8

Some Botanical Consequences of Tectonics and Orogeny

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1. The Gramineae of South Asia

A study of the members of the major plant family, the Gramineae/Poaceae, provides an opportunity, in South Asia in particular, to relate or calibrate the various botanical processes involved in their evolution with regionally significant geological events of a tectonic or orogenic nature. This chapter is primarily concerned with the known or presumed facts of the evolution of cells and nuclei, which must be regarded as fundamental to the morphological and physiological manifestations of botanical evolution, especially speciation, over the geological ages concerned. The emphasis is upon what cytology can contribute to such a broad evolutionary study, rather than upon the minutiae of cell and particularly nuclear structure and behaviour, which are primarily the interest of laboratory cytologists—using appropriate species of the Gramineae as botanical *Drosophilas*.

The grasses of South Asia have already been classified into the subfamilies, tribes, genera, species and other groupings accepted by the taxonomists [12, 37]. It is, however, possible to propose an alternative or supplementary classification, distinguishing in this between species that arrived in South Asia from other regions on tectonic plates or along migration routes, or which evolved (speciated) on the plates or later within the region, in the infinite variety of palaeoclimatic conditions which were created by the geological events, which occurred in or adjacent to the South Asian region. A major fact to be considered in this connection is that, the origin and early evolution of the grass family had not occurred when the rafting of the South Asian Plate from East Africa had begun.

The groups within the gramineous flora of South Asia may be briefly summarized as follows:

a) species of East African/Madagascan affinity, which crossed on the South Asian Plate between the beginning of rafting (late Cretaceous) and collision with Laurasia (Eocene) (See Sec. 2.1 below);

b) the species of the Deccan Plateau which evolved from the above in the rainshadow of the eastern crest of the Western Ghats,

c) xerophytic species of the north-west of the region, which arrived from north-east Africa and the Near East after the establishment of new drought conditions in or following the Eocene;

d) groups of species which became established down to specific contours in the Himalaya and associated ranges, having come from the north (Siberia through Innermost Asia) or the west (Irano-Turanian region).

The grass evolutionist asks the cytologist for evidence which may be available or is still to be found, of genotypical response (especially cells and nuclei) to the great environmental changes which occurred from the geological period under review. What are the cytological criteria for primitiveness, to supplement the morphological and physiological; what are the accepted original stages of evolution of polyploidy [83] and their changes of chromosome complements, and of apomixis; what is the evolutionary significance of isozymes in the cells of wild and cultivated grasses; how do plants (cells) change their photosynthetic pathways as a reaction to progressive exposure to changing environments and altitudes, particularly to ever-increasing aridity in hot and cold climates; what is the cytology of endemism? All these processes of cell structure, physiology and reaction are concerned in the ultimate genetical nature (adaptation) of progeny which arose from the millennia of speciation, which occurred in the grasses of South Asia.

After consideration of some of these questions, necessarily brief in the space available, * case studies relating to some of the above groups of grasses or to individual genera and species, wild and cultivated, will be presented to indicate trends in current research on the cells and their genetical expression and response.

2. Origin, Evolution and Speciation

2.1 GEOLOGICAL AGE AND PLANT SPECIATION

This chapter is based on the acceptance of the theories of plate tectonics rather than those of the expanding earth [58], which are most difficult to reconcile with the known and theoretical aspects of plant biology. The geological facts relating to the movement of the South Indian Plate and the sequence of palaeoclimates are known. From the late Cretaceous onwards, the plate began its long rafted journey (over 50 million years) from a position adjacent to Madagascar and East Africa up to collision, following a 25° change of main axis, and the subsequent probable reduction in overall length of some 2,000 km [174], with the landmass of Laurasia in the Eocene.

The choice of the Gramineae for this study is appropriate, because the whole evolution of that plant family took place during the same period. It is stated that the Gramineae first appeared in the Paleocene, followed in the Oligocene by fossil spikelets of *Stipa*, coincident with the first appearance of high crown teeth in fossil mammals [34]. In calibrating the geological history (and consequent palaeoclimatic history) with the origin and evolution of one plant family, it is necessary to consider current theories regarding the possible ancestors of the Gramineae and the development of primitive forms. There is a need for data on the cytology and consequent genetical behaviour of the first primitive and later more evolved forms of the Gramineae. For example, what are the morphological, physiological and cytological criteria for primitiveness in monocotyledons and/or Gramineae in particular (see Sec. 2.6)?

At this point, it is necessary to refer in passing to alternative views of the place of origin of the grasses—that of C.E. Hubbard, N.L. Bor and repeated by Clayton [34] that the grasses arose in or near the edge of the tropical rainforest, and that of G.L. Stebbins [144] and personal communication (1986), that the grasses arose in the semi-arid savanna and migrated back to the rainforest or

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*The author had planned to take up his long-term study of the Gramineae of Asia in 1987, beginning with a contribution entitled: A Geological Classification of South Asian Grasses, to the second Conference on the Palaeoenvironment of East Asia, Centre of Asian Studies, University of Hong Kong, 9-14 January. He then envisaged starting a book-length work, which would include the conclusions he had reached on the origin, evolution and present status of the Gramineae of Asia, based on over a lifetime's study of the subject, and which would also discuss the views of colleagues from all world, in the form of personal communications, reprints and publications.

out into other semi-arid and more arid environments. Most authorities relate the origin of the grasses to the Commelinales in general and the Flagellariaceae in particular, plants of the tropical forests [33].

> "Now the Bambusoideae, a subfamily defined by certain anatomical peculiarities such as fusoid and arm cells, is both tropical and primitive. Primitive in the sense that some genera have incomplete suppression of axillary buds in the inflorescence and spikelets, and the flowers may retain trimerous symmetry. Among them is a group of small tribes (e.g. Olyreae) known as the bamboo allies, which paradoxically combine the primitive and baroque. This collection of curios, apparently the relics of ancient departures from the mainstream of grass evolution, gives some hint of the diversity that must once have existed in the ancestral stock. They are mostly insignificant broad-leaved inhabitants of the rainforest ground layer, which are often mistaken for other forest families such as Zingiberaceae. By contrast, their near relatives, the true bamboos have become successful competitors in this environment by developing woody tissue and adopting the form of trees."
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> The most likely grasses which first moved from the forest into savanna, "belong to the subfamily Arundinoideae, for this is also primitive; primitive in the sense that it lacks distinctive features, but seems rather to represent the lowest common denominator of subsequent subfamilies. Its notoriously difficult taxonomy suggests that it is now reduced to dismembered fragments around a core which has become extinct.
>
> "Subfamily Chloridoideae is easy to place, for it abuts onto Arundinoideae, and indeed the boundary between the two is difficult to establish. It ushers in a new development, the Kranz syndrome. This is a set of anatomical characters associated with C_4 metabolism, in effect an extra loop in the photosynthetic cycle (the basic form of which is known as C_3), that renders it more efficient in high temperatures [154, 160]
>
> "Subfamily Panicoideae presents more problems. It has also evolved the Kranz syndrome, in fact two different versions of it (the MS and PS types of Brown, [15]), but some genera of Paniceae still retain the older non-Kranz anatomy and C_3 metabolism. Moreover, there are no direct links between the main tribes, Paniceae and Andropogoneae. The situation is still rather confused.
>
> "Finally, subfamily Pooideae seems to represent a new venture for the grasses, an adaptation to cold climates and invasion of the temperate steppes. It has retained the primitive C_3 pathway, for the more advanced form offers no advantage in a cool climate. This suggests a relationship with Arundinoideae, a few of whose genera have shown their ability to penetrate deeply into the temperate zone" [33].

In the present context, one must ask whether the initial stages of evolution of the Gramineae had begun before the South Asian Plate had been biologically separated (that is, 2,500 km away) from the African mainland and Madagascar, and if so, how far had it progressed from the primitive begin-

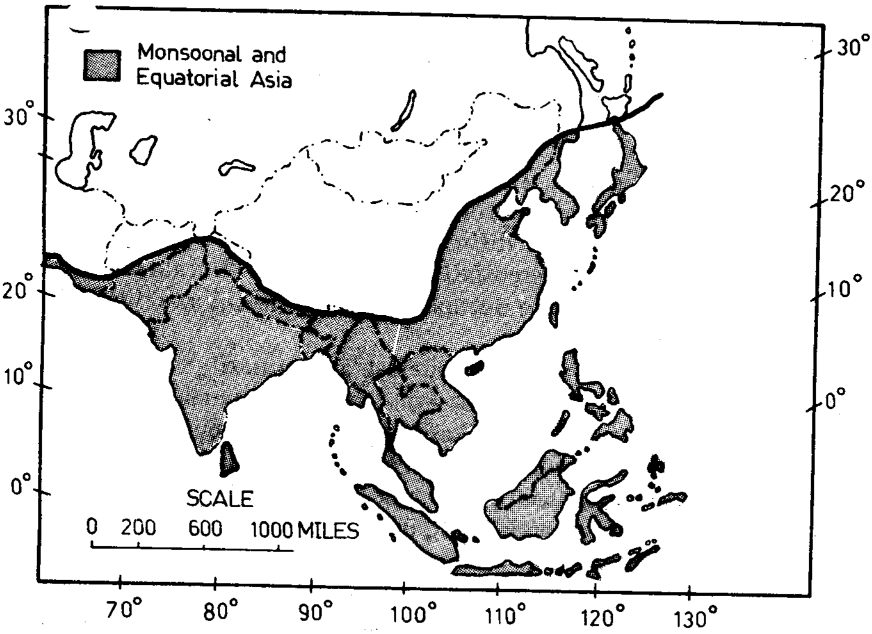

Figure 1.

nings. Did subsequent evolution through the early stages of the Tertiary follow parallel lines on both the African mainland [13, 20, 21, 52] and the Plate?

