Skewed Distribution of Species Number in Grass Genera: Is It a Taxonomic Artefact?

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ABSTRACT

The grass family (Poaceae) comprises about 10,000 species distributed in some 785 genera, seven large subfamilies and a few small ones. The distribution of species in genera appears skewed toward monotypic genera and those with few species. This pattern follows the hollow curve distribution documented by Willis. Explanations of the pattern have been attributed to statistical, biological and taxonomic factors. This study explores potential biological and statistical explanations for species distribution in Poaceae. Patterns of species distribution in the family and its major subfamilies were investigated, and the influence of age, habit and habitat on these patterns was assessed. Results showed that species distribution is not only skewed for the number of small genera but also for the total number of species in larger genera. Phylogenetic position does not appear to explain species distribution in the family and in fact refutes the age and area theory proposed by Willis. Genus size appears to be correlated with habit where larger genera are predominantly perennial. Genera with mixed annual and perennial species do not reflect the hollow curve pattern. These patterns of species distribution may be explained by polyploidy and hybridisation, two prominent features in the evolution of the family.

11.1 INTRODUCTION

A striking pattern for distribution of taxa in their respective higher categories points to a skewed distribution towards monotypic and small groups. This phenomenon was first documented by Willis and Willis and Yule in a study of the flora of Ceylon (Sri Lanka). They dubbed this pattern the...
hollow curve distribution (HCD) and indicated that such a pattern exists at all taxonomic levels. Willis and Yule\(^2\) asserted that the longer the group has existed, the more area it will occupy. They further stated that monotypic genera are in general ‘beginners’ and are descendents of larger ones. The HCD was later demonstrated in other organisms, such as arthropods, birds and mammals\(^3\)–\(^7\). Although this skewed pattern is evident across a broad range of biological diversity and at all taxonomic levels, explanations of its causes vary, and different hypotheses and models have been proposed (see Hodkinson and Parnell, Chapter 1; Davies and Barraclough, Chapter 10; Parnell et al., Chapter 16).

Willis\(^1\) cited biological, historical, mathematical, psychological and statistical elements as potential causes of the HCD. Willis and Yule\(^2\) stressed age and area as the principal factors behind the biological patterns of diversification and the emergence of the HCD. Dial and Marzluff\(^5\) indicated that early authors favoured deterministic explanations, whereas more recent authors incline toward stochastic models. In a study aimed at determining patterns and causes of species diversification, Dial and Marzluff\(^5\) compared species distributions in 85 taxonomic units from six groups of animals and one group of plants to those predicted by five null models. Their sample comprised 53 taxonomic assemblages based on traditional classifications and 32 based on phylogenetic schemes. They found that real assemblages were dominated to a significantly higher extent by one unit than predicted by all five models. They also noted that the pattern is evident in both traditional and phylogenetic schemes and concluded that such skewed distributions reflect real differences in the evolutionary successes of the groups. Dial and Marzluff concluded that overdominance of an assemblage by one unit is a common and nonrandom feature of taxonomic diversity distribution and proposed that such a pattern might be the consequence of differences in life history traits such as fecundity, age of first reproduction, longevity and mobility. Cardillo et al.\(^6\) studied the pattern of diversification in 76 genera (210 species) of Australian mammals and contrasted the observed distribution with the Poisson and geometric models. They observed that species distribution based on real data is significantly different from those predicted by Poisson and geometric null distribution, with the observed distribution having more species poor and species rich genera than predicted by the models. Scotland and Sanderson\(^7\) tested the HCD in birds and the three angiosperm families Fabaceae (legumes), Orchidaceae (oroids) and Asteraceae (asters or daisies). They compared their new model, simultaneous broken tree (SBT), with distributions based on real data, the simultaneous broken stick (SBS) and the geometric distribution. Their study showed that the SBT model overestimated the monotypes and dominance (large genera), whereas the SBS underestimated them. Consequently, they suggested that lack of fit between real data and the SBT model is taxonomic and not evolutionary, contending that taxonomists are averse to studying genera that are too large or too small.

