EVOLUTIONARY TRENDS IN THE GRASSES (POACEAE): A REVIEW

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INTRODUCTION

Poaceae (Gramineae) are one of the largest vascular plant families, containing between 650 and 785 genera, and 10,000 species (Clayton & Renvoize 1986; Watson 1990; Watson & Dallwitz 1992). Only Asteraceae (Compositae), Fabaceae (Leguminosae), and Orchidaceae contain more species than Poaceae (Watson 1990). Poaceae are also one of the most ecologically and economically important plant families (Thomasson 1987). Grasses and grasslands are distributed worldwide and account for 25–45% of the world's vegetation. Grasslands support diverse invertebrate and vertebrate communities (Hilu 1985), and are important elements in the development and stabilization of soil. Most human food comes directly or indirectly from grasses, either directly in the form of rice, maize, wheat, millet, and barley, or indirectly in the form of cows, sheep, pigs, and poultry raised on grasses or grains. Grasses have many other economically important uses, including bedding for humans and animals, thatch for mats and roofing, and reeds for fences, walls, and flooring. Bamboo is used as construction scaffolding in Asia.

Researchers have attempted to determine the origins of the Poaceae, and the evolutionary path that grasses have followed in becoming one of the dominant plant families on Earth. This paper will describe what has been learned to date about grass evolution.

PHYLOGENETIC ORIGINS

The evolutionary origin of the grasses is uncertain, obscured by the lack of unambiguous links between Poaceae and other monocotyledons (Clayton & Renvoize 1986; Stebbins 1987). Morphological similarities between grasses and sedges (Cyperaceae) were once thought to reflect a close relationship between these families. However, plant taxonomists now attribute these similarities to convergent evolution, and place Poaceae and Cyperaceae in different orders (Dahlgren et al. 1985; Clayton & Renvoize 1986; Clifford 1987). The nearest liv-

ing relatives of the grasses are now thought to exist among either the Joinvilleaceae, Flagellariaceae, or Restionaceae (Clayton 1981; Clayton & Renvoize 1986; Stebbins 1987). The family Joinvilleaceae is the leading candidate, having been identified as a sister group to Poaceae (Soreng & Davis 1998). Similarities in certain chloroplast DNA sequences suggest that members of the genus *Joinvillea* (Joinvilleaceae) may be the plants most closely related to Poaceae (Davis & Soreng 1993).

Taxonomic evidence (Clayton & Renvoize 1986; Watson & Dallwitz 1992) and cladistic analysis (Kellogg & Campbell 1987; Davis & Soreng 1993) support the division of Poaceae into three evolutionary sub-groups. These groups are the Bambusoideae, the Panicoideae/Arundinoideae/Chloridoideae, and the Pooideae. The Bambusoideae retain the greatest collection of primitive characters, and are considered the ancestral grouping by most authorities. The Bambusoideae are thought to have originated in tropical forest-edge habitats, suggesting that Poaceae as a whole probably evolved from tropical forest-edge species (Clayton & Renvoize 1986; Stebbins 1987; Renvoize & Clayton 1992).

From this presumptive forest-edge origin, grasses evolved along three different developmental trajectories, each adapted to a different general habitat type. The Bambusoids evolved to become tropical forest inhabitants, the Panicoids, Arundinoids, and Chloridoids occupied open savannas and warm prairies, and the Pooids became adapted to cool-temperate habitats (Renvoize & Clayton 1992). The grasses have adapted most successfully to open habitats, particularly habitats impacted by grazing, fire, and drought (Stebbins 1981; Coughenour 1985; Renvoize & Clayton 1992).

FOSSIL RECORD

While a late Cretaceous origin (more than 63 million years ago = >63 MYA) of the family is still debated (Takhtajan et al. 1963, in Daghlian 1981; Linder 1987; Stebbins 1987; Crepet & Feldman 1991), there is ample fossil evidence that grasses had evolved as a distinct taxonomic group by the Eocene epoch, 40–60 MYA (Daghlian 1981; Stebbins 1981; Clayton & Renvoize 1986; Thomasson 1987; Renvoize & Clayton 1992). Grass fossils have been found in African and South American Eocene formations (40–60 MYA), and in Eurasian (12–18 MYA) and North American (15–25 MYA) Miocene deposits (Clayton 1981; Daghlian 1981; Stebbins 1981; Coughenour 1985; Thomasson 1985; Stebbins 1987; Thomasson 1987; Crepet & Feldman 1991). Reports of Cretaceous grass fossils are considered erroneous, the result of specimen misidentification or misclassification (Thomasson 1980).