Were the several cytological and genetical phenomena of the South Asian grass flora introduced at progressive stages with exposure to the ever-increasing moisture stress characteristic of the geologically induced palaeoclimates—abnormal meiosis, aberrant chromosome composition, polyploidy, apomixis, adoption of new photosynthetic pathways, types of isozymes, etc? In brief, how much of the speciation which occurred is a reflection of genotypic response to continuously changing environments, and how much to adjustments (progressive or mutational) in the basic cytological composition and genetical behaviour of the species involved [75, 149]? Nagendra Prasad and Janaki Ammal (1985) found that speciation "is occurring at a fantastic speed in the diploids of Silent Valley, Kerala", a relict of original virgin forest. It would be interesting to conduct observations on cell genetics among the Gramineae (particularly the possibly ancient aquatic or semi-aquatic types described for Sindhudurg District in the Western Ghats) [1].

In assessing the significance of palaeoclimatic change in the evolution of the Gramineae, it is necessary to consider the possible sequence of palaeoclimates, which existed on the plate before and during its movement from Africa to Laurasia. Were there, then as now, arid regions in Madagascar [115] and therefore also on the Plate? Were vestiges of these initial arid regions retained as the Plate crossed the Equator, or were they and their vegetation cover replaced by one adapted to a climatic sequence subtropical/equatorial/subtropical?

2.2 STRESS

Consideration of the effect of stress on speciation [82] involves a decision between two markedly contrasting outlooks on the whole question of the reaction of the genotype to environmental change.

In their study of floral differentiation in *Triticum* Frankel and Roskams [49] state that "the reproductive organs of plants as a rule are effectively buffered against genetic and environmental perturbation" and that it is this constancy which is the main difficulty in research into the genetic and physiological control of differentiation of reproductive organs. Variations which might help to make the normal better understood are thought to be rare and destructive.

This view is that, abnormalities at meiosis are primarily expressions of the genotypical composition of the plant—that they are due to the action of genes governing degrees of *absence* as well as *presence* of biochemical characters or substances, to so-called innate genetic imbalance, or sterility loci and alleles determining sterility, to autonomous genetic systems of the organelles and interaction between mitochondria and nuclear genes, to a locus (Ph) on the long arm of a chromosome [41], to the genetic regulator [72] to the effect of the 5BS chromosome on the duration of meiosis [7], or to the location of the Ba gene which plays a major role in the control of normal floral development [48].

On the contrary, it is necessary to ask, first whether and under what conditions and in which particular species, abnormalities during and after meiosis can be regarded primarily as an expression of reaction to various forms and intensities of environmental stress. That stress would be caused by insufficiency of water and of soil nutrients and by the presence of high and fluctuating temperature, before and during the period of flowering. Stress operates on the uptake and movement within the plant of the crude nutrients, which are precursors to the complex biochemical substances essential in the formation, development and maturation of the germ cells. The nature, direction and rate of that movement are governed by the specific vascular structure in the stems and within the flower or inflorescence.

With this interpretation, physiological, morphological and biochemical factors are seen as governing the degree to which the genotype or the particular genetic system may be permitted or induced to express itself in overall reproductive efficiency and in the production of normal or abnormal gametes and zygotes, according to the combination of conditions obtaining at any particular time and place.

Unfortunately, it would appear that those who study cytological reactions and genetical consequences of various forms of stress stop short of examining conditions of nuclei and chromosomes in mitotic and meiotic divisions. Petolino and Collins [106] have reviewed the literature (182 references) on cellular approaches to the obtaining of response to environmental stress in plant breeding; stress due to water deficiency (see [70]); excessive temperature and the presence of excessive salt and metals. Reference is made by Petolino and Collins [106] to the use of cellular selection techniques by cell lines of haploid and diploid *Nicotiana* and *Capsicum* with enhanced response to chilling temperatures. The cellular selection resulted in alteration of mitochondrial activity, known to be related to temperature tolerance in whole plants [40]. It appears that the increased chilling response was epigenetic in nature. Exposure of tomato plants to low temperatures during pollination and fertilization resulted in the differential survival of the gametophytes with cold-tolerance genes. Only those pollen grains able to germinate and elongate under low temperature would function in fertilization and contribute genes to the progeny [175].

Important research on water stress is in progress at the Central Arid Zone Research Institute, Jodhpur, Rajasthan, regarding the effects on both growth and yield, but again, without reference to the normality or abnormality of mitotic and meiotic cell divisions basic to the expression of this measure of economic production [51, 79, 80, 165].

Canadian workers have evaluated tolerance of cobalt, copper, nickel and zinc in clones of *Agrostis gigantea* [68] and in *Deschampsia caespitosa, Hordeum jubatum* and *Poa compressa* [116].

Many observations have been made on plant growth and reproduction without sufficient concern for the basic mitotic and meiotic cell divisions to which these are the ultimate manifestation. Grime [55, 56] has applied his hypothesis of plant strategies to experiments on flowering response to drought stress in species of *Urtica* [11]. Grime has proposed that differences observed in plants coincide with lower xylem water potentialities and higher mortalities in *Urtica urens,* and is consistent with plant strategy theories reflecting life history and reproduction to frequency of habitat disturbance.

Rozijin and van der Werf [120] have studied effects of drought treatments applied in different stages of the life cycle and allocation of biomass in the vegetative and reproductive phases of winter annual species of the genus *Aira.* Biomass allocation showed greater differences between species than between the treatments, especially in the reproductive phase. The proportion of biomass allocation to reproductive organs was affected by the drought treatments, but there is no reference to actual cytological response.

2.3 ISOHYETS AND CONTOURS

Boundaries between major geological ages are of great significance in biological evolution—for example, the Cretaceous/Tertiary mass extinction of fauna, major changes in type of vegetation (gymnosperms to angiosperms). But these are not so relevant to the history of the Gramineae in South Asia, as the many boundaries between one type of ecoclimatic condition to another. These have been and are still being of great significance in the cytogenetical evolution of the grasses. Examples are:

a) isohyets of the north-west of the region, ranging from the low, spasmodic and biologically ineffective rainfall of the western zones credited with, say, 10 cm of rainfall per annum, to the zones with reasonably adequate monsoonal rainfall;

b) the crest of the Western Ghats, where rainfall drops so markedly on the eastern side;

c) altitudinal contours in the mountains of the north and in the Nilgiris and other lesser mountains.

After the initial creation of new boundaries following the catastrophic introduction of arid conditions in the Eocene and the later establishment of the rainshadow on the Deccan Plateau, the borders between arid and semi-arid and the more humid would have fluctuated in relation to relatively minor climatic changes. The high rate of speciation caused by the effect of excessive physiological stress on the genecological composition and behaviour of grasses following the Eocene became much reduced with the establishment of a reasonably stable but fluctuating monsoonal pattern. The efficiency of the light rains of the arid and semi-arid areas became much less later, with the advent of man as an agent in general devegetation, and the renewed exposure of grass species to high intensities of desiccation at the ground level. The effect of the environment on the genotypes at this time was expressed by increase in the proportion of progeny of perennials adapted to greater stress, or by the increase in the proportion of drought-escaping annuals, now cytologically and genetically fixed and unable to revert to the perennial state.

There are in the Himalayas and associated ranges a number of contours which represent climatic and vegetational boundaries (see [86, 110, 111], for a comparison with European conditions), which have had and to some extent still have, a considerable significance in grass distribution and speciation. In the interpretation of species distribution along altitudinal gradients [66], three borders in these mountains are of primary significance and call for extended research on the cytology of the grass species involved:

a) the border between monsoonal and humid-temperate environments

b) the border between humid (cold) temperate and the alpine semi-arid (cold)

c) the upper border between alpine semi-arid and high alpine arid.

The most significant of these boundaries in the present connection is the first, generally around 2,000 m contour. This may be said to be the limit of tolerance of humid temperate conditions by monsoonal species and the lower limit of tolerance of monsoonal conditions by the grasses of the humid temperate environment.

Basing conclusions on the study of the cytology of the Gramineae from lower to higher altitudes in the north-western Himalaya, north of Chandigarh, P.N. Mehra (personal communication, 1973) considers that variability in populations of a species at both the taxonomic and cytological levels is most likely, as one approaches the ecoclimatic borders of its distribution; in other words, that stress at the peripheral portion of distribution may accentuate the intensity of variation. Abnormal meiosis is ascribed to such causes as environmental factors, extensive vegetative multiplication, browsing by animals, and "genomic instability as reflected in the various meiotic aberrations and subsequent production of sterile pollen." It has, however, been noted that certain variations in ambient temperatures do affect meiosis, and lack or excess of critical elements in the soil may well do likewise.