In this study, the grass family (Poaceae) is chosen to assess the potential influence of some biological traits on species distribution in genera. Biological traits examined here are habit, eco-geographic preferences, habitat and polyploidy. Genus size is also considered in a phylogenetic context using a consensus tree for the grass phylogeny. The grass family is chosen because of its large size (approximately 10,000 species and 785 genera), wide distribution over diverse habitats, variation in habit that provides a sizeable sample and wealth of data on chromosome number and polyploidy. This study is based on real (observed) data and does not include null model assessments.

### 11.2 THE GRASS FAMILY (POACEAE)

Poaceae is the fifth most species rich flowering plant family. It spans the globe in distribution and uniquely forms large stretches of grass-dominated communities, the grasslands. Grasses are found at almost all altitudes and latitudes that allow plant life to exist, and its species are among the pioneers in primary and secondary succession communities. Various species and lineages of grasses have evolved ecophysiological, anatomical and morphological adaptations that have allowed them to flourish and radiate in a variety of habitats ranging from humid tropics to seasonal tropics to temperate regions and from xeric to aquatic\(^8\)–\(^10\). The major grass subfamilies also tend to display
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geographic/ecological preferences; for instance, Bambusoidae are found predominantly in tropical regions, Pooidae generally occupy temperate areas, Chloridoideae tend to flourish in drier habitats and Ehrhartioideae (Oryzoideae) exist in wet environments. Certain grass lineages, such as pooids and bambusoids, employ a C$_3$ type of photosynthetic system, whereas others, such as Chloridoideae, have C$_4$ types. Grass species range in life span from annuals to biennials and from short-lived perennials to long-lived perennials. In the latter type, some woody bamboo plants may live for over 100 years before they flower, set seed and die.

Grass reproduction is intriguing. The flowers lack a showy perianth and are reduced to mostly three or six stamens and an ovary enclosed in bracts, features that promote wind pollination. They have adopted various forms of sexual reproduction, like outcrossing, inbreeding and cleistogamy, and added asexual means of reproduction such as apomixis, vivipary and vegetative propagation. Hybridisation and polyploidy are common in grasses. These features are evident in the estimated 80% polyploidy and the predominance of allopolyplody. Basic chromosome numbers in grasses are remarkably variable, covering a range of $x = 2–14$ and 18, having somatic numbers that range between $2n = 4$ and $2n = 263–265$, and with a 2C DNA content that varies from 0.7 in *Chloris gayana* Kunth to 27.6 in *Lygeum spartum* L., an impressive 40-fold range. Chromosome number and structure and DNA content have undertaken a number of evolutionary pathways that include numerous reversals.

To place the pattern of variation in genus size in a phylogenetic context, a robust phylogeny for the grass family is required. Our understanding of grass systematics has recently made major leaps with the application of molecular approaches to the family. General consensus exists on the delimitation of the major grass lineages and the patterns of their divergence (see GPWG; Hilu; and Hodkinson et al., Chapter 17). These phylogenetic hypotheses are based on sequence information from different genomic regions and sometimes incorporate structural characters. The consensus grass phylogenetic tree depicts a basal grade of Anomochloa, Streptochaeta, Pharoideae (Pharus) and Puelioideae (Puella and Guaduella) following this grade, the remaining nine recognised subfamilies fall into the strongly supported PACCAD (Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Aristidoideae and Danthonioideae) and the less substantiated BEP (Bambusoideae, Ehrhartioideae and Pooidae) clades (reviewed in Hilu). Therefore, our deep understanding of grass phylogenetics and systematics can provide a reliable guideline for evolutionary trends at various taxonomic levels, including patterns of variation in genus size.