Early attempts at fossil grass classification were hampered by a poor understanding of taxonomic relationships among living grasses, and the depauperate fossil floras on which these classifications were based (Thomasson 1980). The prevalence of parallel evolution within the family also hindered the proper classification of both living and fossil grass species (Clayton & Renvoize 1986; Stebbins 1987). Compounding the problem was the fact that fossil grass pollen,

while distinctive at the family level, was of very little use in distinguishing among grass genera or species (Thomasson 1980).

While there are no clear fossil links between the grasses and other monocot families, careful examination of the available fossil record has improved our taxonomic understanding of Poaceae. Changes in fossil floral structures support the hypothesis that the hardened lemma and palea of certain North American grass species co-evolved with mammalian and/or invertebrate herbivores (Thomasson 1985; Thomasson 1987). These structures are thought to have evolved to increase the chances that a seed would survive mastication and passage through a herbivore gut (Thomasson 1985). Comparison of microscopic morphological characters such as phytoliths and micro-hairs helped clarify taxonomic relationships among fossil grasses (Thomasson 1987). Similarly, the discovery of Kranz anatomy in certain fossil grasses increased our understanding of relationships among fossil and living grasses. Kranz anatomy, which first appeared in Miocene (ca. 25 MYA) grass fossils (Thomasson 1987; Hattersley & Watson 1992), is a distinct and easily identified arrangement of photosynthetic bundle sheath cells, and is diagnostic for the C_4 (Hatch-Slack) carbon fixation pathway. C_4 physiology is a taxonomically important trait because C_4 grasses only occur in the warm prairie and savanna-adapted Panicoideae, Arundinoideae, and Chloridoideae. C_4 physiology is not found in the tropical forest-adapted Bambusoideae or cool temperate-adapted Pooideae (Clayton & Renvoize 1986).

EVOLUTIONARY DIVERSIFICATION

Diversification occurred as grasses adapted to life in open terrestrial habitats (Clayton 1981; Renvoize & Clayton 1992). Key adaptations arising during diversification included the reduction in size and number of floral parts, the development of wind pollination, and morphological and physiological adaptations that allowed grasses to tolerate and even benefit from grazing pressure, fire, and drought (Stebbins 1981; Clayton 1981; Connor 1981; Coughenour 1985).

Floral and reproductive evolution

Analysis of living and fossil floral morphology supports the hypothesis that grass flowers evolved by reduction (Clifford 1961; Connor 1981; Stebbins 1981). The modern grass flower (floret) is typically wind pollinated and composed of three stamens, two stigmas, and a single-chambered ovary with two lodicules at its base. These structures are covered and protected by the lemma and palea until the flower opens (Clayton 1990). One or more florets attached to the same stalk (rachilla) and subtended by a pair of bracts (glumes) comprise a spikelet, and one or more spikelets comprise an inflorescence. By contrast, the primitive grass flower was insect pollinated and had three bracts, three lodicules, six stamens, three stigmas, and a one- to three-chambered ovary (Clifford 1961; Connor 1981).

Floral reduction is associated with the transition from insect to wind pollination (Clifford 1961). In the grasses it involved the reduction of stamen numbers

from six to three, two, or one, stigma numbers from three to two or one, and the reduction of the perianth (petals and sepals, collectively) to one to three small lodicules (Clifford 1961). Large, showy flowers, which function to attract pollinators, require a substantial energy expenditure to construct and maintain. Such attractants are not needed in wind-pollinated plants, and so are often greatly reduced or completely absent (Mauseth 1988). In this way, floral reduction resulted in a large energy savings for any species achieving it. The energy saved could be channeled into other maintenance or survival functions. However, while solving one set of problems, floral reduction created a different set of potential problems in grasses.

Small flowers make small targets for wind-borne pollen. In addition, grass pollen is the shortest-lived pollen among the angiosperms (Clayton & Renvoize 1986). While sometimes carried long distances by the wind, grass pollen is viable for only a few hours, resulting in an effective pollination range of a few tens of meters under most circumstances (Clayton & Revoize 1986). Further, grass flowers open for only 2–3 hours when they do flower, perhaps to minimize the introduction of pathogenic fungal spores during anthesis (Clayton & Renvoize 1986). These factors all reduce potential pollination success.

