 1981) and has also a taxonomic significance, cf. the genus *Hordeum* (Baum 1980).

Elytrigia repens being a young species of hybrid origin from the Pleistocene – Holocene period (Prokudin following Tzvelev, 1982) as well as a segmental autoallohexaploid (Dewey 1974) provides a special opportunity to study the variation patterns.

MATERIALS AND METHODS

In four separate areas of Poland (vicinity of Wrocław, Stołowe Mts., Gorce Mts., Podhale) 66 samples of seeds of *Elytrigia repens* (L.) Nevski were collected. In the Podhale region the seeds of *Elymus caninus* (L.) L. were also gathered. This species was geographically overlapped with some accessions of *E. repens*. Accessions of *Elytrigia intermedia* (Host) Nevski were taken from the author's grass collection to compare with two previous species. The whole material was grown in the collection of *Triticeae* at the Botanical Garden of the Wrocław University. For random samples ($n = 10$ to 30 spikes) from 66 accessions of *E. repens*, 4 of *Elymus caninus* and 5 of *Elytrigia intermedia* ten characters of spike were measured (see also Fig. 1):

Fig. 1. Diagrams of the spike and spikelet in *Elytrigia*. ms – median spikelet, mrs – median rachis segment, la – lemma awn, ga – glume awn, lff – lemma of the first floret, g – glume.

1. Length of spike (without awns)
2. Number of spikelets per spike
3. Length of median spikelet (with awns)
4. Number of florets in median spikelet
5. Mean length of glume in median spikelet (without awns)
6. Mean length of the glume awns in median spikelet
7. Length of lemma of the first floret in median spikelet (without awn)
8. Length of the lemma awn of the first floret in median spikelet

9. Length of palea of the first floret of the median spikelet
10. Length of median rachis segment (measured below median spikelet),

and also some character ratios:

11. $1/2$ (mean length of rachis segment)
12. $3/10$ (growth relation within a spike metamer – between spikelet and rachis segment)
13. $5/6$ (length growth relation within glume)
14. $7/8$ (length growth relation within lemma)
15. $7/9$ (length growth relation within the first floret).

The accessions were planted under uniform soil and climatic conditions. Within some accessions heteromorphic individuals were selected. The material was submitted to one-way classification in a completely randomized design. Pearson's coefficients of correlation were calculated to study interrelations between traits of a spike. The most informative characters were selected by means of multiple regression with use of the MAXRES statistics. The discriminative value of a character set in relation to the taxa studied was established by using the Wilks' lambda statistics. For purpose of taxa classification canonical variate analysis (CVA) as well as cluster analysis were applied. The statistical and numerical analyses were performed according to Bartkowiakowa (1982) and Kucharczyk (1982) at the Computer Centre of the Wrocław University.

RESULTS

Character correlations

Table 1 presents an example of a matrix of Pearson's correlation coefficients for one compact group of accessions of *Elytrigia repens* selected after canonical variate analysis (CVA). The most spike characters are significantly correlated. The most distinct interrelations are outlined within the Table. This is most important that they describe components of the median spikelet and a rachis segment just beneath it. Both awns, of the glume (no. 6) and of the lemma (no. 8), exhibit weaker correlations within a spikelet. The number of spikelets (no. 2) show the weakest correlations with other characters of the spike. The characters nos. 12, 13, 14 have a small number of significant coefficients with value > 0.500 . The matrix for *E. intermedia* (Table 2) shows a half of the amount of significant coefficients than the presented matrix for *E. repens* (counted in relation to all the possible ones in the matrix). The number of spikelets (no. 2) in *E. intermedia* correlates highly with characters: 5, 7, 9, 10, 11, 12. Some coefficients in the outlined area are insignificant because the species is awnless.

Choice of the representatives

Table 3 shows the differentiation of sets of representative characters for the three taxa analysed. Sets of two to five representatives in *E. repens* exhaust more the variation of characters not present in the set when compared to the other two taxa (smaller value of MAXRES evidences this). There are no special similarities in relation to any sets of representatives but in *E. repens* and *E. caninus* measurements of both awns are informative for the trait set. For five-representative sets the MAXRES value is close to 0.500. One can accept these sets as satisfying for the description of each taxon and as correlated sufficiently with the set of characters not being the representatives.