11.4 RESULTS AND DISCUSSION

Considering the whole grass family, it is evident that species distribution is strongly skewed towards monotypic or small genera (Figure 11.1A), following the HCD depicted by Willis and also discussed by Clayton and Renvoize and references therein. In Poaceae, 35% (230) of the genera are monotypic, and those with one or two species represent almost half (315) of the total number of genera. In fact, 78% (506) of the grass genera are relatively small, containing 10 or less species. Due to their small size and large proportion, these genera encompass only 15% (1,416) of the grass species. In contrast, only 3% (22) of the grass genera contain 100 or more species. Those 3%, however, encompass an astonishing 50% (4,820) of the species in the family. Therefore, although
the distribution curve is strongly skewed toward small genera, the overwhelming majority of species (dominance) is found at the other end of the curve (Figure 11.1B). Excluding the two ends of the spectrum in terms of genus size and species distribution leaves genera with 11–99 species that make up 19% of the genera (123) with 35% (3,418) of the species, and an average of

**FIGURE 11.1** The distribution of genus size in the grass family. (A) The pattern follows the HCD with predominance of monotypic and small genera. (B) Species concentration (dominance) occurs at the opposite end of the curve. (Data from Clayton and Renvoize\textsuperscript{11} and Watson and Dallwitz\textsuperscript{19}.)

<table>
<thead>
<tr>
<th>Table 11.1: Distribution of Species in Grass Genera</th>
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<td><strong>Number of Genera</strong></td>
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<td>Poaceae family</td>
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<td>Monotypic genera</td>
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<td>Genera of 1–10 sp.</td>
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<td>Genera of 100 and more sp.</td>
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<td>Genera of 11–99 sp.</td>
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*Note: Statistics calculated for the whole family, annuals, perennials and genera with mixed annual and perennial species (noted as mixed genera). Also noted is the distribution of species in genera as grouped into three arbitrary categories: 1–10 species, 11–99 species and 100 and more species. Data obtained from Hila et al.\textsuperscript{14} and Watson and Dallwitz\textsuperscript{20}.***
28 species per genus. The species distribution in this group is in sharp contrast with the two extremes, where an average of 2.8 species per genus for genera containing 10 or less species and 219 species per genus for genera with 100 or more species is found (Table 11.1).

### 11.4.1 AGE AND DIVERSIFICATION

Although the skewed distribution towards monotypic or very small genera is evident in Poaceae and elsewhere, explanation of its causes has varied. Willis and Yule\(^2\) proposed the concept of age and geographic distribution to explain the HCD originally documented by Willis\(^1\). They asserted that large genus size is a manifestation of age and wide distribution and that those genera have given rise to small ones with restricted distribution. Considering this scenario, one may expect genera at the base of the grass family tree (taxa sister to the rest of the grasses), as well as those at the base of major lineages (PACCAD) and the individual subfamilies, to be large in size while genera in terminal lineages would be small in size. However, this is not evident among extant grasses (Figure 11.2); the four basal lineages in the grass phylogeny are represented by monotypic to very small genera: *Streptochaeta* (two to three), *Anomochloa* (one), *Pharus* (five to six), *Puelia* (six), and *Guaduella* (eight). The early diverging lineages are not the ancestors of the other grasses; it is not known how diverse the stem lineages (ancestors) leading to the split of these basal lineages and their sister group were. However, it is clear that the early diverging lineages are not diverse in all cases examined here.

When geographic distribution is considered, *Streptochaeta* is restricted to shady places from Mexico to Argentina, *Anomochloa* to the forest of tropical America, *Pharus* to shady places of tropical America and the West Indies, *Puelia* to shady places of Sierra Leone and Angola and *Guaduella* to tropical rainforest of Africa. The pattern of small basal taxa is also evident in individual major grass lineages. *Micraira* appears as the sister genus to the large PACCAD clade (not shown);

