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Grass Systematics and Evolution: Past, Present and Future

Abstract

New knowledge has greatly increased understanding of grasses as biological entities. The Poaceae occupy an isolated position among the Liliopsida (monocotyledons). The nearest related family is the monogeneric Joinvilleaceae. Grasses probably originated in open tropical savannas having seasonal drought, where the major subfamilies also differentiated from each other. The phylogenetic tree of the family is probably highly reticulate due to repeated cycles of polyploidy and hybridization. Morphological trends have been mostly bidirectional, although those within the spikelets and florets have been chiefly toward reduction. Mosaic evolution, consisting of different rates for different characters in the same line, has been common. Chromosomal diversification has consisted of increase in overall size, alterations of banding patterns, and structural rearrangements, both large and cryptic, at the level of hundreds or thousands of DNA base pairs. Various correlations suggest that increase in nuclear DNA content at the diploid level has at least in part an adaptive significance associated with differences in cell elongation and proliferation.

The contributors to this Symposium have provided ample evidence to show that the evolution of a major plant family can be better understood only by a true meeting of minds: a dialectic based on presentation, analysis, and synthesis of information from many sources. Following the lead of pioneers like Prat (1936), with respect to morphology and histology, and Avdulov (1931), with respect to chromosomes, the variety of different approaches to the evolution of grasses has steadily increased during the past half century, so that Poaceae are now one of the better known of major angiosperm families.

Moreover, the taxonomic synthesis has greatly broadened its base. In the 1920s, it rested almost entirely on morphological characters that could easily be seen in

dried specimens. Due to advances in histology, anatomy, chromosome cytology, embryology, and biochemistry of proteins and nucleic acids, as well as a broadened vista on ecological relationships and natural selection, botanists concerned with grass systematics and evolution can now regard species and genera not as piles of dried herbarium specimens but as living, evolving entities. In his opening address, Dr. Pohl has fully justified the thousands of hours spent in painstaking research that has brought this knowledge to light. Considering the widespread occurrence and ecological diversity of grasses, their dominance over vast regions of our globe, and their prime importance to humankind, we, the experts, may congratulate ourselves on having become authorities on the most important single family of organisms in the world of life, rivaled only by the human family itself.

Systematic Position, Age, and Origin of Poaceae

I shall not review all of the important points that have been brought up in this Symposium but shall confine my attention to those about which I feel most competent to pass judgement. In doing so, I shall emphasize the contributions that information about Poaceae can make to a better understanding of plant evolution in general. First, what are the relationships of the Poaceae? My answer to this question is essentially the same as in a recent publication (Stebbins, 1982). The family occupies an isolated position in the Liliopsida (monocotyledons). The only family sufficiently similar to serve as an "outgroup" for determining polarity of character states within the Poaceae is the monogeneric Joinvilleaceae (Tomlinson and Smith, 1970). The Restionaceae, which Campbell and Kellogg (this volume) recognize as a possible sister group, as well as the Centrolepidaceae and Flagellariaceae, are so much more specialized than the least specialized grasses in certain characters that they are useless for this purpose. As *Joinvillea* itself occupies an isolated position, and connections between it and families that have less specialized characters are obscure, the conclusion becomes inevitable that connections with other major families have been largely obliterated by extinction. Hence, it is highly probable that the position of Poales relative to other orders of the superorder Commelinidae (Commelinales, Cyperales) will always remain obscure, unless evidence from DNA and protein similarities can make it clearer.

Second, when did they evolve? Fossil evidence reviewed by Thomasson (this volume) indicates that the family may have first appeared in the Late Cretaceous (Table 15.2) (Santonian or Senonian ages). For many millions of years, however, they appear to have been relatively uncommon. In the Northern Hemisphere, fossil pollen and other remains do not become abundant until late in the Oligocene or early in the Miocene. They may, however, have become dominant much earlier in parts of South America. The Eocene mammalian fauna of that continent included species of grazers, similar though completely unrelated to modern horses (Patterson and Pascual, 1968). Although actual pollen, leaf, and seed fossils are scanty or lacking, soils dated as Eocene in age contain siliceous fragments similar to those found on contemporary grass leaves (Frenguelli, 1930; Andreis, 1972). Consequently, the first grass-covered savannas may have arisen in South America during the Eocene. The possibility cannot be excluded that savannas containing grasses also existed in Africa during the Eocene.

