Morphological identification of genomic genera in the Triticeae

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Our goal was to determine whether the genomic groups of perennial species Triticeae having solitary spikelets could be identified morphologically and, if so, to construct identification keys that could be used for this purpose. If so, it would strengthen the argument for recognizing such groups as genera. We conducted Discriminant and Random Forest® analyses of 61 characters scored on 218 herbarium specimens representing 13 genomic groups. In addition, we closely examined some additional characters that came to our attention, evaluating our findings on specimens not scored for the two kinds of analysis. Random Forest® analysis was almost always more successful in distinguishing the genomic groups, whether separating all 13 groups or a subset of the 13. The results suggest that it is usually possible to identify the genomic group to which a specimen of perennial Triticeae with solitary spikelets belongs on the basis of its morphology but that doing so will require examination of characters that have not been considered particularly important in the past. Among these are the length of the middle inflorescence internodes, the width of the palea tip, and the morphology of the glumes. Generic descriptions and keys have been posted to the web (see http://herbarium.usu.edu/triticeae). They include all the genera that we recognize in the tribe, not just those included in the analyses, and will be improved as additional information becomes available.

Key Words: Genomic group, solitary spikelets, inflorescence, palea tip, glume.

Introduction

Botanical names are an important and conspicuous mechanism for communicating information. The amount of information they convey is limited by their brevity, existing knowledge, and the taxonomic philosophy of the person promoting a particular treatment. The International Code of Botanical Nomenclature (McNeill et al. 2007, referred to after this as the “Code”) states only that the name of a species is a binomial, with the first word being the name of a genus. Most of us also learned that species in the same genera are, in some sense, more closely related to each other than to members of another genus, a statement that reflects a philosophical position, not a requirement of the Code. It is this apparently simple philosophical statement that is behind most nomenclatural disagreements, including those in the Triticeae. The problem is deciding how best to determine which taxa are “more closely related”. Another area of disagreement is the relative importance that should be attached to having a system that reflects relationships and one that is easy to use.

In 1984, Løve and Dewey independently proposed using genomic constitution to determine generic boundaries in the Triticeae, species with different genomic constitutions being placed in different genera. They argued that these genomic genera would better reflect phylogenetic relationships within the tribe; Dewey added that they would be a useful guide for plant breeders. The response from taxonomists was largely negative (see, for example, Baum et al. 1987, Kellogg 1989, Seberg and Petersen 1998). In this study, we focused on one of the objections expressed: that the genomic genera could not be distinguished morphologically, a factor that makes their adoption impractical, if not impossible, for collectors and other field-oriented scientists. Our goal was to identify morphological criteria for distinguishing different genomic groups within the perennial Triticeae with solitary spikelets.

There have been two previous studies of the relationship between morphology and genomic constitution in the Triticeae. Salomon and Lu (1992) studied seven taxa representing two genomic groups, StY and StH tetraploids (genome symbols from the International Triticeae Consortium; http://herbarium.usu.edu/Triticeae/genmsymb.htm) and found a correlation between genome constitution and both palea apex shape and the shape of the teeth on the palea keels. They cautioned, however, that more species needed to be examined before it could be concluded that these features were a reliable means of distinguishing between the two groups. Baum et al. (1995) conducted discriminant analysis of nine characters scored on 290 specimens representing 100 species in...
four genomic groups, P, StH, StYP, and StY. The resulting functions correctly identified the genomic group of the specimens 73% of the time in their jackknife analyses.