TABLE 1. Matrix of the significant correlation coefficients for spike characters in *Elytrigia repens* ($n=90$, $r \times 100$)

Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
15	62...	—	63...	63...	63...	68...	64...	36...	23.	62...	71...	—	-44...	-23.
14	-25.	—	-35..	-37...	-25.	-51...	-32..	-83...	-29..	-25...	-27.	-24.	44...	
13	-55...	-49...	-41...	-44...	-24.	-85...	-36...	-47...	-22.	-35..	-31..	-24.		
12	27.	—	56...	59...	41...	35..	47...	48...	48...	—	—			
11	59...	—	84...	72...	88...	60...	83...	50...	64...	88...				
10	63...	—	80...	68...	84...	62...	80...	43...	66...					
9	40...	—	82...	65...	83...	49...	89...	62...						
8	39...	—	64...	59...	56...	66...	65...							
7	60...	—	94...	80...	94...	70...								
6	71...	45...	71...	69...	59...									
5	59...	—	94...	82...										
4	63...	23.	92...											
3	68...	23.												
2	81...													

., ... ,... Significance levels at $\alpha = 0.05, 0.01, 0.001$, respectively.

Coefficients between characters, components of a spike metamer, are outlined.

TABLE 2. Matrix of the significant correlation coefficients for spike characters in *Elytrigia intermedia* ($n=70$, $r \times 100$)

Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
15	—	—	33.	—	63...	—	80...	44..	55...	71...	71...	-76...	—	47..
14	—	—	—	—	46..	—	47..	84...	39.	40..	—	-37.	—	
13	—	—	—	—	—	39.	—	—	—	—	—	—	—	
12	—	88...	—	—	-62...	—	-80...	-33.	-70...	-70...	-83...			
11	37.	-79...	62...	—	82...	46..	90...	—	86...	86...				
10	32.	-75...	61...	—	87...	38.	91...	35.	86...	86...				
9	35.	-66...	68...	33.	90...	—	94...	32.						
8	—	—	—	—	39.	—	41..							
7	—	-76...	63...	—	90...	—								
6	—	—	37.	—	—									
5	47..	-52...	79...	44..										
4	58...	—	83...											
3	64...	—												
2	—													

., ... ,... Significance levels at $\alpha = 0.05, 0.01, 0.001$, respectively.

Coefficients between characters, components of a spike metamer, are outlined.

Choice of the discriminants

Values of Wilks' lambda, presented in Table 4, are the basis to establish the characters with the strongest discriminative power for species: *Elymus caninus*, *Elytrigia intermedia*, and *E. repens*. In turn the best discriminants are: length of lemma awn, mean length of rachis segment, length of glume, length of glume awn, length of spikelet and number of florets in spikelet, i.e. nos. 8, 11, 5, 6, 3 and 4.

Ordination of forms (Figure 2)

Along the axes of the first two canonical variates the accessions of *E. repens* form a distinct group without the possibi-

ty of division into subunits. Within the diagram areas signed A and B include the accessions having awned and compact versus awnless and loose spikes, respectively. A scattering of points within diagram is independent on their geographical distribution. *Elymus caninus* is very distant from *Elytrigia repens*. *Elytrigia intermedia* is within a range of variation of *E. repens*, especially in relation to the values of canonical variate I. The values of canonical variate II do not support such a picture. However, *E. intermedia* is once again located within the range of variation of *E. repens* when the third canonical variate is considered. Discriminative power of canonical variates is strictly related to their eigenvalues, i.e. I = 26.5, II =

TABLE 3. Analysis of representation of spike characters for three taxa of *Triticeae*

Number of representatives	<i>Elytrigia repens</i>	<i>Elytrigia intermedia</i>		<i>Elymus caninus</i>		
		MAXRES		MAXRES	MAXRES	
1	6	950	5	937	10	995
2	1, 7	759	5, 13	820	3, 9	938
3	5, 7, 10	674	3, 5, 13	777	3, 9, 11	848
4	2, 3, 6, 7	556	11, 12, 13, 14	632	2, 6, 8, 12	668
5	5, 6, 8, 11, 15	402	2, 3, 6, 13, 14	422	2, 6, 8, 9, 12	510

MAXRES x 1000 and the numbers of characters as representatives are given in Table.

