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CYTOLOGY AND GENETICS OF FORAGE GRASSES[1]

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INTRODUCTION

A large proportion of the species of Gramineae have been used at one time or another for forage. Certain of these, the tame hay and pasture grasses, are grown almost exclusively for this purpose. The millets and sorghums are important as human food in some regions, particularly in Asia, but these grasses are grown fairly extensively in the United States as temporary hay and pasture or silage crops. The cereals (wheat, oats, barley, corn), although cultivated primarily for grain, are used also for grazing, hay or silage in some instances. In addition to the cultivated grasses, a large number of species make up the native pastures—the range of the western United States and similar native grassland areas elsewhere in the world. Some of these species, included in the genera *Andropogon, Agropyron, Bouteloua, Stipa* and others, occur abundantly and constitute an important part of the herbage. Others occur sporadically and are important for grazing only in limited areas or for a short time during the growing season. In recent years, with the increased attention given to maintenance and reestablishment of the ranges, the more important wild species have been seeded on extensive areas. Thus some of these wild species are becoming cultivated grasses.

Cytological and genetical investigations of the grasses have been initiated primarily for two reasons, first, to serve as an adjunct to morphological data in studies of the taxonomy and phylogeny of the Gramineae, and second, to provide fundamental information for the improvement of species by breeding. In relation to the

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systematic and phylogenetic studies, chromosome numbers of numerous species have been determined, polyploidy and intraspecific chromosome races have been discovered in many genera and species, and several interspecific and intergeneric hybrids have been investigated. Increased appreciation of the importance of forage plants, which led to the initiation of many grass breeding projects during the last two decades, added a great stimulus to cytological and genetical investigations of the more important species. These investigations include studies of meiotic behavior within species and in interspecific hybrids, origin of polyploidy, cytogenetics of polyploids, inheritance, and linkage relations.

Although the cereal grasses—*Triticum, Avena, Hordeum, Secale, Oryza, Zea*—are used, in some cases extensively, for forage, they are chiefly of importance for their grain. The genus *Aegilops* is of interest primarily because of its phylogenetic relation to *Triticum.* Literature dealing with these genera will be included in the present review only when the results seem to have a direct bearing upon the cytology and genetics of the forage grasses.

KARYOTYPE ANALYSIS AND PHYLOGENY

The value of cytological investigation as an aid in establishing systematic and phylogenetic relationships among species and genera was recognized by many (*e.g.,* 240, 241). Hunter (153) pointed out that, in respect to taxonomic significance of karyotypic peculiarities, first place is taken by basic number and size of chromosomes. Next in order of importance come idiogram types, characterized by changes in length and structure of the arms of individual chromosomes. Limitations of karyotype analysis in systematics have been emphasized (*e.g.,* 24). Morphologically similar chromosomes in diverse species may not be homologous. Furthermore, variations in chromosome shape and size may occur in strains of the same species; the latter character particularly is known to be under genotypic control (101, 542). Despite these limitations, chromosome numbers, size and morphology provide critical information regarding phylogenetic relationships when used in conjunction with morphological, geographical and ecological studies (*cf.* 24).

Several investigators (*cf.* 21, 153) have attempted to construct a natural system of classification of the Gramineae. Consideration of these systems is not within the scope of this review. The first

large-scale attempt to use cytological information as an aid in classification of the grasses was that of Avdulov (21), but other extensive investigations of this kind have also been reported (71–74, 120, 153, 224, 516, 525). In addition, detailed determinations of chromosome numbers have been given for species in the tribes Festuceae (77), Phalarideae (269, 359), Oryzeae (376) and Paniceae (60), in the genera *Bromus* (100), *Festuca* (242), *Poa* (18, 52, and others), *Glyceria* (75, 76), *Agropyron* (364, 365, 502), *Hordeum* (14, 135, 363, 541), *Deschampsia* and *Aira* (138), *Danthonia* (63), *Agrostis* (511), *Alopecurus* (188, 534), *Bouteloua* (124), *Paspalum* (59, 487) and *Sorghum* (128, 157, 198, 253, 443), and in miscellaneous species (202, 268, 313 to 316, 326, 330, 481, 490, 512, 524). Determinations of one or a few species are found in many reports. Although the authors, in most instances, did not deal with the general problems of phylogeny and systematics, the chromosome numbers reported are invaluable in presenting a more complete picture of the relationships among species, genera, tribes and subfamilies.