Our study began as an investigation of the Australasian Triticeae, superficial observation of which suggested that they could be distinguished morphologically from other members of the tribe. All the Australasian species are perennials with one spikelet per node and all, so far as is known, have the W genome. In the polyploids, it is combined with one or more of the St, Y and H other genomes. Löve (1984), who restricted Agropyron to the crested wheat grasses, placed the diploid Australian species in Australopyrum and the polyploid species in Elymus because the diversity of their genomic constitution was not known in 1984. Connor (1994) argued for recognition of the morphologically distinct genus endemic to New Zealand. Its species (1994) argued for recognition of the morphologically distinct genus endemic to New Zealand. Its species have since been shown to be HW tetraploids. The remaining Australasian species are usually included, together with some Asian species, in Elymus sect. Anthosachne (Löve 1984, Connor 1994, Jacobs et al. 2009, but see Yen et al. 2006). Thus our interest in providing a better generic treatment for the Australasian Triticeae required that we identify morphological characteristics for distinguishing all the genomic groups of Triticeae that include perennial species with solitary spikelets. Almost all these species were included in Elymus sensu lato by Löve (1984), the exceptions being the diploid genera Agropyron P genome), Australopyrum (W genome), and Festucopsis (L genome). For convenience, we refer to the groups by the appropriate generic name (Table 1) even though some of the species we examined do not have combinations based on such names. The Asian species that have been included in Anthosachne are StY tetraploids, i.e., members of Roegneria.

Materials and Methods

We examined herbarium specimens of all the Australian species of perennial Triticeae and representatives of the Asian and American genomic groups that include perennial species with one spikelet per node. The species we included are those with known genomic constitution (see http://herbarium.usu.edu/Triticeae/genomes.htm). We excluded Secale, Dasypyrum, and Leymus because those of their perennial species that have solitary spikelets are rarely placed in the wrong genus. The specimens used came from CANB, CHR, MO, NSW, and UTC (herbarium codes from Index herbariorum; http://sweetgum.nybg.org/ih/). The New Zealand specimens were identified by Dr. Henry Connor, the remaining Australasian specimens by Jacobs. The non-Australasian specimens came from UTC and MO. Many of the Asian specimens had been identified by Drs. Bjorn Salomon and Bao-Rong Lu. The remaining specimens were identified by Rollo and Barkworth. Several references were used for this purpose, notably Bor (1970), Tutin (1980), Cope (1982), Tsvelev (1983), Koyama (1987), Salomon (1994), Lu (1995), Assadi (1996), Edgar and Connor (2000), Wu et al. (2006), Barkworth et al. 2007 and Jacobs et al. (2009). Voucher information is presented in the appendix.

Seventy nine characters (Table 2) were chosen for the initial examination. They were selected based on previous work, floristic treatments, and our own observations. Of the 79 characters: 52 were continuous, nine meristic or ordered, and 18 qualitative. Only the continuous and ordered characters were used in the discriminant analyses.

Our intent was to examine five specimens per species, but in some instances we were unable to obtain that many. Recognizing that our samples probably did not include the extremes of variation for the species involved, we attempted to create an artificial maximum and minimum for each species.

<table>
<thead>
<tr>
<th>Genomic composition</th>
<th>Generic name</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>Agropyron</td>
<td>Eurasia</td>
</tr>
<tr>
<td>St</td>
<td>Pseudoroegneria</td>
<td>Eurasia and North America</td>
</tr>
<tr>
<td>W</td>
<td>Australopyrum</td>
<td>Australia, New Zealand, and New Guinea</td>
</tr>
<tr>
<td>StH*</td>
<td>Elymus</td>
<td>Eurasia, North America, South America</td>
</tr>
<tr>
<td>StY</td>
<td>Roegneria</td>
<td>Eurasia</td>
</tr>
<tr>
<td>HW</td>
<td>Stenostachys</td>
<td>New Zealand</td>
</tr>
<tr>
<td>StYW</td>
<td>Anthosachne</td>
<td>Australasia</td>
</tr>
<tr>
<td>StYP</td>
<td>Anthosachne</td>
<td>Asia (Tibetan Plateau)</td>
</tr>
<tr>
<td>StYH</td>
<td>Campeistachys</td>
<td>Eurasia</td>
</tr>
<tr>
<td>StYHW</td>
<td>Conmorechioa</td>
<td>New Zealand</td>
</tr>
<tr>
<td>StP</td>
<td>Douglasdeyeka</td>
<td>Iran and western Asia</td>
</tr>
<tr>
<td>E+</td>
<td>Thinopyrum</td>
<td>Eurasia (a genomically mixed and poorly understood group, united by their possession of the E genome).</td>
</tr>
<tr>
<td>L</td>
<td>Festucopsis</td>
<td>Albania</td>
</tr>
<tr>
<td>Xp</td>
<td>Peridictyon</td>
<td>Southwestern Bulgaria and northern Greece (not included)</td>
</tr>
<tr>
<td>StHNSxM</td>
<td>Pascopyrum</td>
<td>North America (not included)</td>
</tr>
<tr>
<td>NSxM*</td>
<td>Leymus</td>
<td>Eurasia, North and South America (not included)</td>
</tr>
</tbody>
</table>
Table 2. Characters and method of scoring. If a feature such as an awn was not present, it was scored “not applicable”.