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**FIGURE 11.2** A consensus tree for the grass family on which genus size is mapped for basal lineages of the grass family and its major subfamilies. (The consensus tree is based on trees obtained from GPWG\(^17\) and Hilu et al.\(^18\); information on genus size is from Clayton and Renvoize\(^11\) and Watson and Dallwitz\(^19\).)
the genus comprises eight species confined to Australia (not shown). Considering the base of individual subfamilies for instance (Figure 11.2), in Pooidae, both *Brachyelytrum* (shady places of woodlands in North America, Japan and Korea) and *Nardus* (Europe and Western Asia) are monotypic; in Chloridoideae, *Triraphis* includes seven species found in Africa and Arabia and one species in Australia; and in Ehrhartioideae, *Streptogyna* contains only two species distributed in the forest shade from West Africa to Southern India and Sri Lanka, and Mexico to Brazil. Therefore, genus size at the base of individual subfamilies is small, but geographic distribution varies. In contrast, a wide range of genus size exists at the terminal branches that include monotypics and large genera. Thus, the size of early diverging genera in the family and the subfamilies is small rather than large. The small size and mostly restricted distribution may either represent the prehistorical geographic pattern or could be the outcome of species extinction and endemism. Cardillo et al.\(^6\) indicated that diversification rate is an outcome of a differential rate of speciation and extinction. In conclusion, age alone cannot be used to explain genus size or the predominance of small-sized genera.

### 11.4.2 Habitat and Ecophysiologically Related Traits

Next to be examined is the potential impact of ecophysiological factors and habitat on genus size. To address the potential underlying impact of these traits on species distribution, three subfamilies with different preferences have been chosen: Bambusoideae with tropical and forest habitats and \(C_3\) photosynthesis; Chloridoideae with drier habitats and \(C_4\) photosynthesis; and Ehrhartioideae with primarily aquatic or wet habitats and \(C_3\) photosynthesis. Deviation from the HCD would be construed as a potential influence of one or more of these variables on mode of diversification.

Comparing species distribution in these three subfamilies, skewed distribution towards small genera (HCD) is evident (Figure 11.3; Ehrhartioideae is not shown). Similarly, concentration of the majority of the species in a few large genera (dominance) matches what has been documented for Poaceae as a whole (distributions not shown). Consequently, these results do not point to differences in habitats as potential factors that impact species distribution. Bambusoideae is of special interest

![Figure 11.3](image)

**FIGURE 11.3** Genus size distribution in Bambusoideae (A) and Chloridoideae (B). Genus size distribution follows the HCD. The two subfamilies differ in their ecophysiological preferences and photosynthetic systems.
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here as, due to infrequent flowering, taxonomic decisions are in some cases based on vegetative characters, a situation that may favour a trend toward splitting but not lumping of species in a genus. Consequently, one would expect species distribution to be skewed away from monotypic or very small genera and to favour relatively larger ones; this assumption is based on potentially higher variation amongst populations in vegetative characters relative to reproductive traits. In this case, taxonomic factors would become more pronounced in assessments of species distribution. This, obviously, does not seem to be the case (Figure 11.3A).

Thus, these contrasting subfamilies all show the HCD despite having differing geographic distribution, photosynthetic pathways and other adaptive traits correlating to ecological factors.

11.4.3 IMPACT OF LIFE HISTORY ON GENUS SIZE

The next question to ask is whether life history has an impact on genus size across the Poaceae. Different life forms exist in the grass family as a response to adaptation to scores of environmental conditions. This chapter focuses on plant longevity and groups species into annuals and perennials. Perennialism in the grass family has a very wide scale, as it can span a life history period from a few years to over 100 years. To address life history as a factor, grass genera are labeled as annuals, perennials or mixed. In the latter case, a genus is labeled as such when it encompasses both annual and perennial species regardless of their proportions.

The number of genera composed of perennials in Poaceae is almost three times that of the number of genera composed of annuals (371 versus 134), leaving 146 genera with a mixture of annual and perennial species (Figure 11.4A, Table 11.1). The difference between genera composed of annual species and those composed of perennial species becomes more acute when the number of species in each group is considered. Genera composed of perennials contain 10 times as many species as genera composed of annuals (3,824 versus 384). The number of species (5,446) in mixed genera is high (Figure 11.4B, Table 11.1). On average, the number of species in genera composed of annuals is 2.9, in genera composed of perennials 10.3, and in mixed genera 37.3. These differences are statistically significant at the 5% level ($\chi^2 = 39, p < 0.05$).