From his extensive investigations of chromosome numbers, size and morphology in the grasses, Avdulov (21) attempted to construct a more natural system of classification. Karyological data were correlated with morphology of flowers, shape of first leaf, anatomy of leaves, structure of starch grains, and ecological distribution. On the basis of these data, he divided the Gramineae into two sub-families, the Sacchariferae and Poateae. The latter was further subdivided into Phragmitiformes and Festuciformes. The Sacchariferae have small chromosomes in multiples of 9 or 10, the Phragmitiformes have small chromosomes in multiples of 12 (this group has many features characteristic of a primitive type), and the Festuciformes have large chromosomes in multiples of 7 or less. Cytologically, evolution has proceeded, according to Avdulov (21), in the first stage by a reduction in number and an increase in size of chromosomes. The decrease in number finally continued without a corresponding increase in size to genera with 6 and 5 as the basic number. This procedure is more true of the Festuciformes which have passed into the colder regions of the world. The Sacchariferae have remained in the tropics, and the chromosome number has not fallen below 9. The final stages of evolution have involved also changes in disposition of the chromatin in the chromosomes, *i.e.*,

in chromosome morphology. Avdulov (21) agrees with Levitskiĭ (239, 240, 241) in considering the more symmetrical chromosomes as more primitive, the derived types having unequal length of arm. This view has been substantiated by findings in *Allium* (236), *Vicia* (491) and *Crepis* (24).

Hunter (153) proposed minor modifications to Avdulov's classification, but, in general, his results supported Avdulov's conclusions. As already pointed out (153, 525), more complete cytological information is required for a number of tribes before an accurate evaluation of the systematics and phylogeny of the Gramineae can be given.

CHROMOSOME NUMBERS

The chromosome numbers of numerous species have been reported in recent years, making available for summary a more extensive list than has been compiled previously (125 to 127, 267, 550). In Table 1, 805 species in 142 genera are recorded. These do not include species of *Triticum, Aegilops, Secale, Avena* or *Zea.* The arrangement of tribes and genera follows Hitchcock (150), and the species are listed, so far as possible, in ascending order of chromosome number.

In 360 species the somatic numbers are multiples of 7. Multiples of 5 occur less frequently (163 species), followed in order by 6(85), 9(82), 8(7), 13(7), 17(5) and 11(3). In compiling these data, species with multiples of 10 were counted as multiples of 5, since it was impossible in many species to determine from chromosome numbers alone whether the basic number was 5 or 10. Similarly, some species included among those with $x = 6$ have numbers that are multiples of 12. Species with $2n = 36$ might be hexaploids ($x = 6$) or tetraploids ($x = 9$). In nine cases it was impossible to determine from related species whether $x = 6$ or 9. Variable chromosome numbers were reported in 16 species, nine of *Poa,* three of *Bouteloua,* two of *Alopecurus,* one of *Deschampsia* and one *Saccharum.* Apomixis occurs in some of the *Poa* species, thus accounting for perpetuation of variable aneuploid numbers. In *Alopecurus,* variability may be attributable to the high degree of polyploidy (120).

The basic number could not be determined in 56 additional species, including 39 of *Stipa* in which somatic numbers of 24, 28, 32,

34, 36, 40, 42, 44, 46, 48, 64, 66, 68, 70 and 82 are known. In each of five *Glyceria* species and, similarly, in several others, multiples of 7 and of 10 have been reported by different authors. It seems probable in such instances that the species was incorrectly identified by one of the authors or that the count was in error. In a few cases, numbers differing by two to four chromosomes were reported, the discrepancy resulting probably from errors in counting or the occurrence of aneuploids.