| VEGETATIVE CHARACTERS: Growth habit (not rhizomatous, rhizomatous). CULM: height (cm); thickness at middle of first internode (mm); peduncle length (cm); nodes (number); trichome length middle of first internode (mm); trichome length top of first internode (mm); trichome length on first culm node (mm); trichome at top of peduncle. BASAL LEAVES: trichome length on sheath (mm); trichome length upper surface (mm); trichome length lower surface (mm); trichome length on first internode (mm); surface trichome length (mm); surface trichome density (0, 1, 2, 3, 4). TOP LEAF: ligule length (mm); blade length (cm); angle (declined, perpendicular, ascending, erect). |
| REPRODUCTIVE CHARACTERS: INFLORESCENCE: length (cm); rachis extension length (mm); posture (drooping, nodding, inclined, erect); nodes (number); disarticulation (in rachis, below spikelet, below florets); lowest internode length (cm); middle internode length (cm); spikelets per node, lowest node (number); spikelets per node, mid-spike (number); pedicel length (mm); rachis cross-section shape (lunate, semi-circular, trapezoidal); trichome length rachis surface (mm); trichome length rachis edge (mm). SPIKELET: length (mm); florets (number); orientation to rachis (radial, tangential). LOWER GLUME: length (mm); shape (not applicable, rectangular, lanceolate, linear, horn-shaped); tip (not applicable, aristate, acute, obtuse); width (mm); hyaline margin width (mm); awn length (mm); veins (number); midvein trichome length (mm); surface trichome density (0, 1, 2, 3, 4). UPPER GLUME: length (mm); width (mm); shape (not applicable, rectangular, lanceolate, linear, horn-shaped); symmetry (symmetric, asymmetric); tip (not applicable, aristate, acute, obtuse); hyaline margin width (mm); awn length (mm); veins (number); keel (number); keel prominence (not prominent, prominent); midvein trichome length (mm); midvein scabrous (yes, no); surface trichome length (mm). LEMLA: length (mm); veins (number); awn length (mm); midvein trichome length (mm); back trichome length (mm); margin trichome length (mm); awn curvature (not applicable, straight, up to 90 degrees, more than 90 degrees). PALEA: apex width (mm); width at midlength (mm); keel cilia length (mm); palea tip shape (acute, rounded, truncate). |

using the lowest and highest values, respectively, from descriptions in the references cited above, but they contained too few of the characters in our list to permit use of such artificial records in our analyses.

The species studied represented 13 of the 16 genomic groups of perennial Triticeae (Table 1). Three groups are unispecific: Festucopsis, Peridictyon (Seberg et al. 1991), and Connorochloa (Zhang et al. 2009, Barkworth et al. 2009). Two groups, Elymus and Thinopyrum, are known to include variants of the basic constitution for their group: Elymus, which consists primarily of SrH tetraploids also includes a few hexaploids that are either SrSH (e.g., E. repens) or SrHH (e.g., E. patagonicus; Dewey 1972). Thinopyrum, as treated here, includes species with just the E genome or both the E and the St genome. The latter species are sometimes placed in Trichopyrum (Löve 1986, Yen et al. 2005).

The ability of individual quantitative characters to distinguish the groups was explored by examining box and whisker plots for each character. These have been posted to the web at http://herbarium.usu.edu/triticeae/idgenomicgenera.