Third, where and under what conditions did the Poaceae become differentiated from other families? A common belief is that the earliest grasses were adapted to tropical rain forests (Bews, 1929). This belief is based on the fact that the Bambusoideae, usually regarded as the least advanced with respect to floral characteristics, are rain forest dwellers. In partial agreement with Tsvelev (1976, 1983), I have the following objections to this hypothesis. In the first place, all modern bambusoids are specialized with respect to various vegetative characteristics. These specializations differ greatly from one to another subdivision or from one genus to another (as between *Streptochaeta*, *Bambusa*, and *Anomochloa*). Forms intermediate between these genera are unknown. If the tropical rain forest were the center of origin, one would expect to find there not only diversity, but also occasional links between different groups. The actual situation is best explained on the hypothesis that the ancestors of the modern archaic, but not primitive, bambusoids entered the rain forest early in the evolutionary history of the family, and have remained there as stabilized relicts.

An even more important point, emphasized by Tsvelev, is that the earliest evolution of Poaceae as well as later differentiation involved adaptation to wind pollination. Hence they most probably originated in sites exposed to wind, such as open or semiopen mountain tops or slopes.

I find one difficulty with this hypothesis. The fossil record of vertebrates does not point to the existence of mountain-dwelling herbivores during the Late Cretaceous. As one of the most distinctive features of most Poaceae is the highly developed intercalary meristem at the base of their leaves, which enables them to regenerate after grazing, a logical assumption is that this manner of adaptation to grazing played an important role in the early evolution of the family. Consequently, a habitat containing large herbivores, such as many of the Cretaceous dinosaurs, would appear to be more likely. Open savanna habitats are an important feature of the landscape in some parts of the Amazon and Orinoco basins in South America. They are dominated by modern wind-pollinated monocotyledons, particularly Poaceae and Cyperaceae. Counterparts of these open habitat plant associations may well have existed during the Cretaceous Period and have

contained the original ancestors of their present inhabitants. The following scenario is suggested.

Poaceae evolved from *Joinvillea*-like ancestors in moist tropical or subtropical lowlands, where soil conditions favored herbaceous rather than woody vegetation, as in the llanos of the Orinoco Basin. Selection pressures for the origin of the most distinctive vegetative and reproductive characteristics of the earliest grasses could have been as follows. Heavy sympodial rhizome systems would provide resistance to the trampling of large herbivores. Regeneration after grazing, at least during moist seasons when the tropical sun would maintain high energy budgets of lowland plants, would be enhanced by greater development of basal meristems of their leaves. Increased silicification of epidermal cells would increase resistance to phytophagous insects. Condensation of compound racemes to form racemes of spikelets would not only intensify pollen clouds formed by simultaneous anther dehiscence, and so facilitate mass transport of pollen by air currents and moderate winds, but also increase the size of the target for the transported pollen. Transformation of a scalelike perianth similar to that of *Joinvillea* to fleshy lodicules would aid in opening and closing of florets in response to diurnal shifts in temperature and moisture.

Surely, several other scenarios are possible, and perhaps equally plausible. This one is presented to show that grasses could and probably did evolve in tropical or subtropical, continually or seasonally moist habitats in response to selection pressures that most probably existed during the geological period when they are believed to have first evolved.

Fourth, under what conditions and when did the subfamilies differentiate from each other? In the absence of a fossil record, this question is difficult to answer. Nevertheless, the pattern of genera in each of the seven major groups recognized in this Symposium indicates that at least four of them differentiated from a primitive and ancestral complex, now completely extinct, early in the evolution of the family. Small, relatively primitive and relictual genera occur in the bambusoids *(Streptochaeta)*, arundinoids *(Arundo)*, pooids *(Ampelodesmos)*, and eragrostoids *(Vaseyochloa, Swallenia)*. The other three major groups may be secondarily derived, the stipoids from the primitive pooids, and the panicoids and andropogonoids both from the arundinoids via *Arundinella* and related genera.

If this hypothesis is correct, the evolutionary "tree" of the Poaceae should be represented not as a typical tree having branches divergent from a main axis or "trunk," but a pattern intermediate between a much branched shrub and a *Hydrodictyon*-like network, as shown by Clausen (1951, Fig. 76) for the Asteraceae, subtribe Madiinae. Moreover, since most of the major groups, and even individual tribes, became independently adapted to increasing aridity and more efficient wind pollination, parallel evolution with respect to individual characteristics has taken place to a greater extent than in most other angiosperm families, and to a far greater extent than in any group of animals. As explained in a later section, genomic differentiation and allopolyploidy, like that which now prevails in the Triticeae, have been features of evolution in Poaceae ever since they originated, so the hypothesis of a reticulate pattern of evolution for the entire family is highly probable.

Phylogenetic Trends: Morphology and Histology

Based on earlier presentations in this Symposium, as well as extensive literature, a number of phylogenetic trends can be detected. Most of these trends are bidirectional. They are radiations from a postulated character state that is intermediate and primitive, rather than a steady progress in any particular direction. The principal bidirectional trends are summarized in Table 33.1.