The grass inflorescence may have evolved to compensate for the reduction in the number of stamens and stigmas found in individual grass flowers (Clifford 1961). An inflorescence presents many more flowers, and a larger total cross-sectional area, to the wind than one individual flower could present. This increases the opportunity for wind-borne pollen grains to encounter a receptive stigma.

Other reproductive adaptations found in grasses include the development of cleistogamy (self-fertilization prior to, or in place of, flower opening) and apomixis (parthenogenic development of an unfertilized embryo) in some grasses, and a marked increase in vegetative propagation among many grass species (Clifford 1961). Cleistogamy, which occurs in at least 300 grass species (Clayton & Renvoize 1986), provides some opportunity for genetic recombination, though only through meiotic cross-over events. Apomixis, like vegetative propagation, is a form of asexual reproduction, producing offspring genetically identical to the parent (clones). While of little utility to fertile diploid individuals, apomixis may benefit polyploid species. Polyploidy often produces chromosomal mis-matches that result in partial or complete sterility. Apomixis may increase the prospects of successful reproduction in such species (Renvoize & Clayton 1992). Vegetative and apomictic clones can be at a competitive disadvantage when facing rapidly changing environmental conditions. However, like their parents, they are often very well suited to local conditions, a potential advantage when the habitat is stable and competition is fierce.

Co-evolution with herbivores

The co-evolution of grasses and grazing vertebrate herbivores was another important factor in grass evolution (Clayton 1981; Stebbins 1981). Grasslands and the hypsodont tooth first appeared in the fossil record about 60 MYA, during the Eocene (Stebbins 1981; Coughenour 1985). Since that time, grasses

evolved basal and intercalary meristems, a hardened lemma and palea to protect ingested seeds, and rhizomatous, trample-resistant sod. Grasses also shed the ability to produce defensive secondary metabolites (e.g., tannins, alkaloids) during this period. These co-evolutionary adaptations permitted horse-like mammals to utilize grasses as food, and grasses to thrive under a grazing regime that suppressed competing plant species (Clayton 1981; Stebbins 1981).

Coughenour (1985) noted that grasses existed as a distinct taxonomic group for "quite some time" before abundant grazers appeared, and has suggested that the adaptations attributed to grazing could have arisen in response to drought, competition, or the need for physical support rather than in response to grazing pressure. Nonetheless, the major grass adaptations attributed to grazing pressure appeared in the fossil record at about the same time as did vertebrate adaptations associated with a grazing habit (Stebbins 1981; Thomasson 1987), leading most authorities to accept the co-evolution hypothesis (Clayton 1981; Stebbins 1987).

Fire adaptations

Fire was a factor in grass evolution even before the appearance of vertebrate grazers (Clayton 1981). Fire benefits grasses by killing taller competitors, maximizing the light and nutrients that grasses can obtain (Weaver 1968). Annual production of grass litter increases the frequency of grassland fires, which reduces the overall fuel load and the maximum temperature of a grassland burn. Cooler-burning fires are less likely to damage basal grass meristems and subterranean grass roots and rhizomes, permitting them to rapidly sprout after a fire, intercept light, occupy space, and recycle nutrients before competitors can become established (Weaver 1968).

Drought adaptations

The climate in African, South American, and North American grassland regions shifted from warm, humid sub-tropical conditions towards cooler, semi-arid conditions between 25–60 MYA, during the Oligocene and Eocene epochs (Stebbins 1981). Several grass adaptations suggest that this climatic shift influenced grass evolution. Grasses evolved an extensive network of highly ramified roots, allowing them to efficiently scavenge moisture from the soil. When available soil moisture was insufficient to support metabolic processes, above-ground grass stems and leaves died. Grasses survived these dry periods in underground buds on roots and rhizomes.

Grasses also evolved the C_4 carbon fixation pathway during this period. C_4 grasses have a much lower CO_2 compensation point, the point at which photosynthesis equals respiration, than C_3 grasses (C.P. equals 5 parts per million for C_4 grasses versus 50 parts per million for C_3 grasses). This means that C_4 grasses maintain higher CO_2 diffusion gradients into their leaves than C_3 grasses. This is important because higher gas diffusion gradients permit C_4 grasses to maintain relatively high photosynthetic rates with partially closed stomata. Plants transpire less water with partially closed stomata than they do with fully-opened stomata. Thus, the greater CO_2 diffusion gradient in C_4 grasses results in greater

water use efficiency in C_4 grasses compared to C_3 grasses; that is, C_4 grasses used less water per unit carbon fixed than C_3 grasses. Greater water use efficiency confers a competitive advantage to C_4 grasses in hot or dry habitats.