We used both Discriminant Analysis (DA) and Random Forests® (RF) to determine whether some combination of the characters could be used to distinguish the genomic groups and, if so, to identify the relative importance of the individual characters in making such distinctions. Only the quantitative and meristic characters were used in these analyses. DA uses a succession of linear combinations of the character values to classify the groups, with each successive function weighting the characters in such a way as to maximize the additional separation of the groups. RF builds on classification trees (CT). CTS are built by recursive binary division of the records until the groups are separated or no improvement in separation can be achieved. RF fits many classification trees to a data set and then combines the predictions from all the trees. It uses many (e.g., 500) bootstrap samples of the data to create multiple classification trees. In each sample, 63% of the records occur at least once. The trees are used to predict the membership of the excluded records with the final disposition reflecting the majority rule, ties being split randomly. RF supersedes classification trees, being a more accurate classifying procedure and one that is minimally impacted by small perturbations in the data (Cutler et al. 2007).

Because of their different approaches, DA and RF also differ in their identification of the most important characters for distinguishing groups. In DA, only one of a set of highly correlated characters will be given high weight because the other characters add only minimally to the discriminating power of a function. RF ranks all the characters that are useful for classifying the groups without regard for their correlation.

We used both methods to examine whether the records could be placed into the appropriate genomic groups and which characters were most useful for achieving this goal. In addition, we looked at the ability of the methods to separate the species containing a particular genome from the species not containing that genome and at two subsets of the records, those of the northern hemisphere St containing species and those of the four groups examined by Baum et al. (1995). We used SYSTAT 12 (Systat Software Inc. 2007) for developing the box and whisker plots and DA. Software for RF is freely available at http://www.math.usu.edu/∼adele/forests.

In practice, taxonomists rely on morphological keys for plant identification. To create such keys, we first developed descriptions of the genomic groups in this study, drawing on knowledge gained while scoring the specimens, our previous experience, and descriptions in the references used for identification. In addition, we entered information on the distribution of individual species, as reported in various floras. This information was then used to generate maps showing the species density of each genomic group by country, or, for the former Soviet Union, by the floristic regions used.
by Tsvelev (1983); by state for the USA; and by province or territory for Canada. The resulting maps were stored as JPEG files. We used Fact Sheet Fusion (CBIT 2009), to create a web page for each genus. This program aids in creation of linked pages that include thumbnail images linked to larger versions of the image resources. The pages were posted to http://herbarium.usu.edu/triticeae/genera.

The descriptive information was used to construct both a dichotomous and multi-access key. Dichotomous keys dictate which characters are used for identification and the order in which they are used. Multi-access keys enable users to select the characters they wish to use and the order in which they use them. In Lucid, the user may also click on the “wand” icon to determine which of the remaining characters would narrow down the possibilities most. If this character is not available or is one the user does not feel comfortable using, the next best characters can be determined by successively selecting the “wand plus arrow” icon. In both the dichotomous and multi-access key, the names of the taxa are linked to the descriptive pages.

We used Phoenix (CBIT 2004) to create an interactive version of the dichotomous key and Lucid (CBIT 2008) to develop the interactive multi-access key. Phoenix permits a user to skip one couplet in the key and includes links to the descriptive pages for the genera but does not provide the flexibility of true multi-access keys such as Lucid. The keys incorporate images designed to aid in interpreting the characters and links to the descriptive pages. They are ongoing projects. In addition, we have posted a PDF version of the text material in the dichotomous key to the web. All three keys can be accessed via http://herbarium.usu.edu/triticeae/keys.

Results

Two hundred and eighteen specimens, representing 78 taxa and 13 genomic groups, were formally scored for the numerical analyses. Several additional specimens from the listed herbaria were examined more informally in the course of developing the descriptions and keys.

Qualitative characters

Most of the qualitative characters examined were either so constant among the groups or so similarly variable within each group as to be of little value by themselves for identification. For instance, all the specimens had truncate ligules. In most taxa, the ligule edges were irregular, although some specimens of <i>Australopyrum calcis</i> had denticulate ligules and one species of <i>Anthosachne</i> had ciliate ligules. The inflorescences almost always appeared to be erect but in some genera a minority of the specimens had drooping inflorescences. This is, however, a character that it is difficult to score reliably from herbarium specimens. Three of the genera (<i>Elymus</i>, <i>Pseudoroegneria</i>, and <i>Thinopyrum</i>) include a few rhizomatous species or species that are sometimes rhizomatous but even in these genera most species are not rhizomatous. In <i>Stenostachys</i> and <i>Connorochloa</i> the rachis was consistently lunate in cross-section whereas in <i>Thinopyrum</i> it was consistently trapezoidal but both shapes are also present in other genera.