With respect to growth habit and inflorescence, all of the general trends are bidirectional. They can be traced from a state that in general resembles the outgroup genus, *Joinvillea*, either toward reduction or toward elaboration. Reduction is by far the most common, which reflects the fact that during the Tertiary Period, when diversification was at its height, the new habitats available to occupation by grasses were increasingly dry, cold, or both. Under these conditions, different evolutionary lines would be expected to evolve in similar directions, giving rise to a multitude of examples of parallel evolution. In particular, the character states reduced annuals, filiform or linear leaves, few panicle branches, and in particular sessile as well as single-flowered spikelets have evolved independently so many times that they are virtually useless for interpreting relationships unless accompanied by other characters. Trends of elaboration include increased stature and secondary woodiness; extensive rhizome formation, from sympodial to monopodial rhizome patterns; increase breadth and secondary complication of leaf structure (pe tioles, diversified ligules, auricles, Kranz anatomica structure); increased number of panicle branches, partic ularly the emergence of several branches at a single node elongation of branches, particularly those that are slende and drooping; and an increase in number of florets pe spikelet (Stebbins, 1982). These trends have also occurre repeatedly, particularly in association with occupation more favorable or shaded habitats where vegetation dense and competition intense. Nevertheless, while th end points of reduction, particularly with respect to spik lets, often characterize entire tribes, those of elaboratio rarely do so, and are often confined to a single species or cluster of related species.

The genetic plasticity of grasses with respect to grow habit and inflorescence morphology is well illustrated the diversity found in some of the larger genera, such

TABLE 33.1. Bidirectional trends in grass morphology

Character	End points of reduction	End points of increase or elaboration
Overall size	*Micraira, Schismus, Scribneria, Vulpia, Muhlenbergia filiformis*	*Dendrocalamus, Arundo, Stipa coronata, Elymus condensatus, Saccharum, Imperata*
Clumping (caespitose) vs. spreading (rhizomes)	*Danthonia, Festuca* sect. *Ovinae, Muhlenbergia* spp., *Panicum* spp.	*Arundinaria, Phragmites, Ammophila, Spartina, Buchloë, Sorghum halepense*
Leaf breadth and vein number	*Danthonia* spp., *Stipa* spp., *Festuca ovina, Muhlenbergia* spp., *Schizachyrium* spp.	*Bambusa, Arundo, Elymus condensatus, Uniola latifolia, Zea mays*
Panicle branches and peduncles, number	*Danthonia unispicata, Brachypodium distachyon, Nardus, Orcuttia, Coleanthus, Monanthochloe, Muhlenbergia filiformis*	*Zizania, Phragmites, Elymus condensatus, Anthoxanthum, Zingeria, Muhlenbergia* spp., *Panicum capillare, P. maximum*
Panicle branches and peduncles, length	*Streptochaeta*, Triticeae, *Lolium, Scribneria, Nardus, Cynodon, Digitaria, Zea*	*Zizania, Bromus arvensis, Agrostis scabra, Muhlenbergia capillaris, Panicum laxiflorum*
Spikelets, floret number	*Streptochaeta, Chusquea, Olyra*, Oryzeae, Stipeae, Agrostinae, *Muhlenbergia*, Paniceae, Andropogoneae	*Brachypodium, Glyceria* sec. *Euglyceria, Pleuropogon, Eragrostis unioloides, Uniola*

Stipa, Elymus (s.l., including *Leymus, Elytrigia*, and *Psathyrostachys*), *Muhlenbergia*, and *Panicum*. In some of them, stature ranges: from 50 cm to 3 m in *Elymus*, from 15 cm to 2 m in *Stipa*, and from 10 cm to 120 cm in *Poa*. *Elymus, Muhlenbergia*, and *Panicum* contain densely caespitose as well as extensively rhizomatous species. Leaf breadth ranges from 1 mm to 4 mm broad with 16 veins in *Taeniatherum* to 3 cm broad with 75 veins in *Elymus condensatus*. All of these large genera exhibit a wide range of spikelet number per inflorescence, from 10 or less in dwarf plants of the smallest species to several hundred in such species as *Stipa robusta, Elymus condensatus, Muhlenbergia rigens*, and *Panicum maximum*. Similar diversity exists in number and length of panicle branches and of spikelet peduncles.

An unusual trend of elaboration occurs in the rachis of advanced genera of Andropogoneae *(Manisuris, Hackelochloa, Coix, Tripsacum)*.