A basic number of 12 was postulated for the Bambuseae (21, 596). Since species with $2n = 54$ occur, the basic number may be 6, however, instead of 12. A majority of species in Festuceae, Hordeae, Aveneae and Agrostideae have chromosome numbers in multiples of 7. Exceptions occur in each tribe, however. *Phragmites, Schismus* and *Oryzopsis* have $x = 6$ or 12, *Sporobolus* and *Melica* have $x = 9$, *Eragrostis* and *Aleuropsis* have $x = 10$, and *Dupontia* and *Aristida* have $x = 11$. In *Pleuropogon,* the three species reported have $x = 8(77)$, although one collection of *P. californicus* had $2n = 14$. Variations in basic number occur also among species in some genera. *Danthonia, Triodia* and *Trisetum* have species with $x = 6$ and 7; *Milium,* $x = 7$ and 9; *Briza* and *Glyceria,* $x = 7$ and 10; *Koeleria* and *Deschampsia,* $x = 7$ and 13; *Lepturus,* $x = 7$, 9 (or 6) and 13; *Orcuttia,* $x = 6$ (or 12), 8 and 13; and *Muhlenbergia* and *Sporobolus,* $x = 9$ and 10. The extensive aneuploid series in *Stipa* has been noted above.

Chromosome numbers of too few species of Zoysieae, Chlorideae, Phalarideae, Zizaneae and Melinideae are known to indicate the predominant basic number in these tribes. In the Oryzeae, $x = 12$ (or 6) in all species reported except *Lygeum spartum* ($2n = 40$).

Basic numbers of 9 and 10 (or 5) predominate in the Paniceae, Andropogoneae and Maydeae. Four species of *Pennisetum* have $x = 7$, while $x = 6$ (or 12) occurs in some species of *Paspalum,* the two species of *Arthraxon* and in *Tristachya hispida.* Aneuploid series, similar to but less extensive than that found in *Stipa,* occur in *Digitaria,* two species having $x = 8$, an uncommon basic number in the Gramineae. Three species of *Echinochloa* have $x = 17$.

In consideration of the great preponderance of species with chromosome numbers in multiples of 7, it might seem logical to conclude, as Wanscher (584) did, that 7 is the primary basic number of the Gramineae. A difficulty, however, in drawing con-

clusions from the high frequency of species with $x=7$ is that chromosome numbers have not yet been determined for a large proportion of grass species. In Table 1, chromosome numbers are given for species in 142 genera, whereas Hitchcock (150) lists 159 genera of grasses in the United States alone. Furthermore, 7 occurs as a basic number more commonly in the Festuceae, Hordeae, Aveneae and Agrostideae that have their distributions mainly in the temperate and cold regions of the northern hemisphere. Species and genera of these tribes have, in general, been investigated more extensively than those of the tropics and southern hemisphere.

Other evidence has been offered also to support the assumption of 7 as the primary basic number. Huskins and Smith (158) concluded from occurrence of quadrivalents at meiosis in *Sorghum* species and from the existence of duplicate genes in *Zea mays* that these species with $2n = 20$ were polyploid, probably with a primary basic number of 7. Powers and Clark (373) arrived at the same conclusion from a statistical study of pairing at diakinesis in partially asynaptic *Zea mays*. The variability and frequency distribution of paired and unpaired chromosomes were in agreement with the hypothesis that the ten pairs of chromosomes responded as seven independent units.

Five also has been proposed as the primary basic number (120, 130, 317, 362). Five is the lowest basic number found in the Gramineae and seemed, therefore, to be the logical primary basic number (120). Evidence considered (120) to support this hypothesis is secondary association in units of five at metaphase I and II, occurrence of quadrivalents in supposedly diploid species, and bivalent formation in haploids. Secondary pairing of bivalents in five groups was reported in *Oryza sativa* (262, 484) and *Puccinellia vahliana* (120). In the latter case, the two bivalents in each associated group were morphologically similar.

Quadrivalents at diakinesis were reported in *Oryza sativa* (484), and a single quadrivalent has been found in certain plants of the diploid ($2n = 14$) species, *Puccinellia vahliana* (120), *Festuca pratensis* (377), *Dactylis aschersoniana* (281) and *Briza media* (204). Flovik (120) regarded quadrivalents in the diploid species as evidence that 7 was a derived number, presumably from 5. The case of *Briza media* was considered (120) particularly significant because of the existence of *B. minor* with $2n = 10$. On the other hand, some

workers have attributed the quadrivalents to structural hybridity (204, 281, 377). Kattermann's (204, 205, 206) results with *B. media* seem particularly conclusive in that regard.