Other physiological adaptations confer competitive advantage to C_4 grasses in hot or dry habitats. The optimal temperature and light levels for photosynthesis are higher in C_4 grasses compared to C_3 grasses. C_4 grasses are better adapted than C_3 plants to open terrestrial areas where hot, dry conditions and/or frequent fires have eliminated tall woody competitors.

The evolution of the C_4 pathway was one of the key adaptations that allowed Poaceae to dominate dry savannas and open tropical plains (Renvoize & Clayton 1992). C_4 panicoid, arundinoid, and chloridoid grasses were competitively superior to C_3 bambusoid and pooid grasses in hot, dry climates with high ambient light levels. However, C_3 grasses can compete effectively with C_4 grasses in relatively cool, moist, low-light habitats. The C_3 grasses, better adapted to cooler, more mesic conditions, became common components of forest-edge vegetation, and the dominant plants of northern and southern cool-temperate plains (Renvoize & Clayton 1992).

The absence of C_4 species in the Bambusoideae and Pooideae (Clayton 1981) and the morphological characteristics of known C_3-C_4 intermediates (Hattersley 1987; Hattersley & Watson 1992) support the hypothesis that C_3 tropical forest-edge grasses represent the ancestral condition in Poaceae (Renvoize & Clayton 1992).

Polyploidy

Polyploidy, the occurrence of more than two complete sets of chromosomes in a cell nucleus, has played an important role in grass evolution. Polyploidy occurs more often in Poaceae than in any other angiosperm family, with perhaps 80% of grass species having undergone a ploidy change at some point in their evolution (Stebbins 1985). However, the degree to which polyploidy has occurred in the grasses varies greatly among genera. Only 14% of species in the genus *Melica* have undergone a ploidy change, whereas 91% of all species in the genus *Stipa* have done so (Hunziker & Stebbins 1987).

Most plant polyploids are the product of sexually-functional non-reduced gametes (Harlan & de Wet 1975). Non-reduced gametes occur when homologous chromosomes pairs fail to separate during the final step of gamete formation, so the gametes carry a double complement of chromosomes. Fertile polyploids generally contain an even number of chromosome pairs (4n, 8n, etc.), though at least one fertile, permanent triploid grass species (*Andropogon ternatus*) has been documented (Hunziker & Stebbins 1987). The most common base chromosome numbers in Poaceae are 7, 9, 10, and 12, but base chromosome complements vary widely within the family, ranging from $2n = 6$ in one *Iseilema* species to as high as $2n = 265$ in *Poa litorosa* (de Wet 1987; Hunziker & Stebbins 1987; Stebbins 1987).

Polyploidy occurs either between species by interspecific or intergeneric hybridization (allopolyploidy), or within a species when genetically differentiated sub-populations of that species come back into contact and hybridize (autopoly-

ploidy by "secondary contact," Stebbins 1985). Hybridization often induces sterility. However, a ploidy change can sometimes restore fertility to otherwise sterile intermediates by doubling the chromosome complement following a hybridization event (Stebbins 1956).

The competitive advantage conferred by a ploidy change was once thought to take the form of greater resistance to temperature extremes or drought, or an enhanced ability to colonize new habitats (Stebbins 1987). It is now known that the impact of a ploidy change can be less apparent, and that not all polyploids are competitively superior (Stebbins 1987). Chromosome doubling by itself does not necessarily confer increased fitness. The mutations and hybridization events that often accompany polyploidy, or the genetic reconfiguration that often follows a ploidy change, are generally responsible for improvements in fitness (Stebbins 1987).

To a lesser extent, grass evolution has involved karyotype evolution. Reciprocal translocation, accessory chromosome alteration, mutation of repetitive DNA sequences, and transposition have all been linked to differentiation among grass species (Flavel 1986; Hunziker & Stebbins 1987), and the integration of transposable elements has been identified as a potential locus of evolutionary novelty (Hunziker & Stebbins 1987).

CURRENT STATUS

Research continues into the origins of the grasses, and new avenues of inquiry are being explored as new methods of investigation become available. Knowledge of the evolutionary relationships among the grasses will improve as new fossils are found, and as microscopic examination of existing grass fossils proceeds (Thomasson 1987). However, significant progress in this direction awaits the discovery of fossil intermediates that clearly link grasses to other monocots.