MAXRES stands for the maximal loss in information due to the limitation of the number of representatives in relation to the initial set of characters.

TABLE 4. Choice of spike characters with the highest value of discrimination for *Elymus caninus*, *Elytrigia intermedia* and *Elytrigia repens*

Numbers of characters in the discriminative set															Wilk's lambda
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	0.0563
-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	0.0195
-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	0.0063
-	-	-	-	+	+	-	+	-	-	+	-	-	-	-	0.0028
-	-	+	-	+	+	-	+	-	-	+	-	-	-	-	0.0014
-	-	+	+	+	+	-	+	-	-	+	-	-	-	-	0.0008
-	-	+	+	+	+	-	+	-	-	+	-	-	-	+	0.0005
+	-	+	+	+	+	-	+	-	-	+	-	-	-	+	0.0004
+	-	+	+	+	+	-	+	-	-	+	+	-	-	+	0.0003
+	-	+	+	+	+	-	+	-	+	+	+	-	-	+	0.0002
+	+	+	+	+	+	-	+	+	+	+	+	-	-	+	0.0002
+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	0.0001
+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	0.0001
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.0001

+ or - : a character present or absent in the discriminative set

15.8, III = 7.2. This power is significant for all the selected fifteen eigenvalues.

Heteromorphic individuals in *E. repens*

Some plants of *Elytrigia repens* create within themselves the spikes differentiated morphologically. A cluster analysis made for plants of fifteen accessions (one spike has been an OTU) showed for the phenon line arbitrarily chosen, e.g. for the Euclidean distance = 20, that more clusters have been set apart (Fig. 3). Heteromorphic plants have no special position in the CV diagram (see Fig. 2). The shape of dendrogram (numerous clusters), range of the distances in the matrix (low values) and range of distances in a set of the shortest ones (high values) can be accepted as indices of heteromorphism (Fig. 3).

DISCUSSION

Eight matrices of correlation coefficients were analysed (one for *Elymus caninus*, one for *Elytrigia intermedia* and six for *E. repens*). There are considerable differences with re-

spect to the number of significant coefficients between matrices of *E. repens* (67 to 98 % of significant coefficients). These differences indicate the dissimilarity of accessions in relation to the development of particular organs of the spike, providing additional evidence of polymorphism. Low percentage of significant correlations within a matrix may also prove small integrity during development of the spike as it was for interrelations of caryopsis traits between ancient and recent tetraploid wheats, cf. *Triticum dicoccoides* versus *T. polonicum* (Kosina 1995a).

Part of the spike characters can be recognized as being connected with metameric organization, that means they describe longitudinal growth of the spikelet and rachis segment attached below this spikelet. Those would be: length of spikelet, number of florets in spikelet, length of glume, length of lemma, length of palea and length of rachis segment, i.e. nos. 3, 4, 5, 7, 9 and 10. In the given matrices these characters are distinctly interrelated - this would indicate the metameric structure of the spike. This also corroborates the data in other grasses presented by Scagel and Maze (1984) that variables which are spatially adjacent or developmentally sequential are more strongly correlated than those further apart. Correla-

Fig. 2. Distribution of accessions of *Elytrigia repens*, *Elytrigia intermedia* and *Elymus caninus* along the first two canonical variates in an analysis of spike characters. A and B denote positions of extreme accessions with awned, compact versus awnless, loose spike, respectively. Accessions with heteromorphic individuals are encircled. Applied set of discriminants: nos. 3, 4, 5, 6, 8, 11.