Bivalents were observed occasionally at metaphase I of meiosis in haploid plants of *Secale cereale* (238, 348), *Triticum monococcum* (*cf.* 120, 159) and *Hordeum distichum* (552). This has been interpreted (120) as supporting the hypothesis that $x = 7$ is a derived number. A similar suggestion was offered by Tometrop (552). On the contrary, Levan (238) did not consider bivalent formation in haploid *Secale cereale* as evidence of secondary diploidy derived from $x = 5$. In contrast to haploids, no evidence from metaphase pairing was found in triploid *Lolium perenne* (300) of homology between chromosomes of the haploid set.

Species with $2n = 10$ occur in *Briza, Anthoxanthum* and *Sorghum*. Flovik (120) considered that species with $x = 10$ were derived from these primary types. Multivalents at meiosis in *Sorghum vulgare* (158) may indicate that this species is a tetraploid instead of a secondary polyploid, as suggested by the authors (158). On the other hand, Garber (128) did not find multivalents in *Sorghum* spp. with $2n = 20$ and questioned the derivation of the *Eu-sorghum* ($2n = 20$) from the *Para-sorghum* ($2n = 10$) group. A related species of the Andropogoneae, *Hyparrhenia hirta,* has $2n = 30$, however, supporting the assumption of $x = 5$ in this tribe (128). Likewise, 15 bivalents are formed in *Narenga porphyrocoma* (166).

Gates (130) and his students, particularly Pathak (362), consider that the number of chromosomes of the haploid set with nucleolus organizers has a bearing on the degree of polyploidy involved. The occurrence of two such chromosomes in some grasses with $2n = 14$ was interpreted as an indication of polyploidy in these forms, thus supporting the assumption of 5 as the primary basic number (130, 362). The unreliability of number of nucleolar chromosomes in determining the existence of polyploidy has been pointed out (31, 300).

Avdulov's (21) conclusion that 12 is the primary basic number was based largely on his assumption that more primitive forms, *Bambusa, Oryza, Ehrharta* and *Phragmites,* have numbers in multiples of 12, whereas some of the more specialized and recently derived groups have numbers in multiples of 5, 6 or 7. Yamaura (596) also considered 12 the basic number in the Bambuseae, but

Hunter (153) questioned this because of the occurrence of species with $2n = 54$. Evidence of polyploidy has been reported in *Oryza sativa* (272, 317, 358, 484) and *Ehrharta* spp. (359), suggesting that 12 may not be the primary basic number. Contrary to the assumption of polyploidy in *Oryza sativa,* bivalents occur rarely or not at all in interspecific hybrids involving this species (149, 318). Furthermore, no species are known in the Oryzeae with any number other than $x = 12$ (except *Lygeum spartum*—$2n = 40$). *Phragmites communis* has been reported with 36, 48 and about 96 chromosomes (Table 1), suggesting a basic number of 6. In this regard it is noteworthy that *Phragmites* may be one of the most primitive grasses; fossil representatives belonging to the genus are known from the middle Tertiary Period and especially from Myocene deposits (120). Six has been found also as the basic number of some species of *Danthonia* which are among the most primitive of the Aveneae (63).

Examination of chromosome numbers in conjunction with evidence available at present on phylogenetic relationships in the Gramineae does not seem to provide critical evidence regarding the primary basic number. The data on chromosome numbers are, in themselves, incomplete, and addition of new data may alter appreciably the frequency of various basic numbers. Furthermore, inaccuracies no doubt exist both in the identification of certain species and in determination of chromosome number. An instance of the first difficulty is found in Church's (74) discussion of Avdulov's (21) data for species of *Spartina.* In order that the cytological analysis be more nearly complete, there is need for supplementing the data on chromosome numbers with information on chromosome morphology, meiotic behavior in species and interspecific hybrids, genetical relationships, and methods of reproduction. Finally, these cytological data must be correlated with morphological, ecological, geographical and paleontological data in order that a more natural phylogenetic system may be devised.