Investigators are using biochemical techniques to study taxonomic and evolutionary relationships among the grasses (Hilu 1987; Kahler & Price 1987; Chapman 1992; Soreng & Davis 1998). Molecular biologists have developed powerful tools to study the nucleotide sequences of RNA, and the nucleotide and gene sequences of nuclear and chloroplast DNA of living taxa. Evolutionary relationships can be deduced by comparing selected nucleotide or gene sequences among taxa and assuming that greater similarity between the taxa reflects less evolutionary divergence between them. These analytical techniques are being applied to the study of evolutionary relationships among living grasses, and may represent the best hope for uncovering the origins of the family.

Cladistic analysis is also being applied to Poaceae to improve our understanding of grass taxonomy and evolution (Kellogg & Campbell 1987; Kellogg & Watson 1993; Soreng & Davis 1998). Traditional taxonomic methods are based on morphological similarities (petal number, stamen count, ovary position, etc.) among taxa. Cladistics examines evolutionary similarities to determine taxonomic relationships. In cladistic analysis, evolutionary relationships (phylogenies) are determined by the number of evolutionarily recent ("derived") traits

shared among taxa; the greater the number of shared derived traits, the closer the taxonomic relationship.

Cladistic methodology can be applied to many different types of data. Cladistics has been used to study morphological character sets (Baum 1987), and rates of evolution in nucleotide sequences in chloroplast DNA restriction sites (Davis & Soreng 1993) and nuclear ribosomal RNA (Hamby & Zimmer 1988). Cladistic studies have generally supported the conclusions drawn from taxonomic evidence about the evolutionary origin of the family (Kellogg & Campbell 1987; Davis & Soreng 1993; Soreng & Davis 1998).

SUMMARY AND CONCLUSIONS

Grasses evolved as a distinct taxonomic group in the late Cretaceous or early Tertiary period. While exact taxonomic relationships are not yet known, the nearest living relatives to Poaceae are thought to be in the Joinvilleaceae, Flagellariaceae, or Restionaceae. Taxonomic evidence and cladistic analysis support the division of Poaceae into three evolutionary groups: the Bambusoideae, the Panicoideae /Arundinoideae /Chloridoideae, and the Pooideae, with the ancestral family line rooted in the Bambusoideae. Each of these groups evolved to become best adapted to a different set of environmental conditions, the bambusoids to tropical forests, the panicoids, arundinoids, and chloridoids to open savannas and warm prairies, and the pooids to cool-temperate habitats.

The fossil grass record dates from the Eocene, but contains no direct evidence of the links between Poaceae and other monocotyledons. Careful examination of existing fossils has clarified taxonomic relationships among living taxa.

Key evolutionary adaptations in the grasses include the reduction in size and number of floral parts, the development of wind pollination, and morphological and physiological adaptations that allowed grasses to tolerate and even benefit from grazing pressure, fire, and drought. Polyploidy, which occurs more often in Poaceae than any other vascular plant family, has had a great impact on grass evolution.

While the origins of Poaceae are not yet known, the addition of molecular techniques and cladistic analysis to our research tool box offers hope that we will one day fully understand the taxonomic relationships and evolutionary origins of the grasses.

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CONTEMPORARY PLANT SYSTEMATICS. By Dennis W. Woodland. Third edition, 2000. Hard-cover; xiv + 570 pages. Andrews University Press, 213 Information Services Building, Berrien Springs, MI 49104-1700. Telephone 616. 471. 6134. ISBN 1-883925-25-8. $64.99.

Plant taxonomy or systematics is an academic subject that may be taught in a number of ways. For each of these approaches, one or more suitable textbooks are available. Some plant taxonomy courses (such as the one I took at Iowa State almost 30 years ago) stress family recognition, teach-ing students the characteristics of major angiosperm families. Instructors of such courses might se-lect *Guide to Flowering Plant Families* by Wendy Zomlefer (University of North Carolina Press, 1994). Such courses may have a strong phylogenetic focus, examining both the processes of evolu-tion and the cladistic patterns of relationships they create. Instructors of such a course might select *Plant Systematics: A Phylogenetic Approach* by Walter Judd, Christopher Campbell, Elizabeth Kel-logg, and Peter Stevens (Sinauer Associates, 1999). For other students, taking plant taxonomy means that much of their time will be spent collecting and keying out species of the local flora. In doing so, they might rely on a field guide such as *Gleason's Plants of Michigan* by Richard Rabeler (Oakleaf Press, 1998). Yet other instructors emphasize principles and methods, teaching students the kinds of