Mehra and Ramanandan [90] recorded meiotic aberrations in different degrees in 13 out of 28 species and recorded comparative morphology of the intraspecific cytological races of 28 species of grasses (Pooideae) of the western Himalaya, collected at elevations ranging from 1,500 to 4,300 m. These are species of temperate genera, occurring here at one of the southern limits of their south Asian distribution, few of which set seed; if they do so, the seeds are mostly sterile.

A companion paper on the Panicoideae [91] describes the cytology and distributional pattern of 23 species at or near their altitudinal limit on the monsoonal/temperate border in the western Himalaya (Chandigarh/Simla); in only five of the species examined is some degree of disturbance at meiosis recorded, an interesting contrast with the Pooideae. Again, in a study of species of the Andropogoneae and Paniceae in the central and eastern Himalaya (Nainital and Darjeeling respectively) Mehra and Sharma [92, 93] report a high degree of disturbance of meiosis only in a pentaploid of *Pennisetum orientale*. Among the temperate species of the western Himalaya, partial or complete breakdown of meiosis is noted in *Poa alpina, P. bulbosa, P. nemoralis* and *P. pratensis* [94].

For the further clarification of the nature of the genotypic response to the climates of increasing altitudes in these mountains, it will be necessary to conduct cytological field studies of grasses of temperate adaptation along altitudinal transects. These would extend from the lower contours at the limit of their tolerance of monsoonal conditions, up through elevations of maximum adaptation promoting normal growth and reproduction, to the higher levels where physiological and cytological reactions are limited by intolerance of the semi-arid cold.

2.4 ALTITUDE

If any species of the Gramineae were growing in the southern parts of Laurasia during the Oligocene and subsequent geological ages, along the northern shores of the Tethys, they must have experienced a very unusual sensation, the rise of the ground beneath their feet, as it were. They progressively faced the uplift of their environment from an initial average 1,000–2,000 m altitude in a tropical to subtropical environment, to altitudes extending up to 8,000–9,000 m in a humid-temperate to cold-arid environment.

In plants facing such environmental changes, disruption of meiosis (reproduction) will probably precede cessation of mitosis (growth) in the somatic tissues. To cope with this situation, plants would need to have the capacity *either* to migrate down to elevations which could still provide the environmental conditions to which they are adapted physiologically and genetically, *or* they should have the capacity to produce, within the range of variation in their progeny, a certain proportion of viable offspring, better able to grow and reproduce in progressively more extreme environments, variation within the total genotypical scope of the species.

Escape mechanisms would include characters of types with greater physiological response (speciation), higher polyploidy from lower ploidy populations (see Sec. 2.7); types with changed photosynthetic pathways, or capacity to produce certain porportions of annuals (therefore winter- and/or drought-escaping) from predominantly perennial and thus less viable progeny [113].

2.5 ENDEMISM IN THE GRAMINEAE

In discussing speciation as the main driving force of chorology, Clayton [31] states that "one of the traditional approaches to the problem is through endemism, and attmepts to distinguish between centres of origin and refugia. The frequency of one-country endemics has been mapped by Clayton and Cope [35], revealing classical centres in Fouta-Djallon and Ethiopia, but elsewhere the pattern is very confused. The highest counts occur in South Africa, Madagascar, Peninsular India, South-East Asia and Australia, where isolation is clearly an important factor. Otherwise, they are strongly correlated with mountain topography (the pediplain of the Congo-Zambezi watershed is an unexplained exception), and form long chains rather than discrete centres. In short, the concept of endemic centres, at least in its simple form, is shown to be somewhat naive and not particularly helpful. The geography of speciation remains an open question, but I would suggest that the striking difference between the mountains and the plains lies not so much with active speciation in the former, as with ruthless extinction in the latter."

Endemics are regarded as having one restricted region or area of distribution. There are two types [81]:

a) a young species or genus which may not yet have attained its maximum area as determined by its dispersal barriers—an endemic in the strict sense;

b) old or relic species, occupying a much smaller area than before, an element that is surviving but not contributing to floral evolution—an epibiotic.

Members of the Botanical Survey of India have contributed a number of studies on endemism and patterns of distribution of angiosperms (including Poaceae) in various parts of India [100]. The nature of endemic taxa is assessed on the basis of [101]:

1) taxonomically isolated endemic taxa,
2) disjunction in their distribution, and
3) presence of fossils.

Families with the largest representation of endemics are the Fabaceae and Acanthaceae, followed by Poaceae and Asclepiadaceae [102]. The survival of palaeoendemics in the Eastern Ghats is dependent on biotic, climatic and edaphic factors, as well as on the genetic structure and past history of their populations, in accordance with the gene-pool/niche interaction theory [148]. The isolation of narrow endemics due to various environmental barriers is more pronounced in the Eastern Ghats than the Western Ghats, where there is a more continuous mountain system, and a more humid climate. The endemic plants of Maharashtra have been listed by Almeida and Almeida [2] of India and Sri Lanka by Sarkar [127].

There is no doubt that a comprehensive study of the grass endemics of India, dealing especially with habitat, geological age and cytology, would produce data highly relevant in the present context, as that dealing specifically with endemics of gypsum deserts in North America in particular [161]. Gypsum is a common surface evaporite in warm or hot regions of low rainfal throughout the world. Enormous deposits were formed during the Mesozoic, 150-240 myBP, but these were subsequently covered by the calcareous or siliceous deposits of the Cenozoic. Tectonic and erosional forces have re-exposed this fossil gypsum or its anhydrite form [4], for example in the Sierra Madre region of Mexico. "Strange and bizarre plant endemics tend to develop upon such substrates, especially where the surrounding flora is rich and the gypsum outcrops of long standing. Genera include a number of Poaceae, which occur in a latitudinal range from 24° N to 47° N in North America; the sparseness of endemics at high latitudes is probably due to the more recent exposure or re-exposure of glacial outcrops as plant habitats.

Turner and Powell [161] state that "comparison is needed between diploid ancestral types versus tetraploid-derived counterparts of gypsous and non-gypsiferous plants. Preliminary data indicate (from chromosome counts of 125 species of 55 genera) that, within a given taxonomic group, diploids are more common among gypsiferous taxa than among their non-gypsiferous counterparts. Gypsophylic elements may thus be more relict in their specialized habitats.

Some closely related taxa also grow on saline soils; some of the endemics may reflect a physiological jump from saline to gypsum soils. Even so, the morphological differentiation of these contrasting species suggests that the availability of such habitats has been sufficiently long to trap ancestral relics, or else their occupancy was early enough, so as to provide sufficient time for morphological differentiation via micro-adaptational mechanisms.

Probably relevant to the further study of the origin and evolution of endemism in South Asia is a paper on edaphic endemism by Raven [117], referring to an earlier essay of 1962 by Harlan Lewis—a model for speciation in a marginal populations under conditions of extreme selective pressure and concomitant severe reduction in population size. Following the trend towards increased aridity operative in south-west North America since at least the mid-Oligocene, numerous pockets of species usually found in moist regions have been cut off. Such isolation has been accentuated since the Pleistocene and Recent times by increase in altitude.

> "In effect, the region constitutes a gigantic 'tension zone' between temperate and tropical biota . . . It therefore appears reasonable that this process as outlined by Lewis has played a large role in the proliferation of the narrow endemics so characteristic of the region. As much as 29 per cent of the vascular plants of California are endemic—an amazing proportion for a continental region . . . I suggest that there may be a direct connection between the edaphic endemism so prevalent in dry regions and catastrophic selection . . . Many workers suggest strongly that in plants, the occupation of unusual soil types almost inevitably involves the formation of genetically distinct races . . . Marginal populations apt to be growing on substrates, unusual for the species as a whole would be the very ones most likely to undergo catastrophic selection, and as a result be fixed at adaptive modes different from those of the main body of the species."

2.6 CELL AND NUCLEAR EVOLUTION

Takhtajan [152] was convinced that the monocotyledons were derived from dicotyledons, having acquired their characters while they adapted strongly during a phase of evolution to aquatic or at least marshy habitats. The main groups have gained in homogeneity and most orders are placed in a logical sequence . . . in Commelinacae. The orders are placed in a series from a more Lilialean to an advanced Poalean sequence, with the Restionales just above Poales.

Dahlgren believes that the closest group to the grasses is *Joinvillea* (Joinvilleaceae), followed by *Flagellaria* (Flagellariaceae). Other closely related groups are the Restionaceae (in which Ecdeiocolea and Anarthriaceae should be included) and Centrolepidaceae. "It would not surprise me either, if grasses and palms shared a common ancestry far back in the middle Cretaceous" (Dahlgren, personal communication, 1986 [38]).

According to Stebbins [144] the earliest grasses "were herbs with stems having few to many nodes, relatively simple racemose or paniculate inflorescences, and spikelets with numerous florets, the bracts or glumes being undifferentiated like those of primitive bamboos". He disagreed with Prat [107] and Bews [8] that the bamboos were ancestral to the other tribes, believing with Arber [3] that their tree-like habit was a secondary specialization [183]. Stebbins considers the grasses existed in the middle Cretaceous in tropical or subtropical climates, and that from that extinct group, a series of lines adapted to different habitats evolved. "Three of these lines had unusual success. The first two developed primarily in the tropics. These were Panicoideae and the Chloridoid-Eragrostoid line", probably from closely related ancestors, which evolved by retaining primitive leaf epidermis, caryopsis, embryo and seedling and specialization in leaf anatomy. The third dominant line, the Festucoideae, are the principal grasses of temperate climates. Their large chromosomes are probably a later specialization [4]. Stebbins notes that while some temperate orders have small chromosomes, the Commelinaceae, Liliales, Leguminosae and Polemoniales also have large chromosomes. "The relationship between chromosome size, cellular metabolism and growth is a subject which certainly deserves attention, and about which new discoveries of considerable evolutionary significance might be made" [144].