<i>Stenostachys</i> and <i>Footerocopsis</i> are both reported to have spikelets that are radial, rather than tangential to the rachis (Tutin 1980, Connor 1994). In <i>Stenostachys</i>, the glumes are tangential to the rachis but the florets are radial or almost so. In <i>Footerocopsis</i>, only some of the spikelets appeared to be radial to the rachis, others appearing tangential. Examination of fresh material is needed to clarify the situation.

Attempts to score the palea tips according to the terms used in existing descriptions (e.g., acute, obtuse, emarginate, truncate) were unsatisfactory. It seemed to depend on a combination of factors, including caryopsis maturity and width.

Quantitative characters

The box and whisker plots have been posted to the web at http://herbarium.usu.edu/triticeae/idgenomicgenera. They show that a few genera were almost distinct from all others with respect to a single character. For example, <i>Australopyrum</i> differs from almost all other taxa in having long culm hairs and <i>Stenostachys</i> and <i>Connorochloa</i> have glumes that are unusually narrow distally. In general, however, the range of values among the genera exhibits considerable overlap.

Discriminant analyses

Of the 208 records for which there were complete data, 98% were assigned to the correct genus when all the data were used in the analysis. With Jackknife analysis, however, the success rate was only 80%. Eliminating the poorly represented genera had almost no impact on these results. The first three discriminant functions accounted for 28.1%, 18.2%, and 16.2% of the total dispersion, respectively, for a total of 62.5%. The first and second functions separated <i>Australopyrum</i> and <i>Stenostachys</i> from the remaining genera. <i>Connorochloa</i> was distinguished by the first and third functions and <i>Anthosachne</i> was almost completely separated by the second and third functions. Thus the Australasian genera were distinguished from all the remaining genera on the first three functions.

When the four groups examined by Baum et al. (1995) were analyzed (Kengyilia, <i>Roegneria</i>, <i>Elymus</i>, and <i>Agropyron</i>), our jackknifed classification success rate was only 69%, 4% lower than the 73% that they obtained. As in their study, the greatest confusion was between <i>Elymus</i> (<i>StH</i>) and <i>Roegneria</i> (<i>StY</i>).

Random Forest Analysis

Because RF can use records with some missing data, the number of records in the complete analysis was 218, ten more than for DA. Of these, 85% were placed in the correct genome group (Table 3). All the specimens of <i>Stenostachys</i>, <i>Footerocopsis</i>, <i>Anthosachne</i>, and <i>Australopyrum</i>, were correctly classified and 98% of the specimens of <i>Elymus</i>. The most poorly classified were <i>Douglasdeweya</i> (80% misclassified),
Kengyilia (71% misclassified), and Campeiostachys 63% misclassified), all of which contain the St genotype and were represented in this study by few specimens. Misclassified specimens of Douglasdeweya were placed in Pseudoroegneria (1), Elymus (2), and Anthoschne (1); misclassified specimens of Kengyilia were placed in Elymus (1), Roegneria (2), Anthoschne (1), and Autrolytriphyllum (1); and misclassified specimens of Campeiostachys in Elymus (6), Roegneria (3), and Anthoschne (1).

Restricting the analysis to the 112 records from the six northern hemisphere St-containing groups (Pseudoroegneria, Elymus, Douglasdeweya, Roegneria, Kengyilia, and Campeiostachys) resulted in 79.5% successful classification, an increase of 8 correctly classified records over that obtained from the complete analysis. For the four groups examined by Baum et al. (1995), the success rate was 89.9%, a notable improvement over the results obtained with DA.

Table 4 presents the results of the analyses when each of the P-, H-, St-, Y- and W-containing species was compared with all the rest of the records. None of the P-containing specimens were correctly identified as such. The classification success rate for the other genomes ranged from 86.9–97.5% when only five characters were used and from 85.96–99.38% when all characters were used. The important characters varied with each analysis. Only the length of the middle internode was one of the top ten characters in all five analyses; palea tip width was in the top ten for three of the analyses.