Trends involving spikelets are fewer than those involving inflorescences and also have fewer examples of elaboration and parallelism. With respect to floret number, the 10 or 12 florets found in *Arundinaria* is as near to the original number as one can guess. Reduction from this number is almost universal. Higher numbers occur rarely, as in *Brachypodium* (15–20), *Eragrostis simplex* (20–50), and *Uniola paniculata* (10–20). With respect to glumes, reduction or elimination occasionally occurs, and elaboration is rare but occurs in *Orcuttia, Sitanion, Avena*, and a few other genera. Direction of trends in the lemma is similar. Rare examples of elaboration are in *Triticum* sect. *Aegilops* and *Neostapfia*. The palea is the most conservative appendage in the family. Variation in nerve number occurs in Oryzeae. In some species of *Agrostis* as well as a few other genera the palea is absent.

Evolutionary trends within the florets themselves are almost entirely reductional. Some of this took place early in the evolution of the family, such as reduction of stamen number. The original condition of six stamens in two whorls exists only in Bambusoideae and Oryzoideae; in all other subfamilies their number is four or fewer. In both lodicules and caryopses, reduction has been accompanied by divergence, so that its end point differs between subfamilies. The details of these trends have been discussed by earlier speakers in this Symposium, and I have reviewed them elsewhere (Stebbins, 1982).

Since the pioneer research of Prat (1936), histological characters have become increasingly important for distinguishing subfamilies and tribes. Nevertheless, as Ellis (this volume) has told us, evolutionary trends are difficult to determine. The Kranz type of internal leaf anatomy, associated with the derived C_4 photosynthetic sequence, originated probably in some ancestral genus of the heterogeneous group Arundinoideae, but present evidence does not permit a decision as to whether it had a single origin or several independent origins. Bicellular hairs, most characteristic of chloridoids (elegantly illustrated in this volume by Jacobs), panicoids, and andropogonoids, probably originated in the arundinoids, as they occur in *Danthonia* and other genera of that group. They are probably reduced from multicellular trichomes, similar to those in *Joinvillea*. Dumbbell-shaped siliceous cells have a similar distribution among tribes, and probably a similar origin. Short, bulliform siliceous cells, found in the pooid group, are reduced from the longer types found in arundinoids and bambusoids. They are another example of reductional trends that are more general in pooids than in any other group.

An important anatomical character is the rudimentary internode found in the embryo, which was investigated extensively by Reeder (1957). Trends in this character follow others in that reduction occurs in Pooideae and

TABLE 33.2. Mosaic conditions of character states in representative subfamilies of Poaceae

Subfamily	Primitive	Advanced
Bambusoideae	Apical reduction of spikelets; 3 vascular lodicules; 6 stamens; small embryo; short embryonic internode; generalized siliceous cells; bicellular hairs present; Kranz syndrome absent	Multiple branching at a node; leaves petiolate; complex rhythm of flowering
Oryzoideae	6 stamens; small embryos; Kranz syndrome absent; generalized siliceous cells	2 lodicules; bicellular hairs absent; basal reduction of spikelets; spikelets always 1-flowered; glumes much reduced
Stipoideae	3 lodicules; Kranz syndrome absent; small embryos	1-flowered spikelets; indurated lemma; 3 stamens; embryonic internode absent; reduced bulliform siliceous cells; bicellular hairs absent
Pooideae	Apical reduction of spikelets; small embryos; Kranz syndrome absent	2 nonvascular lodicules; 3 stamens; embryonic internode absent; bulliform siliceous cells; bicellular hairs absent
Eragrostoideae	Apical reduction of spikelets; generalized siliceous cells; bicellular hairs present	Frequent reduction of lemma nerves; 2 lodicules; 3 stamens; large embryos; embryonic internode elongated; Kranz syndrome usually present
Panicoid-Andropogonoideae	Bicellular hairs present	Basal reduction of spikelets; 2 lodicules; 3 stamens; large embryos; embryonic internode elongate; Kranz syndrome usually present; dumbbell-shaped siliceous cells

elongation in Arundinelleae, Panicoideae, and Andropogoneae.

The trends of reduction in Pooideae and elaboration in Eragrostoideae and Panicoideae-Andropogoneae probably are adaptations to the very different climates in which these groups are dominant. Particularly with respect to reproductive characters, reduction aids in rapid development and maturation, a rhythm that is of particular value in highly seasonal climates. On the other hand, elaboration of complexity may promote greater phenotypic plasticity, which in semiarid warm climates may help to adapt the plant to irregularities in the onset and end of moist seasons.

Mosaic Evolution in Poaceae

Among Poaceae, as among higher plants and animals generally, different characteristics evolve at different rates within the same evolutionary line. Nearly every taxon is a mosaic of relatively primitive and more advanced character states. Table 33.2 illustrates this situation in representatives of each of the major groups. Even in the more advanced ones, a few relatively primitive states exist. The degree of advancement of a particular taxon is expressed not in terms of the degree of advancement of every character, but in the proportion of primitive versus advanced states.