Many of the less successful line, the bamboos, dominant only in the moist forests of the tropics, retained primitive reproductive structures [186] but others are highly specialized. The Arundineae retained the primitive basic chromosomal number of $x = 6$ or 12 [183]. The Oryzeae have retained the primitive six stamens per floret, while the Stipeae, "probably an offshoot of the danthonoid-arundinoid complex, became highly specialized in fruit structure" [144].

In his review of chromosome evolution in the monocotyledons, Sharma [130] refers to Avdulov's recognition of three types of grass karyotypes: $x = 9$ and 12, both with small chromosomes, and $x = 7$ with large chromosomes. Sharma notes that while polyploids have an advantage in new environments, they are less adapted than diploids to their centres of origin.

> "In the millets, and including *Triticum* and *Avena*, the chromosome numbers are 14, 28 and 42. In the Paniceae they are $2n = 72$, whereas in the andropogons the somatic number ranges from 20 to 180, all in

ultiples of ten. The genus *Bromus*, which is one of the primitive taxa of the festucoid complex, has $2n = 14$ in some of the species."

"On the basis of observations so far made, multiples of $x = 5, 6, 7$ and 10 chromosomes are most prevalent in the gresses. . . . . In general chromosomal details of grasses present several interesting features. A high degree of polyploidy is common to many genera. Both structural and numerical alterations of chromosomes have been frequently observed. Interspecific hybridization is not uncommon. Large numbers of cytotypes, especially aneuploid complexes, have been recorded in several genera such as *Cenchrus, Dicanthium, Bothriochloa* and *Poa* [130, 184].

2.7 POLYPLOIDY

Polyploids may be the result of some form of abnormal meiosis in diploids or other lower ploidy levels, when reproduction took place under the influence of some form of stress, especially aridity. Conversely, polyploidy confers certain benefits upon plants which enable them better to meet extreme ecological conditions. Stebbins [147] has noted correlations between polyploidy and occuption of pioneer, disturbed habitats.

It has already been proposed (see Sec. 2.2) that environmental stress has been a major factor in the evolution of the rich gramineous flora of western monsoon Asia—250 genera and 1,250 species [12]. Preliminary indications are that, the forms of abnormal meiosis that may be found in, for example, the species of the plains of western monsoon Asia are associated with relatively slight, sometimes difficult-to-identify but nevertheless significant changes in the chromosome complement of the progeny. But the many plains genera and species which show polyploid series may be presumed to have had an environment-induced origin at some period of history*.

Mehra [87] in a collection of tetraploid accessions of the *Dichanthium annulatum* complex from almost its entire range of distribution; observed some meiotic irregularities ranging from slight, medium or marked, and of the type commonly associated with polyploidy and hybridization between species. But Mehra and Singh [88] explain the chromosomal behaviour noted in the four ecotypes of the *D. annulatum* complex, which they recognize (tropical, Mediterranean, Senegalese and South African) and their hybrids entirely on the basis of cytogenetical data. The forces which attract chromosomes together, which initiate pairing, and which govern behaviour at meiosis are all believed to be genotypically controlled. There is no reference on the microscale of the possible action of environmental factors operating through the nutrition and metabolism of the plant up to the tapetum and so to the

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* This section had remained incomplete at the time of the author's death. He had wished to discuss findings from the following papers here:

Anton, A.M., A.E. Cocucci. 1984. The grass megagametophyte and its possible phylogenetic implications. *Pl. Syst. Evol.* **146:** 117-21.

Crawford, D.J. 1985. Electrophoretic data and plant speciation. *Systematic Botany,* **10:** 405-416.

Ghorai, A., A. Sharma. 1981. Chromosome studies in some Festuceae. *J. Indian Bot. Soc.* **60:** 148-53.

meiocytes which it commands, nor on the macroscale to the geographical cytology of the ecotypes growing in their so contrasting environments.

Where the ecoclimatic border is along an altitudinal zone or contour, a new level of ploidy may be met. For example, Janaki Ammal [71] reviewed the effect of the Himalayan uplift (introducing an association of operative factors other than the aridity/rising temperatures complex stressed here for lower altitudes) in changing the chromosome complex of genera of families other than the Gramineae, which were members of the flora of Laurasia before the Himalaya reached their present height. All polyploids must originally have arisen from diploids, except in the rare cases of reversion by parthenogenesis. High polyploidy is noted in regions near the glaciers of the eastern Himalaya, where the range bends over the plateau of Assam, a region also favouring hybridization at the place of meeting of Indian, Chinese and Malesian floras.

The evolutionary history of the grass flora of the Great Plains of North America is interpreted by Stebbins on the basis of the probable origin and development of eight different polyploid complexes that include common species of this flora. At least some of the modern grasses that inhabit the Great Plains have entered the area from different directions: the mountains in the western United States, Mexico, south-western United States, Asia. The evolution of the grasses in the North American plains repeats a story that is now familiar . . . Since evolution results primarily from population/environment interactions, the greater are the environmental changes, the more drastic will be the alterations of the fauna and flora of a region [146].

Sharma [133] has examined the overall percentage of polyploidy in Himalayan grasses in general and also reviewed whether this polyploidy is related to changes in latitude and climate as between the eastern, central and western parts of the Himalaya. Stebbins [144] estimated that nearly 70 per cent of grass species are polyploids, or more if one includes genera with chromosome numbers which are also derived by ploidy during their evolutionary history. Polyploidy must not necessarily be taken to be only a recent phenomenon; Ehrendorfer and collaboraters [45, 46] refer to palaeoploidy, often the result of profound shifts and reductions in habitat and distribution area. Stebbins [147] considers it a common phenomenon in vascular plants.

Of 697 taxa of Himalayan grasses, 63.4% were polyploids, the incidence decreasing with increasing latitudes, together with change from subtropical (in the east) to sub-temperate (central) and temperate (west, with the Kashmir Hills) climates [133]. Sharma therefore does not agree with the proposal by Love and Love [84] that there is a tendency for an increase in polyploidy in angiosperms with increase in latitude.

2.8 APOMIXIS

Apomixis is a secondary manifestation of what was initially some type of physiological imbalance between bisexual ancestors and their environment, causing failed meiosis in the ovules combined with failure of pollen development in the anthers. Is it correct to talk about genetic control of a derived condition—apomixis—and not about the genetic basis for a physiological capacity or incapacity to react in a certain way to various forms of stress, in various directions associated with abnormal meiosis, only one of which is apomixis? It would be desirable for physiologists to attempt to dilute or eliminate manifestations of apomixis by appropriately designed and timed nutritional experiments on bisexual plants which show a regular or spasmodic tendency to produce apomicts in their progeny. Special attention should be given to example of seasonal and population differences [78].

Bhanwra and Choda [93, 80 references] have extended the earlier review of apomicts in the angiosperms [101], in which 91 grasses belonging to 30 genera were listed as showing apomixis. The recent paper enumerates apomictic taxa which have been reported since Nygren's review, including many South Asian grasses in the tribes: Andropogoneae, Maydeae and Paniceae in the subfamily Panicoideae: Arundineae, Aveneae, Bromeae, Eragrosteae and Phalarideae in the subfamily Festucoideae. The types of apomixis recognized are: apospory, adventitious embryony, diplospory and parthenogenesis, with the unreduced embryo sac being four-nucleate or eight-nucleate. For example, it appears that about 94 per cent of the apomictic species in the Andropogoneae are aposporous and form four-nucleate embryo sacs; these embryo sacs generally possess one egg, two synergids and one polar nucleus, or rarely one egg, one synergid and two polar nuclei. All are pseudogamous, with triploid endosperm in *Bothriochloa odorata, Capillipedium huegelli, Dichanthium annulatum* and *Eremopogon foveolatus*. Polyembryony, due to multiple embryo sacs, has been reported in several species.

Reddy [118] considers apomixis in Pooideae to be primitive, with structures formed as a result of this mechanism being much closer to sexual reproduction. "On the other hand, the mechanism of apomixis has progressively evolved in Panicoideae, reaching the zenith in Andropogoneae with Paniceae as an intermediary."

Bhanwra and Choda [9] believe that spontaneous hybridization between species and genera is essential for the origin of apomixis within a plant group. Most of the apomicts of Reddy in Festucoideae are diplosporous and form eight-nucleate embryo sacs, whereas all the apomicts in the Panicoideae (except *Tripsacum dactyloids*) are aposporous. The apospory occurs in *Agropyron scaber, Chloris* species and *Hierochloe* species, and four-nucleate embryo sacs are found in some species of the tribes Chlorideae and Eragrosteae [16].