### Discussion

Within the Triticeae, most species are perennial and have solitary spikelets. Ten different genomes have been identified among these species, eight of which are present in varying combinations in the numerous polyploid taxa. It is not surprising, therefore, that their taxonomic treatment is controversial. The genetic and cytogenetic information accumulated during the last century furthered our understanding of why it has been so hard to delimit morphologically recognizable species groups, but it has also suggested new ways of looking at the taxa. In this study, we examined the hypothesis that groups of genomically similar species are morphologically distinguishable.

Our results provide more support for this hypothesis than suggested by current taxonomic treatments. Some groups, such as the Australasian taxa, were relatively easy to distinguish. Others, such as Kengyilia, Campeiostachys, and Douglasdeweya, were not well sorted out when all the records were included in the analysis. This is partly attributable to their low representation in the analyses. Both DA and RF tend to favor increasing the accuracy of identification for the larger groups in an analysis in order to improve the overall success rate. Because there are only two known species of Douglasdeweya and few species of Campeiostachys with solitary spikelets, having equal, or nearly equal, species samples for each group is impossible.

The success rate for Kengyilia would undoubtedly be improved if we included a larger sample of the species because our selection included an almost equal number of typical and atypical species. We did not have access to enough reliably identified material to increase the number of species included. The species of Campeiostachys included had solitary spikelets although the majority of species in the genus have two or more spikelets per node. Inclusion of species with 2 or more spikelets per node from both Elymus and Campeiostachys might increase the confusion between these two genera, both of which include the St and H genomes. Douglasdeweya currently has only two species, both of which were described on the basis of plants grown in experimental plots. Discovery of wild-grown material might enable it to be more effectively distinguished from other genomic genera.

Our inability to identify suites of characters that always placed all the specimens in the correct genomic group could be used to argue for adopting a broad interpretation of Elymus. In our opinion, this would be counter-productive because it would conceal what is known about the genetic

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### Table 3. Classification results from Random Forests Analysis.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>E+</th>
<th>HW</th>
<th>L</th>
<th>P</th>
<th>St</th>
<th>StH</th>
<th>StHYW</th>
<th>StP</th>
<th>StY</th>
<th>StYH</th>
<th>StYP</th>
<th>StYW</th>
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<td>3</td>
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<td>0</td>
<td>0</td>
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We developed detailed and parallel species descriptions, which included descriptions of the species they include. In the absence of such descriptions, good descriptions are needed. Before any keys can be constructed, characters are used. Before any keys can be constructed, the author of the key decides the order in which the characters are used. The order in which to provide it, or dichotomous keys, is determined by the user. Such keys are usually presented in one of two forms, multi-access keys, in which the user determines which information to provide and one-to-one keys, in which the information is provided in a fixed order. Nowadays, such keys are run as computer programs and can be modified as more information becomes available.

Users of taxonomic classifications, however, do not wish to run a computationally demanding analysis in order to identify their plants. Consequently, one of our goals was to develop practical identification keys to the genomic groups of the tribe. The keys are intended to permit generic identification of species with one spikelet per node. Moreover, the disposition of some of these species, notably those treated in *Hystrix*, is problematic. At present, it appears that some belong in *Hystrix*, others in *Leymus*. Because they do not have solitary spikelets, such species were not included in this study. Once they have been examined and their appropriate generic membership decided, it may be necessary to modify the existing generic descriptions.

For the sake of those working with the tribe, we posted generic descriptions for all the genera of the tribe to the web (http://herbarium.usu.edu/triticaceae/genera), not just those included in this study. All the descriptions will be modified as more information and images become available. Our original intent was to provide keys solely to the perennial species with solitary spikelets, but we eventually decided to expand them to include all the genera that we currently recognize. The keys are intended to permit generic identification of non-hybrid Triticeae from anywhere in the world. This increases their value to plant breeders and gene bank curators who often hold accessions from distant locations; it makes understanding of the tribe, potentially impeding the development of new insights into its morphology, ecology, and biology by the next generation of field-oriented botanists and plant breeders.