More striking differences in genus size in relation to different life histories can be seen in the plots of the distribution of species across these three classes (Figure 11.5 and Figure 11.6). Plotting the number of genera against genus size, the HCD was evident for perennial genera (Figure 11.5A), paralleling the pattern observed for the whole grass family and for individual subfamilies (Figure 11.1–11.3). Similar patterns are also observed in the annuals (Figure 11.5B). However, when the mixed genera were examined, the pattern of distribution of genus size failed to fit the HCD (Figure 11.6A). For instance, the number of genera with five species is larger than the number of monotypic genera, and genera with four species are as frequent as monotypic genera. This pattern
FIGURE 11.5 The distribution of genus size in perennial (A) and annual (B) genera. Genus size distribution follows the HCD. (Information on genus size is from Clayton and Renvoize\textsuperscript{11} and Watson and Dallwitz\textsuperscript{19}.)

FIGURE 11.6 Deviations from the HCD. Genera containing both annual and perennial species deviate from the HCD at the whole grass family level (A) and in individual tribes such as Andropogoneae (B). A similar pattern is found in other grass tribes such as the Paniceae and Poeae/Aveneae. (Information on genus size is from Clayton and Renvoize\textsuperscript{11} and Watson and Dallwitz\textsuperscript{19}.)
of distribution was also apparent in mixed genera of the tribes Andropogoneae (Figure 11.6B), Paniceae and Poeae/Aveneae (not shown).

The small number of annual genera and their small average size and the substantially larger number of perennial genera and their larger size in grasses are unexpected findings at first glance, as an annual but not a perennial habit is generally considered to favour higher diversification (see Hodkinson et al., Chapter 17). Annuals reach flowering stage in the same season, and variation in length of vegetative (juvenile) period is a matter of days. In contrast, perennials go through juvenile vegetative stages which may extend from months to years. Furthermore, Harper noted that in perennial herbs, such as grasses, years of flowering and seed production are often interrupted by years of purely vegetative growth. Thus regeneration of offspring in perennials, or at least herbaceous ones, is at a lower rate than with annuals. This gives annuals a definite advantage over perennials in terms of rapid generation turnover, increased variability due to more frequent sexual recombination, and potential for higher rate of fixation of adaptive mutations. Considering this scenario, annuals are expected to have better options for enhanced speciation compared with perennials. It has been shown that fast life history is conducive to higher diversification and may increase probability of speciation. Evidently this does not seem to be the case in grasses, as annual genera are by far less species rich than perennial ones. The causes of this pattern of diversification require explanation.

Considering these observed patterns of species distribution in relation to habit, three questions can be posed:

• Why do annual genera tend to be smaller in size, whereas perennial genera are more species rich?
• Why does the HCD theory break down in mixed annual/perennial genera?
• What causes genera with mixed species to be larger in size on the average than either annual or perennial genera?

11.4.4 POLYPLOIDY AND DIVERSIFICATION IN POACEAE

To partly address the above three questions, two of the prominent features of Poaceae, namely polyploidy and hybridisation, were examined to see if they could provide possible answers. Polyploidy and hybridisation are considered as two important biological forces in grass diversity and evolution. Estimates of polyploidy in grasses are as high as 80%, basic chromosome numbers range from \(x = 2\) to 18, and somatic numbers vary from \(2n = 6\) to 265. Hybridisation is common in Poaceae, and wide crosses in nature and under artificial environments are well known. Polyploidy often confers immediate reproductive isolation from parental species and may lead to speciation. This isolation can be achieved whether polyploidy has arisen via hybridisation and chromosome doubling (allopolyploidy) or through simple doubling of the chromosome complement of an individual plant (autopolyploidy). In both cases, chromosome doubling can result in unbalanced meiotic behaviour and subsequent seed sterility (or lowered viability), at least in the first few generations. Mutations to correct chromosome pairing are thus crucial for the success of those polyploid genotypes regardless of their autoploid or allopolyploid nature.