Jeanmonod [75] regards apomixis as an *echappatoir a travers deux modes*, vegetative reproduction and agamospermy. The importance of the latter phenomenon is proved by the large number of agamospermous plants of which many are polyploid. The correlation which exists between agamospermy and hybridization is demonstrated by the presence among agamosperms of a high level of heterozygotes, of hybrid swarms, or uneven polyploids (thus sterile) and of methods of fertilization similar to those of interspecific hybrids [54, 103, 142]. Agamospermous plants do not usually cross, but there are some fertile agamospermous hybrids which are able both to produce fertilized seed and seed resulting from agamospermy in varying proportions. This occurs, for example, with *Hieracium aurantiacum* [140].

According to Grant [54], agamospermy has the advantage of producing copies of a heterozygous genotype with good adaptability, but which ɔuld be lost in normal sexual reproduction. The combined processes of natural hybridization and agamospermy lead to the formation of micro species. The resulting structure is an agamic complex, in which the derived agamospermous hybrids are superimposed on the original sexual species. The genus *Poa* is mentioned among the classical examples. Agamospermous forms are generally polyploid and more widely distributed than the original diploid species.

Shishkinskaya and Larina [137] detected abnormality in the development and structure of the female gametophyte in the polyploid species, *Festuca gigantea, F. valesiaca* and *Koeleria sahuletorum*; most of these corresponded to embryological characteristics associated with apomixis.

Bothriochloa odorata (tetroploid, $4n = 40$), and *Paspalum distichum* (hexaploid, $6n = 60$), both developed aposporous embryo sacs with a pseudogamous mode of reproduction. The megaspore mother cell degenerates as such, or soon after the formation of tetrad. As many as one to five aposporous embryo sacs arise from the cells of the nucleus. The embryo separates, developing from the diploid egg cell. It fails to reach maturity in the ovules where there is no endosperm formation. In *Bothriochloa odorata* the endosperm is triploid and is formed as a result of fusion between diploid pollen nucleus and a male gamete. In *Paspalum distichum* it is pentaploid, as both polar nuclei take part in fertilization [26].

If apomixis is to be regarded as response of ancestral gass types to different forms and intensities of environmental stress, a distinction may be drawn between different types of stress in the environments in which the Panicoideae and Festucoideae originally grew and where they occur today.

Much of the current work on apomixis is related to its use in plant breeding. This is discussed fully in the case studies which follow, with special reference to *Pennisetum* and *Panicum.*

Apomixis "has provided a dynamic reproductive mechanism for genome preservation, polyploid build-up through fertilization of unreduced eggs (the apomict functioning as the male parent in crosses with sexual plants) and survival of derivatives of wide crosses. Brief contact between cross-compatible sexual and apomictic plants has resulted in interspecific transfer of apomixis in these genera. Hybridization of sexual *Cenchrus ciliaris* and *C. setigerus* resulted in a vast array of sexual and apomictic types, some of which might easily be classified as new species if discovered in natural habitat. Obligate apomixis is genetically controlled in *C. ciliaris* and *C. ciliaris* × *C. setigerus.* Two pairs of genus and epistasis are involved."

The primary interest at the moment is in the possibility of controlling and manipulating this "unique reproductive process" in modern grass breeding [6].

2.9 PHOTOSYNTHETIC PATHWAYS*

The only known fossil grass leaves showing both external micromorphological and internal anatomical features on the same specimens have been

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* The author would like to thank Dr. P.W. Hattersley for valuable assistance in this section.

described from the Late Miocene of Nebraska [159]. The internal anatomy of the fossils is typical of grasses using the C_3 photosynthetic pathway, and the combination of characters suggests taxonomic relationships with members of the Arundinoideae (see also [157, 158]).

The origin and evolution of C_4 photosynthesis is an intriguing problem in biology. It is found in at least 18 families of angiosperms, both monocotyledons and dicotyledons, with the majority occurring in the grasses. A fossil leaf fragment collected from the Ogalla formation of north-west Kansas exhibits features found in taxa of the modern grass subfamily Chloridiodeae, including Kranz leaf anatomy. The leaf fragments extend the fossil record of plants that show both anatomical and external morphological features indicating C_4 photosynthesis back to the Miocene [185].

The designation of the Poaceae of South Asia according to their photosynthetic pathways into C_3 and C_4 types is an aspect of plant physiology, which should be considered in the present context. There are, moreover, three biochemical subtypes of C_4 photosynthesis, which differ, in decarboxylation enzyme and site of decarboxylation within the PCR cells known in the Poaceae [60]. Two species of *Panicum* [39] differed in C_4 acid decarboxylation type and in developmental origin of the bundle sheaths in major veins of their leaf blades. A fuller review of the biochemical, physiological and cytological features in C_3 and C_4 grasses has been planned.

Hattersley [61] analyzed the distribution of C_3 and C_4 grasses in Australia in relation to climate. "All but four of 833 native and 292 naturalized Australian grasses have been assigned as having the C_3 or C_4 photosynthetic pathway. . . . In general, C_4 grass species, like C_3 species *increase* in number with increasing rainfall, in their preferred temperature regime. C_4 species are most numerous where the summer is hot and wet; C_3 species where the spring is cool and wet. C_4 species numbers decline with increasing temperature and/or decreasing spring rainfall" (see also [64, 65]).

Hattersley (in press) concludes that there is little that can be said about the evolution of C_4 photosynthesis in plants that is not speculative (see also [10, 15, 112, 141]). Monson *et al.* [99] and Holaday and Chollet [69] have reviewed C_3-C_4 intermediacy.

In their study of the classification of the Poaceae into subfamilies and supertribes, Watson *et al.* [168] review the taxonomic distribution of C_4 photosynthesis—"not a single taxonomic feature but a complex phenomenon or syndrome; this must have arisen separately in several unrelated families, including the Poaceae. The switch from C_3 to C_4 (and/or the reverse?) must have occurred on several occasions. This classification presents one entirely C_4 supertribe (Andropogonanae), one entirely C_4 subfamily (Chloridoideae) (but see Ellis, [47]), two mixed C_3-C_4 subfamilies (Panicoideae and Arundinoideae—rather distant from one another), and one mixed supertribe (Panicanae). The C_4 syndrome appears to be homologous across the grasses. Switching from C_3 to C_4 involves drastic leaf-structural and spatial reorganizations involving mesophyll and mestome sheaths, vascular bundles and suberized lamellae [62, 168]; also precise changes in the localization and kinetics of the Rubisco enzyme and extensive redeployment of pyruvate orthophosphate dikinase. "The probability of arriving at the complete C_4 syndrome and the same variants more than once (let alone several times), by independent evolution via selection of chance mutations must be very small; and it seems improbable that the syndrome should have a different genetic basis from group to group" [168]. Two alternatives to completely independent evolution are suggested: can "one presuppose that the capability for switching to C_4 arose early in the history of the grasses, to be somehow preserved in an inoperative (or not noticeably operative) state, or could there have been clandestine transfer of genetic information?"

3. Some Case Studies

Agrostis

Bor [12] lists 35 species and varieties in South Asia, and Cope [37] lists eight in Pakistan. This is a genus of 150 to 200 species, mainly in temperate and cold regions, especially in the northern hemisphere—generally at higher altitudes in the Himalayan and associated ranges to the west, and in the Nilgiris, annual and perennial types exist.

Rajbhandari [113] examined specimens of nine species from high altitudes in Nepal, mostly in extreme cold/arid environments on alpine and subalpine grasslands. These species are all annuals. Most botanists agree that annuals arose from perennials (E.J.H. Corner, personal communication, 1976), particularly in areas exposed to different forms of physiological stress. One may therefore ask (in relation to Himalayan orogeny) where are or were the nearest perennial forms of *Agrostis, Calamagrostis* or *Deyeuxia*, from which these annual forms evolved, somewhere at a very early geological age, when the Himalayas were lower in altitude? If any Gramineae were present at lower altitudes when the climate was tropical/subtropical before uplift began, or even during the early progressive stages of uplift, they are most unlikely to have been species of these genera. Did *Agrostis* and its close relatives of temperate adaptation come from the west (the Irano-Turanian region) or from the north, along the ancient routes of plant migration from the north of Laurasia, which were followed by other temperate genera and species of the high Himalaya, before these routes were cut by the desiccation resulting from the rise of the Himalaya?

Cenchrus

Bor [12] recognizes seven annual and perennial species in South Asia; Cope [37] as many as five in Pakistan. "*Cenchrus* is distinguished from *Pennisetum* by the transformation of the involucral bristles into a spiny cup. The tendency is barely recognizable in *C. ciliaris*, whose membership of this genus is justified by its intergradation with *C. pennisetiformis*" [37].

Sexual and aposporous apomictic embryo sac development in three *C. ciliaris* genotypes was evaluated *in situ* and *in vitro* at the U.S. Regional Pasture Research Laboratory, Pa 16802 [57]. The *in vitro* culture technique provides a method for studying embryo sac development and physiologic regulation of apomixis. Few investigations into the physiological basis of apomixis have been reported [57, 136, 2·08].

Zeven and de Wet [176] state that *C. biflorus* ($2n = 30, 34, 36$) and *C. ciliaris* ($2n$ = mainly 36) and probably also *C. setigerus* ($2n = 34, 36, 37$) are of African origin; if so, do we have to visualize migration from east Africa to the west and north of South Asia, either by man-borne trade or by land along the Hadramaut and Makran coast? If this is proved, would one not expect to find a graduation from fully sexual to obligate and facultative apomictic types along the migration route, from the African centre of origin into the biological vacuum of the Eocene?