Two conclusions may be drawn from these observations. First, no extant genus is primitive with respect to all of its characters. The original common ancestor of grasses has long been extinct. Second, advancement is not based upon any internal urge toward evolutionary progress, nor upon any set of external conditions that causes natural selection to affect equally all of the characteristics of the plant. The Poaceae thus exemplify a general tenet of Darwinism and the modern synthetic theory of evolution: change is based on a combination of the action of chance and of natural selection that affects different characters unequally.

Nevertheless, Table 33.2 shows that with respect to advanced character states, the Bambusoideae are distinctive in that advancement affects vegetative characters and the rhythm of flowering more than the florets themselves. Nevertheless, as Soderstrom and Ellis point out (this volume), some of the trends observed within the bamboo subfamily are similar to those in other subfamilies, such as sympodial to monopodial type of rhizome, six to three stamens, and reduction from several florets to one floret per spikelet. On the other hand, one trend found in bamboos, from dry caryopsis to fleshy fruit, is not repeated in any other subfamily.

These differences are in accord with selection theory. In the tropical forest habitat, where most bamboos grow, competition among growing individuals is particularly intense, so that increased vigor and rapidity of growth has a strong selective advantage. On the other hand, the favorable flowering season extends almost indefinitely, so that there is no advantage for reduced floral parts that facilitate rapid flowering and seed development. The fleshy fruits of some bambusoid genera have a particular advantage in forests that harbor many species of frugivorous birds and mammals.

The adaptive significance, if any, of the different combinations of advanced characters found in the other subfamilies is hard to interpret. Many of them may have become established largely by chance in small populations, during the early evolution of these subfamilies. Nevertheless, the two groups that inhabit primarily cool climates (stipoid and pooid) share character states of siliceous cells, lodicules, embryos, and mature caryopses, while different states are shared by eragrostoid, panicoid, and andropogonoid subfamilies, which are better adapted to warm climates. More intensive research may reveal some adaptive significance for these differences.

Evolution of Chromosomes and DNA

The evolutionary significance of chromosomal changes has already been discussed (Hunziker and Stebbins, this volume) and so will be mentioned here only briefly. From the early pioneer research of Kihara (1924, 1940) to the elegant recent work of Dewey (1969, 1970a,b, 1971, 1975), Poaceae, particularly the tribe Triticeae, have served as models for the differentiation of genomes via major structural alterations of chromosomes. Chromosomal repatterning at the diploid level, accompanied or followed by polyploidy, has played a major role in the origin of grass species, and perhaps of genera. The issue of whether or not genera should be redefined so as to agree with individual genomes or recombinations of them is controversial. Its resolution via careful discussion among systematists and cytologists is urgently needed. In this connection, the fact should be pointed out that some pairs of species that possess different combinations of genomes, such as *Bromus arizonicus-carinatus* (Stebbins, Tobgy, and Harlan, 1944) and *Stipa cernua-pulchra* (Love, 1954) are so much alike in gross morphology that taxonomists have difficulty in separating them. Separating the members of these pairs by placing them in different genera would be highly confusing.

Grasses are also classic material for recognizing chromosomal repatterning at the molecular level of hundreds or thousands of nucleotide base pairs. The prophetic research of McClintock on transposition of genes among chromosomes of maize is now fully verified by more recent molecular research, and must be recognized as an important source of diversity (Flavell, 1986). I developed the concept of cryptic structural hybridity (Stebbins et al., 1946) based on the observation of high sterility in certain hybrids in spite of good meiotic pairing. Fertility follows somatic doubling using colchicine (Stebbins and Vaarama, 1954). It may be explained by the processes outlined in Flavell. If so, one must conclude that rearrangements at the nucleotide level have played an important role in the origin of the reproductive isolation that separates many grass species.

The problem of repetitive nucleotide sequences and the nature of the large amounts of noncoding DNA in many genera of grasses and other angiosperms is discussed by Appels, as well as Hunziker and Stebbins (this volume). First, differences in nuclear DNA content among species having the same chromosome number are subject to both phyletic increase and phyletic decrease, as is evident not only in Poaceae, but also in other families, such as Asteraceae, Fabaceae, Liliaceae, Plantaginaceae, and many others. The best documented examples of decrease in Poaceae are the specialized annual *Bromus pumilio (Boissiera pumilio)*, ($2C = 3.7$ pg) as compared to other diploids such as *Bromus japonicus* ($2C = 11$ pg) and *B. scoparius* ($2C = 9.7$ pg), and two related annual species of *Poa*, *P. infirma* ($2C = 2.4$ pg) and *P. supina* ($2C = 2.8$ pg) as compared to a related diploid perennial, *P. trivialis* ($2C = 5.6$ pg) (Bennett and Smith, 1976). The trend in *Poa*, reduction in DNA content associated with the shift from perennial to annual growth habit, is found in other genera of Poaceae *(Festuca: Scariosae-Ovinae)* and in Asteraceae and Boraginaceae among dicotyledons. On the other hand, annual species of *Secale*, *Lolium*, and *Hordeum* have nuclear DNA volumes similar to or even greater than related perennials.