Fig. 3. Heteromorphic plants of *Elytrigia repens* described by ranges of euclidean distances. Figures mean a number of clusters (groups of spikes). Extreme phenograms are presented.

tions between length of glume awn and of lemma awn and other organs of spikelet are, however, a little weaker, especially in *Elytrigia intermedia* where awns are almost absent. Development of awns as some exterior structures may be probably more influenced environmentally. As a consequence of that, there may be an increase of variation and a decrease of correlation (see in *Elytrigia repens*). The same interrelation between a main body of lodicule and its hairs was found in the genus *Triticum* (Kosina, unpublished). Such a metameric structure of the spike is also proved very clearly by somatic mutation of spikelet colour in an amphiploid between *Triticum durum* and *Aegilops squarrosa* (Kosina 1989, 1994). Phytomeric structure of the barley spike was studied in details by an interpretation of numerous morphological mutants in barley by Bossinger et al. (1991, 1992). Plant metamers are associated distinctly with merophytes, cell clones of common origin (Barlow 1989). Examples for the above are offered by lower plants but also by spikelet mutation in grass (Kosina 1994)). There was observed clearly a unity of origin of spikelet and rachis segment below it. Similar to this pattern there are patterns of spike disarticulation apparent in wild wheats and also in some other members of *Triticeae* – *Thinopyrum junceum* and *Lophopyrum caespitosum* (Sharma and Gill 1982). This sheds some light on a metamer creation discussed lately by Barlow (1989) and Bossinger et al. (1992).

The sets of representatives for three taxa, despite only some similarity (see length of the glume awn), additionally indicate the differences of the development and morphology of the spike. Furthermore, this conclusion is substantiated by the fact of the close level of MAXRES values (see five-representative sets which are very different). A difference between sets of other kind of most informative traits of the ear was noted, e.g. for tetraploid wheats and their hybrids of the F_1 (Kosina 1981). Reciprocal hybrids, however, kept sometimes identity of such a set. The number of traits needed to get the same amount of information may be very different, cf. micro-traits of caryopsis in *Triticum durum*, integrated developmentally (16 traits) and in developmentally instable *T. turanicum* (21 traits) – Kosina (1995a).

Canonical analysis of discrimination reveals considerable variability existing between *Elytrigia repens* accessions. Such a statement is supported by Prokudin's data (1982) as well as by data on embryo morphology (Kosina 1991). This is created by an open-pollinated system of mating in this species. *E. repens* reveals also some variation in the chromosome number (Petrova 1975) which is distinctly increased by inclusion into it a very close species, *E. elongatiformis* (Dewey 1980). The variability of *Elytrigia intermedia* presented only by several accessions, is also great. This species has the same system of mating. Ample morphological variability in Iranian intermediate wheatgrasses was found by Dewey (1978). Large cytogenetic variation (satellites, C-bands) was described by Xu and Conner (1994) in its ssp. *trichophorum*. *Elymus caninus* is a Eurasian, self-pollinating allotetraploid (Dewey 1979) and its pattern of morphological variation can be expected to be like in wheat. There are no intermediate accessions between *Elymus caninus* and *Elytrigia repens* but there is a small set of accessions of *Elymus caninus* in the study. However, this species collected in Podhale was very uniform. The absence of intermediates is undoubtedly caused by the difference in the mating system between both species. A possibility of hybridization between *E. caninus* and other species of *Triticeae* depends on the distance between plants crossed. *E. caninus*, growing in close proximity, hybridizes spontaneously with *Pseudoroegneria tauri* ssp. *libanotica* (Dewey 1972). A spon-

taneous hybridization between this species and *E. repens* is noted as quite rare (Falkowski et al. 1982, Dewey 1984). Location of accessions of both species in the CVA diagram confirms these data. The first and third canonical variates, when applied, give a distinct proximity between *E. repens* and *E. intermedia*. Similarly, the accessions close to *E. repens*, especially in *E. intermedia* subsp. *trichophora* (Link) A. et D. Löve were distinguished for the set of embryo characters (Kosina 1995b). Successful hybridization between both species is enhanced by their similarity in the mating system and genome composition (Falkowski et al. 1982, Dewey 1984). *E. repens* hybridizes also with other species of the tribe (Hansen 1959, Heneen 1962). A type of intraspecific variation of the spike traits in *Elytrigia repens* does not indicate the existence of taxonomic subunits. This confirms the data of Prokudin (1982) on the polymorphism and its continuity in *Elytrigia repens* like in other open-pollinated species of wide geographical distribution. Such a conclusion is true at least for restricted areas of Poland (this report) and in Ukraine (Prokudin 1982).