Coix (Maydeae)

Bor [12] gives specific rank to *C. aquatica*: although difficult to separate from *C. gigantea* in the herbarium, they have different habits and different chromosome numbers (*C. aquatica* $2n = 10$; *C. gigantea* $2n = 20$). *C. lacryma jobi* is a primitive cereal cultivated in many parts of the tropics. *C. puellarum* is common in south-east Asia (187).

A.B. Sapre and associates at the Botany Department, Marathwada University, Aurangabad, observed chromosomal range in interspecific Indian hybrids [125], meiotic non-disjunction in *C. gigantea* [124], spontaneous emergence of parents in hybrids [126], a spontaneous autotriploid in *C. aquatica* [121], and a group of studies on aneuploids and higher polysomics (nullisomy to pentasomy and hexasomy [122–124]).

Although *Coix* is generally regarded as a primitive genus, there is no reference to cytological criteria for primitiveness. Sapre and Deshpande [126] have, however, noted that one or two chromosomes from *gigantea* species (G) showed behaviour like B-chromosomes when incorporated in the *C. aquatica* genomes (AA) through spontaneous hybridization.

Cymbopogon

Cytological observations are being made at the C.S.I.R. Regional Research Laboratory, Jammu Tawi, India, by V. Verma, S.N. Sobti and associates on the genus *Cymbopogon* (Andropogoneae), a polymorphous group of aromatic grasses—140 species in the tropics of the eastern hemisphere, 20 in India in regions with abundant rainfall, from sea level to 2,000 m elevation. There are nine varieties, cytotypes and chemotypes belonging to six species. Of these, five were diploids ($2n=20$), two were tetraploids ($2n=40$), and two were hexaploids ($2n = 60$). Chromosomes are classified into three groups on the basis of size. Variation in the karyotypes of different species is mainly due to variation in number of chromosomes belonging to these groups.

Karyotypic evolution appears to be taking place through structural differences and repatterning of chromosomes along with general reduction in total chromatin length. On the basis of hybridization studies and karymorphological differences between the two varieties of *martinii* (*motia* and *sofia*), it is suggested that the two varieties be raised to specific status [163].

The base number of chromosomes is found to be $x = 10$, with the possibility of accessory or B-chromosomes. A basic number of $x = 5$ has been suggested for the Andropogoneae, but, being unstable, this became duplicated in the evolution of the tribe [89, 92, 93].

Six species and their varieties (five diploids, one tetraploid and two hexaploids) show morphological diversity, possibly due to gene exchange. Both the diploids and the hexaploids showed fairly normal meiosis with 10 and 30 bivalents respectively. However, the tetraploid species (*C. martinii*, $2n = 40$), formed multivalent configurations, suggesting a segmental polyploid nature [164].

The presence of a comparatively symmetrical karyotype in certain species suggests that they are closely related to the ancestral stock. The karyotypes of comparatively modern species, having varying degrees of symmetry, might have originated from the above ancestral forms by structural changes in the chromosomes and their repatterning, including increase and decrease in size [46, 143, 145].

Dactylis

Dactylis *glomerata* is an important grass of the mountains to the north of South Asia at altitudes with a temperate climate (1,800 to 3,600 m). Cope [37] has not attempted to resolve the intraspecific taxa in Pakistan and Kashmir, but distinguishes the following intergrading subspecies:

- subsp. *glomerata* ($2n = 28$) occurs throughout the range of the species;
- subsp. *bispicata*, also tetraploid, occurring mainly in the southern and western part of the range of the species, but reaching Afghanistan and possibly Pakistan;
- subsp. *himalayensis*, diploid, the most common variant in Pakistan, restricted to the western Himalayas.

In all diploid forms of the species and their F_1 hybrids, meiosis was regular [151]. In all the tetraploid studies, chromosome behaviour resembled that in typical *D. glomerata*, with the formation of a varying number of quadrivalents and bivalents, followed by regular chromosome segregation. The diploid species which the authors discuss constitute only about 5% of the genus; the tetraploids make up the remaining 95%; the latter may have evolved as the result of hybridization, but the high proportion may also be an expression of cytological response to stress at some past stage of migration and evolution.

The use of isozymes to indicate intraspecific groupings has been applied to *Dactylis glomerata* [85]. The results show that most diploid or tetraploid subspecies can be classified in one of the two main geographical groups (Eurasian or Mediterranean), differentiation between them probably having occurred long ago, probably in the Miocene. Diploid and tetraploid subspecies within each climatic group show some similarity, but the genetic diversity is always higher in tetraploids than in diploids. The analogies could be due to phylogenetic relations and/or adaptive convergence. The additional alleles found in tetraploids would be due to the inertia of the tetraploid genetic structure, which slows the rate of segregation. The genetic structure of the Eurasian *himalayensis* and *aschesoniana* subspecies was found to be very close; it is likely that they have a common origin [85].

R. Lumaret (CEPE/CNRS, B.P. 5051, 34033, Montpellier, France) reports in a personal communication (August, 1986) that she has received material from the district of Xianning, north-west Guizhou, collected at 2,200 m. This mater is diploid; no tetraploids have yet been found. The Chinese type is similar in panicle characters to *Dactylis glomerata* ssp. *himalayensis*, supporting the hypothesis that these two types originated from a common ancestor, but there are differences in the leaves. There is no divergence between the types in the chloroplast DNA structure from DNA restriction fragment patterns. Enzyme polymorphism has been studied at six different loci, which code for different types of enzymes. Surprisingly, at the level of each locus, fixation of one allele, sometimes two, was found. This has never before been reported for the genus *Dactylis*. There may have been a dramatic differentiation for this entity, which would indicate a long and significant isolation.

Until sufficient evidence has accumulated, it may be proposed that the types of *D. glomerata* found in the western Himalayas entered this new mountain habitat from the Irano-Turanian region, while those described by Bor [12] and maintained in the herbaria of the Forest Research Institute and the Botanical Survey of India in Dehra Dun reached the Himalaya from the north; they may have been components of the vegetation of the Xizang plateau before the final uplift of the Himalaya along its southern rim and the introduction of increased aridity in the plateau north of the range. In this connection, reference should also be made to the possible significance of the Chitral/Gilgit gap as a dividing line between western and eastern Himalaya, or to the differential rate of speciation through polyploidy in the north-eastern and north-western Himalaya—low stress versus high stress [71].

Dactyloctenium

M.L. Sharma and associates in the Department of Botany, Panjab University, Chandigarh, India, have studied several species and cytotypes of the genus—five species in India, annual and perennial, Eragrosteae. Seed sterility in *D. sindicum* may be due to failure of the pollen tube to reach the embryo sac in most of the ovules, and failure of normal megasporogenesis and megagametogenesis in a low percentage of ovules.

It is most difficult to separate the annuals, *D. aegyptium* and *D. aristatum* using Bor's [12] criteria, as many intermediate forms also occur. On the basis of cytotaxonomic studies on 81 populations from the plains of Chandigarh and eastern Punjab, it is concluded that the *D. aegyptium* complex in the Punjab plains comprises taxa belonging to *D. aegyptium* (L.) P. Beauv. and *D. aristatum* Link., and populations which represent new varieties of *D. aristatum*. A taxonomic key is provided [132, 134]. Leaf epidermal characters have little diagnostic value either at the specific or subspecific level [135].

Cope [37] recognizes three species in Pakistan, *sindicum, aegyptium* and *aristatum*, but notes that the boundaries between species are often ill-defined. "Further collecting and some experimental work are required before this genus can be fully understood."

Panicum

The most primitive representative of the Paniceae, *Pseudolasiacus*, occurs in Madagascar, while most of the genera considered to belong to the same tribe, Microcalamineae, are also African [20, 21]. Bor [12] recognized 32 species as authentic in the South Asian types of the genus *Panicum*, but noted 375 synonyms proposed for specific rank by other taxonomists. Does this indicate degree of speciation within the African genus in response to new environments [173]? Looked at from the South Asian subcontinent, one tends to regard the mesophytic population in India, e.g. *Panicum maximum*, as of early origin on the Plate, and the species of more xerophytic adaptation like *P. antidotale* and *P. turgidum* as more recent arrivals in western monsoon Asia from east and north-east Africa (see also *Cenchrus* in these Case Studies).

Scanning electron microscopy, used to study the anthoecia of *Panicum elegans* from Late Cenozoic deposits in Kansas, revealing that the germination lid has been present in some members of the Gramineae since at least the Late Miocene-Early Pliocene [155].

Current interest in this genus relates to the genetical use of apomixis in breeding procedures. Savidan [128] reported that 500 accessions of *Panicum maximum* collected by Combes and Pernes [36] comprised, when grown in Cote d'Ivoire, 22 sexual diploids ($2n = 16$) among a population predominantly of tetraploids ($2n = 32$) reproducing by apomixis. Hybridization between sexual and apomictic plants gives rise to sexual as well as apomictic hybrids.