The role of mutations in meiotic chromosome pairing is well documented, and simple mutations can result in bivalent associations and subsequently gametic balance (see Hilu). In this case, perennial species would have by far the better chance to accommodate polyploidy, as they can survive beyond a single generation without the need for seed set, increasing the chance of acquiring such mutations. As an annual, correcting chromosome pairing in the first generation is a prerequisite for survival. Should polyploidy be a factor in speciation and larger genus size in Poaceae, then one could expect annuals to be predominantly diploids or low polyploids and perennials to accommodate polyploidy of different magnitude in proportion to genus size. Following this scenario, the size of mixed genera should relate to the proportion of perennial species in the genus and the degree of polyploidy.
To assess the potential impact of polyploidy in grass biodiversity, samples of annual, perennial and mixed genera of various sizes were examined for the presence and degree of polyploidy. Large perennial genera examined are highly polyploid, displaying a series of aneuploid and/or euploid gametic chromosome numbers. Standing out among these genera are Festuca (450 species), Calamagrostis (270 species), Bambusa (120 species) and Rydiosperma (90 species). In Festuca, somatic chromosome numbers reported include 2n = 14, 28, 35, 42, 56 and 70; in Calamagrostis 2n = 28, 42 and 56, or 56-91 (apomicts); Bambusa 2n = 24, 46, 48, 70 and 72; and Rydiosperma 2n = 24, 48, 72, 96 and 120. With the exception of Festuca, diploid types are not found in these genera. In contrast, perennial genera of small size tend to occupy the other end of the spectrum in terms of polyploidy. For instance, the monotypic perennial Calderonella is a diploid with x = 12, Thysanolaena is a diploid based on x = 11, and Asthenochloa and Cleistachne are tetraploids based on x = 9. The perennial small genus Sartidia (4) is also a diploid based on x = 11. This genus is of special interest, as other members of its tribe, Aristideae, are much larger, with Stipagrostis containing 50 species and Aristida 250. However, Stipagrostis contains primarily perennial species with a few annuals, and species are diploid or tetraploid based on x = 11. Aristida on the other hand includes a mixture of annuals and perennials but displays a more extensive polyploid series based on x = 11 or 12 (2n = 22, 24, 36, 44, 48 and 66). These three Aristideae genera display a grade of genus size that parallels their polyploidy levels and habit, suggesting a correlation between species number and polyploidy levels in perennials. It is to be noted that Bambusa belongs to the woody bamboo subfamily (Bambusoideae), a group containing long-lived perennials. Polyploidy is the norm in these, and diploid genotypes/species have for the most part gone extinct.26

Looking at genera with different habits, it appears from examining representative genera that there is a tendency towards lower frequency of polyploidy in annuals than perennials. Asthenochloa and Cleistachne are monotypic annuals, both are tetraploids based on x = 9, most likely rediploidised tetraploids that lack other chromosomal variation. The annual genera Gastridium, Mibora and Elytrophorus each contain two species; they are all diploids. Gaudinia contains four annual species that sometimes behave like biennials; the species are diploids based on x = 7, but occasionally possess a somatic number of x = 15. Larger-size annual genera seem to have been able to accommodate some degree of polyploidy. Examples of those are Sacciolepis (30) with x = 9 and 2n = 16, 18, 36 and 45, and Avena (25) with x = 7 and 2n = 14, 28, 42, 48 and 63. The presence of 5x ploidy level and aneuploid numbers in species of these genera may suggest the presence of some degree of apomictic reproduction, again a system that can accommodate and promote polyploidy by producing seeds without sexual reproduction. In this case, the apparent large genus size may be an artefact of taxonomic splitting caused by apomictic perpetuation of morphologically distinct biotypes.

The second question to be addressed is why mixed genera display a pattern that does not fit the HCD. The answer to this question may relate to the proportion of each life history type in any given genus. If polyploid perennials have an accelerated rate of speciation and the converse is true for the mostly diploid or low polyploid annuals, then the size of a genus with mixed annuals and perennials would depend on the proportion of the two types of species. A mixed genus with proportionally more perennial species would tend to be larger in size than that with higher proportion of annuals. This scenario fits well the large mixed genera Sporobolus (160), Muhlenbergia (160), Isachne (100) and Pennisetum (80), where both annual and perennial habits are present but the annual species are rare. Polyploidy is extensive in all four genera. In Sporobolus, chromosome numbers are based on x = 9 and 10, and somatic numbers are 2n = 18, 24, 36, 38, 54, 72, 80, 88, 90, 198 and 124. Similarly, Pennisetum species display basic chromosome numbers of x = 9, and somatic numbers are 2n = 14, 18, 22, 34, 35, 36, 45, 52 and 54.