The major trend in DNA content in the family as a whole is toward increase, even at the homoploid level. The outgroup genus, *Joinvillea*, has chromosomes of about the same size as those of Bambusoideae, Arundinoideae, and Panicoideae (Newell, 1969). Increase has taken place chiefly in Pooideae, reaching its maximum for diploid species in the genus *Secale*.

The correlation between increased chromosome size, now known to be correlated directly with nuclear DNA content, and adaptation to cool climates was already noted by Avdulov (1931). Bennett (1976) demonstrated a correlation among crop species of both Poaceae and Fabaceae between high DNA content and adaptation to progressively cooler climates. A similar correlation was recorded for different populations of a single species of Asteraceae, *Microseris douglasii* (Price et al., 1981). Grime and Mowforth (1982) noted a correlation between high DNA content and adaptation to a summer dry, Mediterranean climate. They suggest that increased DNA content helps species to grow better under the cool temperature regime that prevails during the moist winter season in such climates.

The meaning of these correlations, if any, is by no means clear. In every family in which they are found, exceptions exist. Among Poaceae, subfamily Pooideae, the most conspicuous exception is the stipoid group, which flourishes in Siberia and the high plateaus and mountains of both North and South America in spite of small chromosomes and low DNA content. If increased DNA content is an adaptation for existence in cool cli-

mates, it is only one of several evolutionary strategies for such adaptation. On the other hand, it is difficult to ascribe the correlations either to chance alone or to the parasitic behavior of extra DNA, as postulated by Doolittle and Sapienza (1980). Chromosomal mechanisms for eliminating excess DNA are postulated just as easily as for increasing DNA content, and numerous examples of (phylogenetic) decrease support the hypothesis that these mechanisms can operate if they are favored by natural selection. Moreover, one does not need to postulate that extra DNA is either intrinsically good or deleterious. The observed correlations suggest that changes in content are somehow associated with adaptive radiation.