The character of a four-nucleate embryo sac structure was used in genetical analysis to differentiate apomitic from sexual hybrids. Sexual biotypes contain only eight-nucleate embryo sacs. All the data from ten different types of progenies fit with a single gene model for the inheritance of apomixis, in which the sexual diploids would have the genotype aa and the apomictic tetraploids the genotype Aaaa; apomixis is dominant. Apomixis in *P. maximum* is often facultative, but with a low percentage of residual sexuality, a rate that remains low following hybridization.

Using the same criteria for sexuality and apomixis (Savidan's simplified embryo sac analyses) in trials with *P. maximum* at the National Grassland Research Institute, Nishinasuno, Japan, Nakajima and Mochizuki [99] recognized how degree of sexuality could be used in a breeding programme: (1) crossing a sexual plant with an apomict to expand genetic variations through genetic recombination, and (2) selecting promising hybrid plants in which heterosis has become fixed by apomixis.

Sinha and others [138, 139] examined two cytotypes with $2n = 18$ or 32. Savidan (personal communication, September, 1986) considers $2n = 18$ "extremely doubtful; all examined cases corresponded to taxonomical mistakes". Meiosis was irregular, characterized by the presence of univalents at metaphase I and laggards at anaphase I. Pollen sterility was high; a number of pollen mother cells also showed desynapsis. The mode of reproduction may be correlated with the meiotic behaviour of chromosomes and the fertility of the gametes.

Scientists in the Department of Agronomy and Botany in the University of Georgia (Athens, GA 30602) have studied the photosynthesis, leaf anatomy, morphology and cytogenetics of hybrids between C_3 and C_3/C_4 species within the *laxa* group of *Panicum*.

> 'There were no differences found in morphology or physiology between the amphiploids and the F_1 hybrids from which they were produced. In the segregating progeny, CO_2 compensation concentration and photorespiration values typical of C_3, but not of C_3/C_4 plants were recovered. Progeny were found from both crosses which possessed O_2 inhibition of apparent photosynthesis typical of the parents, and in the case of the *P. milioides* × *P. laxum* cross, leaf anatomy and overall plant morphology typical of the parents was observed in some progeny. The progeny were found to possess recombinations of various traits associated with reduced photorespiration, so that no correlation existed among O_2 inhibition of apparent photosynthesis, CO_2 compensation concentration, and leaf anatomical traits. One plant was especially noteworthy in possessing leaf anatomy typical of C_3/C_4 plants, but with CO_2 exchange characteristics of C_3 plants" [14].

*Paspalum**

Of this genus, of about 250 species distributed throughout the tropics but mainly in the New World, Cope [37] recognizes three species in Pakistan: *P. dilatatum* (introduced from South America), *P. paspalodes* (closely resembling the more tropical *P. vaginatum*) and *P. scrobiculatum* (a highly polymorphic species which may be a swarm of apomicts) [32]. Accepting 14 species of the genus in South Asia, Bor [12] states that *P. dilatatum* was introduced from South America into India, and has now become established in many hill stations.

Chromosome numbers of most *Paspalum* species are multiples of 10; apomixis is prevalent within the genus and has been an important factor in the evolution of many species [18]. Common *P. dilatatum* is an apomictic, 50-chromosome natural hybrid with three genomes that pair as 20 bivalents and 10 univalents at meiosis. In an effort to circumvent apomixis, Burson [17] undertook a phylogenetic investigation to identify its progenitors, and eventually to resynthesize the species. The genome formulae II, JJ and IIJJ have been assigned to *P. intermedium, P. jurgensii* and the yellow-anthered biotype of *P. dilatatum* respectively, of which the first two species or others closely related may be the ancestors. It was proposed that common *P. dilatatum* (IIJJX) arose from a cross between a sexual tetraploid and an apomictic hexaploid, which may have been *P. durifolium* or another hexaploid species in the section Quadrifaria [17].

A series of papers by Argentinian (Instituto de Botanica del Nordeste, 3400, Corrientes) and American cytologists will be of interest to workers in South Asia (most recent reference [108]). More than 400 species are recognized. Aspects covered include (1) chromosome behaviour, embryo sac development and fertility of *P. modestum* ($2n = 20$), *P. boscianum* ($2n = 40$) and *P. conspersum* ($2n = 60$), wild species which reproduce sexually and may have forage potential; (2) cytogenetic studies on *P. laxum* ($2n = 60$), *P. proliferum* ($2n = 40$) and 20 and 40 chromosome accessions of *P. cromyorrhizon*—meiotic behaviour and embryo sac development suggest that *P. laxum* is a sexual

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* The author is indebted to Dr. Byron Burson for valuable comments and amplification of this section.

allohexaploid and *P. proliferum* an apomictic autotetraploid; $x =$ [illegible] may be the primitive number from which species with $x = 6$ and $x = 10$ were derived; tetraploid *P. cromyorrhizon* is a facultative apomict, whereas the diploid is primarily sexual, but appears to have some potential for apomictic reproduction; (3) cytogenetic relations among *P. notatum* var. *saurae*, *P. pumilum*, *P. indecorum* and *P. vaginatum*—the actual relation of *P. indecorum* to the other species is at present unclear; (4) cytology of intra- and interspecific hybrids between diploid and tetraploid cytotypes of *P. notatum* and *P. cromyorrhizon* indicate they are genomically related, but the sterility of their diploid × diploid hybrid confirmed as separate species.

Most species of the Quadrifaria group are distributed in tropical and subtropical South America [109]. *P. quadrifarium,* a member of the group is distributed mainly between 30 and 39°S. lat. in Argentina, Uruguay and South Brazil. It probably also originated in warm regions, but migration to temperate or less humid regions was accomplished by means of polyploidy and apomixis.

Pennisetum

Cytological investigations on some of the Indian millets, including *P. typhoides* and *P. orientale,* were carried out by Sharma and De [131], who discussed the implications of meiotic irregularities in *P. typhoides.* Recent work on the cytogenetics of this crop of semi-arid environments in Africa and Asia, *P. typhoides,** has been fully reviewed by Hauhar (U.S.D.A. Agricultural Research Service, Albany, GA 94710). Chromosomal hybridization and genetic studies have shown that the wild or semi-wild relatives of pearl millet are not sufficiently isolated from it to deserve specific rank. All annual Penicillarias (a section of the genus *Pennisetum*) have therefore been merged with *P. typhoides,* in which three subspecides are recognized.

There are several semi-wild annual diploid races in the section Penicillaria with which the cultivated pearl millet is interfertile, and essentially forms a single, composite reproductive unit. There is no reference to the possible perennial ancestor of these annual types of *Pennisetum,* which would presumably have arisen in the drought-affected fringes of areas in which perennials were and perhaps still are dominant in the natural vegetation [170].

Based on the more frequent occurrence of B chromosomes in primitive varieties than in selected, commercial varieties, it has been suggested that their occurrence might be used as an indicator of a crop's centre of origin. On that basis, the Sudan [105] and Nigeria [19] have been proposed as the centre of origin of pearl millet, but Jauher [73] does not agree, preferring the Sahel—a good borderline for genotypical response to fluctuating environments (see Sec. 2.3).

All Penicillaria fall into the $x = 7$ group. The only perennial species, *P. purpureum* is tetraploid, and possesses a genome partially homologous to pearl millet (Dujardin, personal communication, September 1986); all other

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* M. Dujardin, University of Geogia College of Agriculture, Tifton, Georgia 31793, disagrees with Jauhar's use of the species name *typhoides,* and considers *P. americanum,* as used by taxonomists such as Clayton, to be correct.

taxa are annual and diploid with $2n = 2x = 14$ chromosomes. In his section on abnormal meiosis, Jauhar [72-74], discusses desynapsis and its genetic basis, the effects of nutrients and ploidy on desynapsis, the effect of the desynaptic gene on B chromosomes and the experimental induction of desynapsis. Other sections of the review deal with haploidy, polyploidy, aneuploids, structural changes in chromosomes and floral biology (protogyny and anthesis). The development of the megagametophyte ahead of the pollen meiocytes is an advantage in outbreeding of pearl millet [114].

The somewhat anomalous occurrence of certain grass species throughout the high Himalayas, Xizang and north into innermost Asia has to be considered in any attempt to use botanical evidence for the Gondwanian origin of parts of the Asian landscape and vegetation. One may regard the genus *Pennisetum* as of Gondwanian (African) origin. Yet Bor [12] refers to *P. lanatum* in the western Himalayas and in Xizang above 1,500 m; also to *P. flaccidum* (= *P. incomptum*) in the Himalayas and Xizing at high altitudes. The staff of the Kashmir substation of the Indian Grassland and Fodder Research Institute reports on a tall form of *P. flaccidum* in the Kashmir Valley and a stunted form at higher altitudes in Ladakh. Cope [37] refers to the distribution of the species as "Pakistan (Sind, Baluchistan, Punjab, Northwest Frontier Province, Gilgit and Kashmir at elevations up to 2,700 to 3,000 m); Himalaya westward to Afghanistan, Tibet and southern China". The Gramineae volume of the Flora of the U.S.S.R. [119] notes the occurrence of *P. flaccidum* in Central Asia, Pamir, Altai, with general distribution in Iran, India (Himalaya), China (Junggar Pendi/Kashgar), Mongolia. Keng Yili [77] gives the distribution of *P. flaccidum* as north, north-west, north-east and south-west China, in addition to Central Asia. Wang Chiwu [167] reports the occurrence of the species in a herbaceous cover on exposed slopes in the valley plains of southern Chahar and Suiyan in association with species of *Artemisia* (approximately 40°N latitude; altitude 800 to 1,000 m). Modern surveyors have noted that *P. flaccidum* forms a steppe on the right (southern) bank of the Yarlung Jiang (Brahmaputra) in Xizang, on the northern slopes of the Himalaya at 4,000 m adjacent to a steppe of the Leurasian *Stipa* [25].