Of greater interest, in many respects, was the identification by RF analysis of the characters that are most useful in distinguishing the genomic genera and of the characters that tend to characterize species that have a particular genome in common. These analyses confirmed Salomon and Lu’s observation that palea tip width is a useful character and suggested several other characters that should be given closer attention such as middle inflorescence internode length and glume shape.

Users of taxonomic classifications, however, do not wish to run a computationally demanding analysis in order to identify their plants. Consequently, one of our goals was to develop practical identification keys to the genomic groups based on morphological features. Nowadays, such keys are usually presented in one of two forms, multi-access keys, in which the user determines which information to provide and the order in which to provide it, or dichotomous keys, in which the author of the key decides the order in which the characters are used. Before any keys can be constructed, however, good descriptions are needed.

Descriptions of genera should be developed from descriptions of the species they include. In the absence of detailed and parallel species descriptions, we developed generic descriptions by combining information from our observations with information from published descriptions and identification keys. This process often required examining specimens to clarify what an author meant by a given phrase, for instance, whether “densely hairy” meant that the hairs concealed all or about half of the underlying surface. Even measurements are somewhat ambiguous, for instance, where does the lemma body end and the awn start? These problems are not peculiar to the Triticeae. They can be addressed, in part, by using images.

In building the generic descriptions, we attempted to take into account all available information, not just that gained through this study. Thus *Elymus* is described as usually having two or more spikelets per node, but with only one in some species although, for this study, we examined only species with one spikelet per node. Moreover, the disposition of some of these species, notably those treated in *Hystrix*, is problematic. At present, it appears that some belong in *Elymus*, others in *Leymus*. Because they do not have solitary spikelets, such species were not included in this study. Once they have been examined and their appropriate generic membership decided, it may be necessary to modify the existing generic descriptions.

<table>
<thead>
<tr>
<th>Char 1</th>
<th>palea tip width</th>
<th>palea length</th>
<th>rachis extension length</th>
<th>palea cilia length</th>
<th>lemma awn length</th>
<th>palea tip width</th>
<th>upper glume width</th>
<th>number of inflorescence nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Char 2</td>
<td>upper glume awn</td>
<td>lemma awn length</td>
<td>rachis extension length</td>
<td>palea cilia length</td>
<td>lemma awn length</td>
<td>palea tip width</td>
<td>upper glume width</td>
<td>number of inflorescence nodes</td>
</tr>
<tr>
<td>Char 3</td>
<td>number of inflorescence nodes</td>
<td>width of hyaline margin on lower glume</td>
<td>lemma margin hair length</td>
<td>lemma awn length</td>
<td>length of middle inflorescence internode spikelet length</td>
<td>lower glume width</td>
<td>culm thickness</td>
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<tr>
<td>Char 4</td>
<td>length of middle inflorescence internode lower glume awn</td>
<td>lemma length</td>
<td>lemma awn length</td>
<td>lemma awn length</td>
<td>length of middle inflorescence internode spikelet length</td>
<td>lower glume width</td>
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<tr>
<td>Char 5</td>
<td>upper glume vein number</td>
<td>auricle frequency</td>
<td>lemma length</td>
<td>number of inflorescence nodes</td>
<td>rachis extension length</td>
<td>lower glume length</td>
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</tr>
<tr>
<td>Char 6</td>
<td>lemma length</td>
<td>length of middle inflorescence internode lower glume awn</td>
<td>lemma back hair length</td>
<td>lemma front hair number</td>
<td>upper glume width</td>
<td>upper glume vein number</td>
<td>anther length</td>
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<tr>
<td>Char 7</td>
<td>lower glume hair density</td>
<td>florets per spikelet</td>
<td>spikelet length</td>
<td>lemma vein number</td>
<td>Inflorescence length</td>
<td>lower glume hair density</td>
<td>upper glume cilia length</td>
<td>anther length</td>
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</tbody>
</table>
them less useful to regional botanists because some of the genera will be absent from their region. With the web-based keys, however, it is possible to specify that the specimen is from Europe, Asia, the Americas, Australasia, or Africa. Like the descriptions, the keys reflect our current knowledge of the genera.