CHROMOSOME MORPHOLOGY

Differences observed in chromosome morphology include size, shape (relative length of the two arms determined by position of the centromere) and presence of secondary constrictions and satellites. Avdulov (21) reported that species included in his Sac-

chariferae and Phragmitiformes had small chromosomes, while species of Festuciformes had large chromosomes. Similar observations have revealed that chromosomes of the Maydeae generally are larger than those of the Andropogoneae (153). In addition to the general size differences exhibited by larger groups, considerable variation has been observed among species of the same genus. *Pennisetum glaucum* has larger chromosomes than is known for any other species of Paniceae (153), the difference, in comparison with *P. purpureum,* being great enough to permit identification of the parental chromosomes in F_1 hybrids (62). Average lengths of chromosomes of *Sorghum versicolor* ($2n = 10$), *S. vulgare* ($2n = 20$) and *S. halepense* ($2n = 40$) were 4.86, 2.24 and 1.98 microns, respectively (198). The much greater chromosome length in the Para-sorghum ($2n = 10$) compared with the Eu-sorghum group ($2n = 20$) was noted also by Garber (128). In *Glyceria,* species with $x = 7$ have large chromosomes similar to those of *Festuca* and of other 7-chromosome grasses, whereas species with $x = 10$ have small chromosomes (75). Nielsen (326) reported variations in length and diameter of chromosomes in root tips of several species. Similar differences were reported for species of *Spartina* and *Andropogon* (75) and for several species of arctic grasses (120). Ghimpu (131) found that the cultivated barleys had a greater total volume of chromosomes than wild species with $2n = 14$. Variations among different plants of the same species have been observed in *Bouteloua* spp. (124), *Lolium perenne* (312, 542) and *Dactylis glomerata* (312).

For use in cytogenetic studies, morphological identification of the individual chromosomes of the genome provides an important tool. Differences in size among the chromosomes within species have been reported for *Lolium* spp. (116), *Melica* spp. (525), *Bromus carinatus* (526), *Sorghum* spp. (128, 157, 163, 198), *Spartina* spp. and *Andropogon* spp. (74), *Festuca elatior* var. *pratensis* (312, 377), *Alopecurus pratensis* (377), *Setaria* spp. (225), *Anthoxanthum odoratum* (359), *Phalaris* spp. (269), several species of arctic grasses (120), *Dactylis glomerata, Lolium perenne, Phleum pratense* (312) and several other species (326). It is probable that careful analysis would reveal differences within genomes in most species of grasses.

Because of variations among plants of the same species and the

influence of fixatives and other conditions on chromosome length, a more critical diagnostic character is chromosome shape, determined by position of the centromere. Variations in this character among chromosomes of the same species have been reported by several investigators (21, 74, 120, 128, 153, 163, 269, 312, 326, 377, 525).

In addition to the primary constriction (centromere), secondary constrictions or satellites form a characteristic morphological feature of certain chromosomes in mitosis. The relationship of secondary constrictions and satellites to the nucleolus was recognized by Heitz (145). Later McClintock (259) demonstrated in maize that nucleolus organization was controlled by a specialized part of the chromosome, the nucleolus organizer. On the basis of these investigations it may be assumed that in most plants two or more chromosomes will have secondary constrictions or satellites in mitotic divisions. Satellites have been observed in *Melica* spp. (525), *Phleum* spp. (292), *Phalaris canariensis* (269), *P. brachystachys* (269) and *Sorghum purpureo-sericeum* (163). Secondary constrictions occur in *Agropyron junceum* (503), *Calamagrostis epigeios* (326), *Stipa pulchra* (326), *Anthoxanthum odoratum* (359) and *Lolium perenne* (300). Both satellites and secondary constrictions have been reported in *Agropyron spicatum* (365), *Muhlenbergia pungens* (326) and *Dactylis glomerata* (312).