The apomictic East African grass, *P. squamulatum* ($2n = 54$) was crossed to tetraploid pearl millet ($2n = 28$) to study potential for germplasm exchange [42]. Fertile apomictic interspecific hybrids appear to be a useful tool for the transfer of genes for apomixis from the wild species to pearl millet. The production of partially male-fertile apomictic back-crosses (*P. americanum* $2n = 4x = 28 \times$ *P. squamulatum* $2n = 6x = 54$) should make it possible to continue gene transfer from the wild species to the crop in succeeding generations [43].

Other research at the University of Georgia College of Agriculture relates to apomictic interspecific hybrids between pearl millet and *P. orientale*, meiotic and reproductive behaviour of facultative apomictic back-cross offspring derived from *P. americanum* × *P. orientale* interspecific hybrids, microsporogenesis, reproductive behaviour and fertility in five *Pennisetum* species, cytogenetics of double-cross hybrids between *P. americanum*-*P. purpureum* amphiploids and *P. americanum* × *P. squamulatum* interspecific hybrids, pseudogamous parthogenesis and fertilization of a pearl millet × *P. orientale* apomictic derivative, and cytology and reproductive behaviour of pearl millet × napier grass hexaploids × *P. squamulatum* trispecific hybrids [44].

Poa

A cosmopolitan genus of 200 species, mainly in temperate regions or altitudes in the Northern Hemisphere, "a very difficult genus to name, partly on account of the wide range of variation displayed, partly because many of the species are closely related" [37]. The relative members of 32 recognized 3 species and 49 synonyms in Pakistan, and the comparable figures for India (species or varieties, 52, synonyms 84) may perhaps be taken as a measure of active speciation [12]. Partial or complete breakdown of meiosis has been noted in *P. alpina, P. bulbosa, P. nemoralis* and *P. pratensis* in the western Himalaya [94].

Kellogg [76], in her biosystematic study of the *Poa secunda* complex, notes that about a quarter of the species occur in the Pamirs and the Himalayas [59]. Some species are fully sexual, others are partial or obligate apomicts; both inbreeding and fully outbreeding and dioecious species also occur [30]. Taxa are recognized primarily on the bases of size of parts and the presence or absence of trichomes and scabrosities in various parts of the plant. The core of any taxonomic revision must therefore involve a detailed analysis of variation in these characters.

Even in the offspring of self-pollinated plants, Kellogg found much morphological variation.

> This variation "could be entirely phenotypic, entirely, genotypic or some combination of the two. If all the offspring of a single plant were apomictically produced, they would be genetically identical, assuming no autosegregation or mitotic crossing-over. Although all the plants were greenhouse-grown, the experiment was not controlled for small differences in environment. At the other extreme, the variation could be all genetic. If all the seeds were sexually produced, then they could all be genetically different. . . . No matter how the variation is explained, however, it is still high enough to suggest that the characters are of minimal taxonomic value. . . .
>
> "In general, my work suggests that much of the presently accepted taxonomy of the genus *Poa* is suspect. The amount of population-level variability in the *P. secunda* complex is not unique in the genus. The genus contains several widespread polymorphic taxa, including *P. pratensis, P. alpina, P. arctica* and *P. glauca*, in which one to many species are commonly recognized. All include numerous entities that have been given specific status at some time in the past, and all are circumboreal, apomictic, and with aneuploid chromosome numbers suggesting some ancestral hybridizations.
>
> "At our current level of knowledge, we can make no claims about evolution within *Poa secunda*. Because there are no characters that can serve as evolutionary markers, we cannot evaluate the various processes

that might have generated the pattern. Hypotheses of fusion of disparate lineages by hybridization, although appealing, are merely plausible suggestions, not subject to test. The roles of polyploidy and apomixis cannot be evaluated. The pattern of variation, in other words, does not illuminate the historical pattern of microevolutionary process" [76].

Rottboellia

"The delimitation of the genera within the group of taxa represented by *Rottboellia* and its closest relatives. . . . has always posed a considerable problem" [162]. Stapf raised Hackel's system of five subgenera to generic rank, creating several new ones, and since that time, the number of genera has steadily increased. Despite the work of many taxonomists, difficult questions remain. A clarification of the genera which occur in Malesia has been made, on the basis of morphological characters and some chromosome counts. . . . "but clearly the last word has not been said. A really stable situation will only be reached when far more data are available, e.g. from anatomy, cytology and, if possible, hybridization experiments," [162].

Christopher [27, 28], University of Kerala, Trivandrum, India, has studied polyploidy in the *R. exaltata* complex in South India [12]. The genus has about 30 annual and perennial species in tropical and subtropical regions of the world (Cope [37] says only four species), and *R. exaltata* is the only species in India and Pakistan. Taxonomists recognize a short and a tall, robust varieties (short $2n = 20$; tall, $2n = 40$). Both showed normal meiosis, with regular bivalent formation, anaphase separation and formation of normal tetrads. The tetraploid taxon is a natural allopolyploid; the short diploid form may be one of its parents. In south India, the species is a compilospecies, the diploid form being very restricted in distribution, the tetraploid widespread.

Sporobolus

The record of $n = 6$ in the pollen mother cells of *S. maderaspatanus* (collected in south India, [29] confirms that for *S. molleri* ($2n = 12$) from East Africa—a comparatively rare basic number in the Gramineae [153]. Meiosis was regular and six bivalents were observed at metaphase I; 90.5% of the pollen was fertile and seed set regular.

Cope [37] notes that *Sporobolus* is a genus of about 150 species of annuals and perennials, mainly in the tropics and subtropics, with some species extending to warm temperate regions; 10 in Pakistan. "A large genus not divisible into well-defined sections, although clusters of closely allied species are readily apparent. Within the clusters, and to a lesser extent between them, the boundaries between species are seldom clear-cut, and the occurrence of intermediates appears to be the rule rather than the exception."

Stipa

Morphological studies of fossil grass anthoecia from Miocene-Pliocene strata in Kansas are cited by Thomasson [156] as evidence for the common ancestry of North American species of *Stipa*, section *Hesperostipa*, and of *Piptochaetium* in *Bothriochloa*. Both species have been distinct from species of *Nassella*, *Oryzopsis* and other *Stipa* since at least the Miocene or Pliocene.

The taxonomic revision of the genus presented by Freitag ([50] University of Kassel, D3500, Federal Republic of Germany) for the area between the east Mediterranean (south-west Asia) and the Himalaya up to Nepal will be of value to Indian botanists, and to Chinese specialists concerned with the genus on the north face of the Himalaya and areas to the north in Qinghai/Xizang. The northern boundary of Freitag's area agrees with that of the *Flora Iranica*[*] for the central part of the area; to the east, it follows the frontiers of Pakistan and India, and in the north-west the main range of the Great Caucasus. The southern boundary is the most natural, since it is here that the genus gradually disappears in the subtropical deserts, semi-deserts, woodlands and forests of western monsoon Asia. The author is familiar with most of the species from his stay in Afghanistan and field visits to the Himalaya, Iran and Transcaucasia.

Concepts differ widely regarding the delimitation of the genus—very narrow by most Soviet authors, wide by western ones [12, 37]. Freitag's revision results in 42 accepted species for the region, includes about 50% of all Euroasiatic species, and covers almost all infrageneric taxa present in Eurasia. The frequently separated genera, *Achnatherum*, *Lasiagrostis* and *Ptilagrostis* are now included in the genus *Stipa*. The significance of the growth form is related to the mode of branching, the ontogenetic development of the shoots and the life span of the individual, with the following types (among others) being recognized: non-rosulate perennials, rosulate perennials and rosulate annuals.

The genus *Stipa* is adapted to temperate, dry climates from lowlands to alpine belt, and exhibits greater diversity in semi-arid and arid climates. About 40% of the species are considered rare, either very restricted endemics, perhaps collected only once and therefore of doubtful status, or they have come from adjacent regions—a few outposts located in marginal areas.

Primitive characters including chromosome numbers of $2n = 24$ are more or less equally distributed in sections *Lasiagrostis* and *Aristella*. The alpine offshoot *Ptilagrostis* has $2n = 22$. The Mediterranean sect. *Macrochloa* is an isolated group of obscure origin with more primitive characters. Freitag's Table 5 : 378 gives presumed evolutionary trends in some characters of the genus, primitive and advanced. Primitive chromosome numbers are 22, 24, 28; advanced numbers are 36, 38, 44.

Cytological data are few, but it is evident that polyploidy is much involved in the evolution of the genus and its sections. However, there is only a limited correlation between chromosome numbers and the height of morphological organization. "Much more cytotaxonomic work is needed to detect the evolution of species and the relationship of the sections within the genus *Stipa*" [50].

[*] **Rechinger, K.H.** (ed.) 1970. *Flora Iranica* no. 70: Gramineae. Graz.

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