In developing the keys to the genomic genera, we drew on information gained from the DA and RF. It was, however, only after conducting additional examination of the specimens and the leads used in other works that we were able to develop the keys that we have posted to the web. The dichotomous key was easier to construct than the multi-access key because we were able to decide in what order to bring out each group. This meant we could bring out the distinctive groups first, using the characteristics that set them apart, and did not need to know about their other characteristics. We are, however, aware that users will find many of the leads in the dichotomous key difficult. Multi-access keys are generally thought to be easier to use but constructing them requires having information about all the characters for all the genera. Because we currently lack such information, the multi-access key is, as yet, incomplete.

The dichotomous key relies primarily on qualitative characters because the range of values for all the quantitative characters overlapped among genera. For instance, most species of *Kengyila* have short rachis internodes at mid-inflorescence, but a few species have long internodes. Similar exceptions exist in all the genera having more than a few species.

Unlike the dichotomous key, the multi-access key features many quantitative characters, because users often feel more confident in using such characters. Their inclusion in the key will enable users to narrow down the possibilities using the characters they prefer but a final determination may require use of the qualitative characters. The multi-access key also includes a distributional character. It should be used with caution because many species of Triticeae have become established beyond their native range. Both the dichotomous and multi-access keys are available at http://www.herbarium.usu.edu/Triticeae/keys.

The absence of detailed, comparable species descriptions means that both the generic descriptions and the keys must be regarded as preliminary. They will undoubtedly require modification as more information becomes available. Modifying multi-access keys is relatively simple; modifying dichotomous keys, including those presented on the web is harder, because it may require rereading all the leads. But providing web-based keys and descriptions makes it easier to address another stumbling block for users, that of understanding what an author meant by a particular term or phrase. Digital files can incorporate illustrative images and drawings at minimal expense. The programs that we used restrict the number and size of the files that they can incorporate, but they can include links to other web sites where such resources are made available in a different style. For instance, Zoomify (2009) permits zooming in on high resolution images, effectively providing the viewer with a magnifying lens (for examples, see http://www.herbarium.usu.edu/triticeae/zoom). CoolIris (2009) facilitates viewing multiple images, thereby enabling visitors to have an overview of the species in a genus, or of variation in a species. Prior to the web, such an overview could only have been obtained by borrowing specimens from multiple herbaria. The only restriction on developing such resources, and it is a significant restriction, is the time and effort involved in obtaining the images and, in the case of images of living plants, preparing the specimens that document them. The greatest restriction on using web-based resources is internet access. In some parts of the world, this is inexpensive and reliable; in others it is non-existent, expensive, unreliable, or some combination of these three. A partial solution to these problems is to make the resources available on a flash drive or compact disk and develop a mechanism for updating the files that does not require a complete download. Those interested in obtaining such copies of the descriptions and keys developed for this paper should write to Barkworth.

The greatest need now for taxonomists working in the Triticeae is to develop detailed, parallel species descriptions and documented distribution maps. In globally distributed taxa such as the Triticeae, this requires collaboration in identifying the characters to examine and how to record their variation. Digital technology can help in this regard, but it will not, by itself, provide the solution.

In the last few paragraphs, we emphasize the role that digital technology can play in the creation of taxonomic resources. It does not, however, address our primary question, whether or not the genomic genera can be identified morphologically. Our conclusion is that they can be, but that it will require examination and clearer description of features such as palea shape, middle inflorescence internode length, and glume shape. We also found that, as is to be expected, genera that have some genomes in common are more difficult to distinguish than those with no genomes in common.

**Acknowledgements**

We thank the curators of the herbaria from which we have borrowed specimens (CANB, CHR, MO) and Drs. B.R. Baum, Henry Connor, B.R. Lu, B. Salomon, Chi Yen, and H.-Q. Zhang for many discussions concerning the taxonomy of the Triticeae and for sharing information with us.

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APPENDIX.

List of voucher specimens, grouped according to their genomic constitution. Not all species have names that reflect their genomic constitution. Most of the specimens of Roegneria and Kengylia were collected in China and have labels that are written in Chinese. I shall try to have them translated, at least to the point where we can list the province in which they were collected, by the time this paper is back from review.