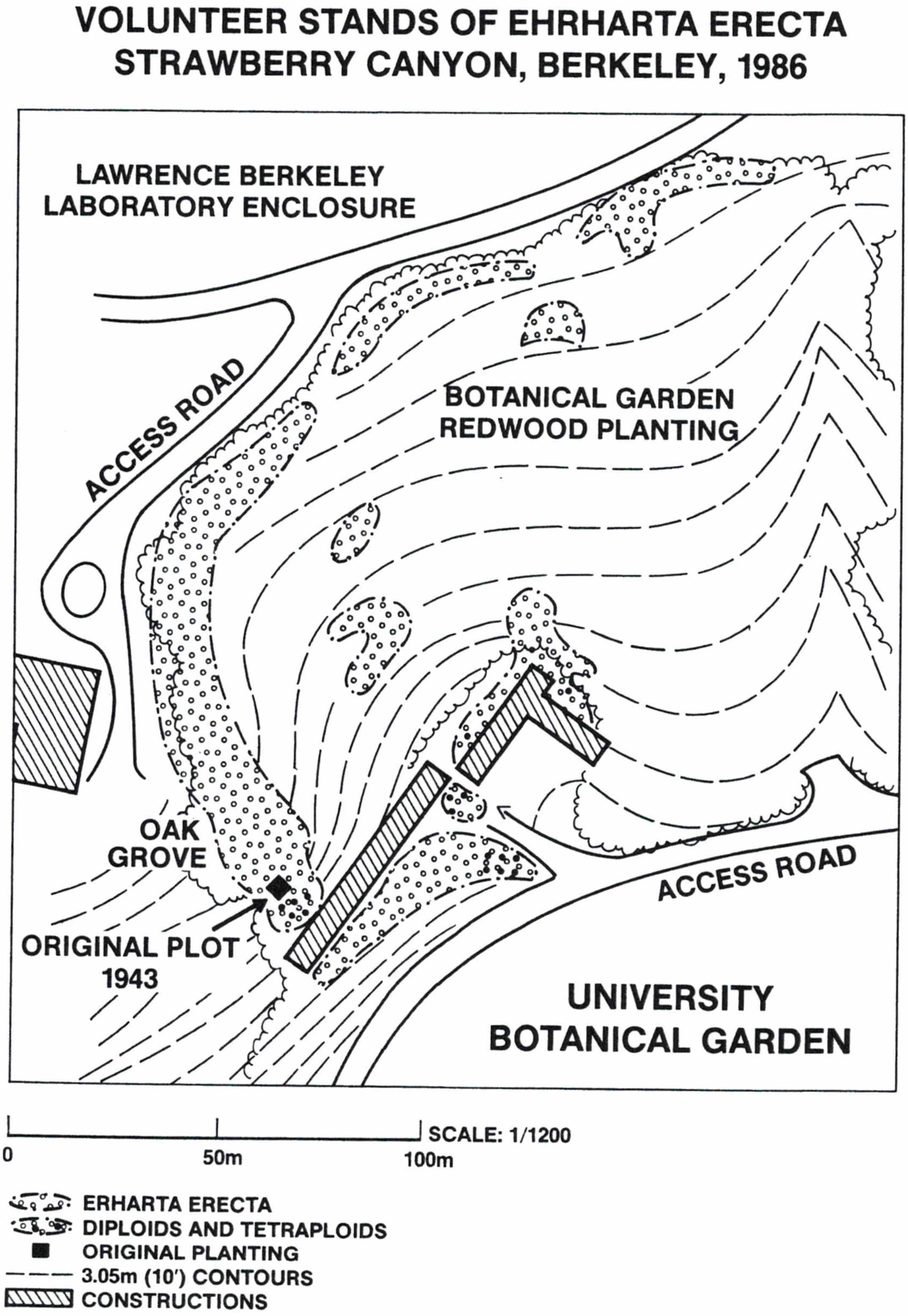
Nevertheless, a direct connection between overall DNA content and any climatic or edaphic properties is hard to imagine. The approach to this problem should be in two steps: (1) Determining relationships between nuclear DNA content and cell behavior, particularly mitotic rhythm. Various observations and experiments indicate that increased DNA content slows the mitotic cycle, particularly by lengthening the period before the onset of DNA replication, and the period of replication itself (Goin et al., 1968; Evans et al., 1972; Cavalier-Smith, 1978). (2) Once more extensive and quantitative data have been obtained on cellular metabolism and the mitotic cycle, the relationship between these characteristics and growth under various ecological conditions should be studied. In particular, the significance of variation between the proportion of size increase due to cell proliferation and that due to enlargement of individual cells should become better known. Among angiosperms, various species of Poaceae are favorable material for such investigations.

The C-banding pattern of chromosomes is particularly valuable in determining relationships within grass genera (Hsu, 1973). This has been carefully analyzed in representative species of *Festuca* by Janice Dawe (unpubl. ms.). From an initial pattern including C-bands in only a few chromosomes in the relatively unspecialized sections—*Scariosae*, *Subbulbosae*, and *Montanae*—two divergent trends of specialization have been recognized. One, leading to the section *Bovinae* and exemplified by *F. pratensis*, consists of a great increase in intercalary heterochromatic bands, so that the mitotic chromosomes of *F. pratensis* are much like those of *Triticum* species. The second trend, highly developed in sections *Ovinae* and *Variae*, involves evolution of large bands of terminal heterochromatin at the distal ends of the chromosomes. Both trends are associated with reduction in overall chromosome size, the reduction being particularly evident in *Ovinae*. Similar trends have been recognized in other plant families. The presence of parallel trends of this kind in several unrelated families is hard to justify on the basis of chance, so that a connection with adaptive physiological properties should be sought. The most likely clue suggests that relationships should first be sought between banding patterns and cell metabolism, particularly cell enlargement and proliferation.

Finally, the significance of the high incidence of polyploidy among Poaceae must be considered. My comments on this topic are an extension of those made in a recent review (Stebbins, 1985). First, new observations were made in 1986 on the now 43-year-old experiment of establishment and relative success of diploid and colchicine-induced autotetraploid *Ehrharta erecta* on a seminatural hillside in Berkeley, California. The results shown in Figure 33.1 amply confirm the conclusion reached earlier, that in Poaceae generally, and probably in most other angiosperms, polyploids produced directly from a single diploid population are usually and perhaps always inferior to their diploid progenitors in their ability to invade and establish themselves in new habitats. The evolutionary success that many polyploids have attained is due not to chromosome doubling itself, but to genetic alterations that accompany or follow the doubling process. The most important source of alteration is hybridization, either between adaptively different populations of the same species, or between different species. Hybridization between differently adapted populations is a radical, disruptive process, especially with respect to segregating progeny. Chromosome doubling counteracts this disruption. In autopolyploids, it does so by means of the buffering action of tetrasomic and other more complex forms of genetic segregation. In allopolyploids, stability is achieved by preferential pairing of structurally similar chromosomes, often aided by the action of specific genes (Stebbins, 1985).