The large genus Paspalum (330) is described as ‘usually’ perennial, indicating more annuals than in the above discussed genera. However, extensive series of polyploidy based on x = 10 and 12 augmented by aneuploidy have been established in this genus. Digitaria contains 230 annual and perennial species. Although it is not described as primarily perennial, it has evolved a wide...
range of polyploidy numbers based on $x = 9, 15$ and $17$; such basic chromosome series appear to have originated via aneuploidy, most likely coupled with hybridisation. *Panicum* (470) comprises both annuals and perennials with no predominance of either habit, but diploidy ($2n = 18$) is seemingly rare, while polyploidy is extensive and based on $x = 7, 9$ and $10$, and $2n = 36, 37, 54$ and $72$. In these cases, it appears that species diversification is augmented by extensive patterns of polyploidy.

At the other end of the spectrum of mixed genera, namely small-sized ones, one would expect either annuals to be found in higher proportion or polyploidy to be rare, or both. *Amphicarpum* (2) is described as an annual and perennial genus; only diploid chromosome numbers have been reported ($x = 9, 2n = 18$). *Tricholaena* contains four species, mostly perennial, that are all tetraploids based on $x = 9$. *Echinolaena* is slightly larger with eight annual and perennial species, but only tetraploidy is found ($2n = 60$). Only diploid genotypes of $2n = 20$ have been reported for *Chionachne* (7), although it is composed primarily of perennial species. Lack of polyploidy may account for the small size of these genera. *Loudetia* (26) is rarely annual, but the larger size is associated with a more elaborate polyploid series based on $x = 6, 12$, and $2n = 20, 24, 40$ and $60$. Moving up in genus size, *Echinochloa* contains 35 annual and perennial species. Polyploidy has progressed considerably in this genus where, based on $x = 9$, odd and even euploidy as well as aneuploidy have been established ($2n = 27, 36, 42, 48, 54, 72$ and $108$). Therefore, it appears that small genus size is correlated with lack of polyploidy, and an increase in genus size tends to be associated with progressive emergence of polyploid genotypes.

The third question is why, on average, genera with mixed annual and perennial species tend to be more species rich. Part of the answer may be found in the combined accelerated rates of speciation of the two life forms through different biological routes. Although perennials take advantage of polyploidy, annuals are also well suited for speciation at the diploid level. In these cases, a combination of rapid generation turnover inherent to annuals and extensive polyploidy in perennials, possibly with apomictic mode of reproduction superimposed, could play a role in determining genus size. This question, however, remains intriguing and in need of further investigation.

### 11.5 CONCLUSION

It is evident from this survey that small genera either have more annual species or less polyploidy, or a combination of both. With increase in genus size, the proportion of perennial species and the incidence of polyploidy increases. This phenomenon could have contributed to the punctuated genus size pattern observed for the mixed genera. It also may explain the correlation between annuals and small genus size and perennials and explosive speciation. Although perenniality combined with polyploidy sets the stage for increased diversity at the species level in Poaceae, other factors such as breeding systems (outbreeding, inbreeding, cleistogamy and apomixis) impose yet additional parameters that could influence speciation. All these factors together should be considered to act in promoting adaptive radiation to exploit a diverse variety of habitats. As such, ecological parameters represent major factors that work in accordance with the genetic factors when degree and patterns of speciation are to be explained. Thus, the nonrandom distribution of species appears to have contributed to the skewed distribution favouring monotypic and small genera and towards that skewed distribution of dominance in terms of species richness. Biological factors, such as habit and polyploidy, appear to have had some impact on these patterns in the grass family. These biological factors may be group specific and should not be overly generalised.

### ACKNOWLEDGEMENTS

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