Some plants of *Elytrigia repens* with distinct large variation of spike morphology (or developmental diversity) have been described by means of the cluster analysis (Euclidean distance, single linkage method). Dendrograms (Fig. 3) present an increase of individual variability (a mosaic) and this is independent of the locality of accession gathering (Fig. 2). The morphological mosaic was also observed in grasses in relation to the spikelet colour and embryo structure (Kosina 1989, 1994; Kosina and Heslop-Harrison, in press) as well as to the structure of endosperm in a wider spectrum of grasses (Kosina 1992, 1995c). Somatic instability was noted for many grasses and it was often associated with a hybrid state of the plant exhibiting profound cytogenetic alterations (Snyder 1951, Nielsen and Nath 1961, Heneen and Runemark 1962, Heneen 1963, Xu and Connor 1994). In *E. repens* such an instability obviously relates to the possibility of ramet (a rhizome) mutation within a single genet. Increased somatic variability was found in the growth rate of ramets within genet in *Lolium perenne* (Richards 1986 after Breese et al. 1965). For this grass two important conclusions are drawn: a) Somatic variation is more frequent in genets that have undergone a long period of asexual reproduction. b) Somatic variation is more frequent in the shoots of young rather than old ramets. This is parallel to the status existing in *Elytrigia repens* and proves the genome mobility (McClintock 1984, Flavell 1985).

CONCLUSIONS

1. In *Elytrigia repens* and *E. intermedia* correlations between spike traits are greater between those which are spatially close and which create a metameric unit.
2. CVA shows a great variation of continuous pattern existing among populations in *E. repens* with respect to spike morphology. There is no possibility to distinguish any intraspecific units.
3. There exist accessions of *E. repens* of similar morphology when compared with *E. intermedia*. That may be an evidence of their past hybridization and genomic affinity. Such accessions were not found between *Elymus caninus* and *E. repens* and it confirms a separation of both species by a mating system.
4. Heteromorphic individuals in *E. repens* create an increased polymorphism by means of ramet (a rhizome) mutation.

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UWAGI O ZMIENNOŚCI MORFOLOGII KŁOSA U WYBRANYCH GATUNKÓW
ELYTRIGIA I *ELYMUS* ((TRITICEAE))

STRESZCZENIE

U *Elytrigia repens*, *E. intermedia* i *Elymus caninus* zbadano strukturę kłosa. Liczba kłosków w kłosie była słabo skorelowana z innymi cechami. Ten sam poziom korelacji charakteryzował kształty (stosunki cech). Korelacje cech ujawniły segmentalną (metamery) budowę kłosa. Istnieje znaczna różnica między macierzami korelacji cech kłosa *E. repens* i *E. intermedia*. Do opisu kłosa wybrano cechy najbardziej informatywne. Są to m.in.: długość ości plewy i plewki, liczba kłosków w kłosie. Długość ości plewki dolnej i średnia długość członu osadki kłosa są cechami najlepiej dyskryminującymi badane gatunki. Rozmieszczenie taksonów w osiach dwu zmiennych kanonicznych wskazuje, że nie jest możliwe wyróżnienie taksonomicznych jednostek wewnątrzgatunkowych u *Elytrigia repens*. Pokrywanie się zakresów zmienności I i III zmiennej kanonicznej u *E. repens* i *E. intermedia* wskazują na pokrewieństwo ich genomów oraz na możliwość krzyżowania spontanicznego obu gatunków. Nie stwierdzono takiej możliwości między *E. repens* i *Elymus caninus*. Rośliny heteromorficzne u *Elytrigia repens* zostały opisane z zastosowaniem analizy skupień. Dowodzą one mobilności genomu w rametach pojedynczego genet.

SŁOWA KLUCZOWE: *Triticeae*, *Elytrigia repens*, morfologia kłosa, analiza kanoniczna, mutacje rametów.