Another important point is that only a fraction of natural polyploids are more successful invaders than diploids of the same genus (Stebbins and Dawe, 1987). This fact points to a highly favorable opportunity for understanding why some polyploids have been particularly successful. In a genus like *Festuca*, which in Europe contains closely related polyploid species, some widespread and others highly restricted, analyses of the genetic properties and origins of differentially successful polyploids would expand greatly our understanding of the reasons for the success of many polyploids.

As discussed elsewhere (Stebbins, 1985), strong indi rect evidence exists in favor of the hypothesis that cycles o polyploidy, including allopolyploidy, have occurred re peatedly during the evolution of Poaceae. The lowes somatic number known in the Bambusoideae anc Oryzoideae, $2n = 24$, may be of ancient polyploid origin a are the numbers $2n = 20$ and $2n = 18$ found in panicoids. I this is so, then phylogeny of the entire family is to som extent reticulate. Extinct genera may well have containe combinations of characters that do not exist in any mod ern genus. This likelihood should be considered seriousl by those who are erecting hypothetical cladograms for th family or for any of its subdivisions.



VOLUNTEER STANDS OF EHRHARTA ERECTA
STRAWBERRY CANYON, BERKELEY, 1986

FIGURE 33.1. Map showing the increasing spread of diploid *Ehrharta erecta* since its initial establishment in Strawberry Canyon, University of California, Berkeley, and the relative stagnation of the colchicine-induced autotetraploid. Base map kindly supplied by the Lawrence Berkeley Laboratory.

Prospects for the Future

With respect to classification at the level of genera and tribes, the Poaceae have now become one of the better known of major plant families. The various modern systems that have been proposed and reviewed in this Symposium agree with each other in their general organization. Improvement is always possible, nevertheless. As reported by Conert (this volume), the major remaining problems concern the subdivision into more natural groupings of genera now placed in the arundinoid group. The analyses of Conert as well as Kellogg and Campbell (this volume) are a fine beginning. They should be supplemented by results from newer techniques; in particular, comparisons between both nuclear and chloroplast DNA sequences of these critical genera would provide much valuable information. For the family as a whole, these techniques plus comparative sequencing of various protein molecules would provide valuable tests of the naturalness of present systems.

With respect to chromosome numbers, biochemical techniques, particularly enzyme analyses that would reveal the presence or absence of duplicate gene loci, would be the soundest approach to settling the problem of whether the gametic number of $x = 12$, which is predominant in modern genera of bambusoids, oryzoids, and arundinoids, is basically diploid or has been derived by ancient polyploidy from $x = 6$ or $x = 7$.

The problem of the 20-fold or even 30-fold difference between extremes among diploid species with respect to nuclear DNA content is one of the more challenging topics in basic problems of evolution. Clearly, these differences have nothing to do with multiplicity of different kinds of genes or with complexity of developmental patterns. They may be in part due to the many-fold repetition of transcribable, essential DNA sequences, but such a function is hard to imagine for most of the DNA present in genera having very large chromosomes, such as *Secale*. On the other hand, the various correlations with differential adaptation to climatic and edaphic factors render highly improbable the hypothesis that increase in DNA content has nothing to do with adaptation, being simply due to chance or to parasitic behavior. The cytologist is almost driven to the hypothesis that in many genera of Poaceae and other angiosperms, a large amount of DNA has a physiological function apart from transcription of RNA, and that for this function the nucleotide sequence is of secondary importance, and in the absence of constraints can evolve very rapidly. A resolution of this problem is very much needed and will most probably be achieved via a combination of comparative investigations in cellular biochemistry and physiology of cellular metabolism.

The age of the family and its subdivisions may be uncertain for some time to come. The investigations of Thomasson (this volume) and other paleobotanists have greatly improved our knowledge of the more recent evolution of the family, but its earlier evolution remains vague and hypothetical. Further progress is most likely to come via discoveries of fossil beds in other continents and from earlier geological epochs that are as rich in grass fruits and microscopic leaf fragments as are those of the central North American plains. Particularly important would be Eocene or older remains from South America or Africa.

The presentations made during this Symposium have shown that the systematics and evolution of grasses is a fruitful, ongoing area of research, the results of which have been and will continue to be of great value to scientists interested in plant evolution, the origin of some of our major food plants, as well as the origin and maintenance of our grasslands—the major resource of food for livestock. As evolutionary science advances and new techniques become available, new and striking results will emerge from this research in the near as well as the distant future.