In most plants a secondary constriction has been reported in only one or two chromosomes in each genome. In contrast, Flovik (120) reported that "all species have secondary constrictions in all or mostly all chromosomes and frequently in an extremely high number, as for instance in *Phippsia* and *Puccinellia*". In some species of these genera, certain chromosomes had as many as three or four secondary constrictions. Similar observations were reported for *Festuca pratensis* and *Alopecurus pratensis* (377). Failure of other investigators to observe the high frequency of constrictions was attributed (120) to the fixing solution used. In most studies of root tip mitoses the primary objective has been determination of chromosome number. Fixation most favorable for chromosome counting frequently is least suitable for determination of constrictions. It seems probable, however, that the numerous constrictions observed (120) are of a kind different from the secondary constrictions reported by others.

The classical investigations on morphology of mid-prophase chromosomes of *Zea mays* (257) provided an invaluable tool for cytogenetic studies of that species (473 and many subsequent investigations). Preliminary investigations with some species (*Lolium perenne, Sorghum vulgare,* for example) indicate that studies of mid-prophase chromosomes will be much more difficult in many other grasses than in maize. Pycnotic knobs in characteristic positions serve as valuable markers in identification of certain individual chromosomes of maize. Such knobs have not been observed in *L. perenne* (312) or *S. vulgare* (254). In *Phleum pratense* ($2n = 42$) three chromosome pairs, presumably one from each genome, have a single pycnotic knob (292).

CHROMOSOME FRAGMENTS

Centric chromosome fragments have been reported in several species—*Alopecurus alpinus, Dupontia fisheri, D. fisheri* var. *psilosantha, Poa alpigena, P. alpigena* var. *vivipara* and *P. alpina* var. *vivipara* (120), *Briza elatior* (22), *Paspalum stolonifera* (23), *Anthoxanthum odoratum* (153), *A. aristatum* (355), *Agrostis trinii* (511), *Sorghum verticilliflorum* (158), *S. purpureo-sericeum* (163, 164), *Festuca elatior* var. *pratensis* (312, 377), *Alopecurus pratensis* (377), *Dactylis glomerata* (377) and *D. aschersoniana* (281). None of these cases has been investigated as thoroughly as the B chromosomes of *Zea mays* (380), but it has been presumed that the fragments may be analogous to the B chromosomes, at least in some cases.

Avdulov and Titova (23) suggested that fragments found in a plant of *Paspalum stolonifera* probably were devoid of genetic material, impoverishment of the chromosomes representing a step in the process of decrease in chromosome number. In *Anthoxanthum odoratum* the fragments (two pairs of large and one pair of small almost spherical fragments) were less deeply stained than the remainder of the chromosomes (153).

The supernumerary chromosomes of *Sorghum purpureo-sericeum* have been studied more intensively than others reported in the forage grasses. Janaki Ammal (163) considered them morphologically identical with the shortest chromosomes of the normal set. At meiosis the extra chromosomes paired with one another, forming bivalents, trivalents and quadrivalents. Janaki Ammal

(163, 164) considered these chromosomes analogous to the B chromosomes of maize and suggested that 5-chromosome sorghums arose from a basic number of 7, the extra chromosomes representing relics of that process. Darlington and Thomas (104) found in *S. purpureo-sericeum* several types of B chromosomes that paired in meiosis when homologous. A very anomalous behavior has been reported for these chromosomes. B chromosomes were found in the microsporocytes of 40 of the 100 plants examined (164). Root tips were examined from 20 of the plants with B chromosomes in pollen mother cells, and in each case only $2n = 10$ was found. A more nearly complete developmental study revealed that the B chromosomes were lost in the radicle before seed ripening (104). In shoot tissue they were lost as the plants reached maturity but persisted in the ovaries and anthers. The B chromosomes were lost in mitosis by their failure to become oriented on the metaphase plate.

The fragments in *Festuca elatior* usually paired with one another or occurred as univalents, but rarely was a fragment paired with a normal chromosome (312, 377). Similar behavior was found also for the fragments of *Alopecurus pratensis* (377).

In hybrids of *Lolium perenne* × *Festuca arundinacea* one F_1 plant and three plants from the backcross to the male parent had an extra centric fragment about one-half as long as the normal chromosomes (366). The origin of such centric fragments may perhaps be accounted for by misdivision of the centromere (102, 472).

The fragment chromosomes may represent, as has been suggested (23, 163), a stage in the evolutionary process of reduction in chromosome number. On the other hand, they may provide, because of their centromere, a ready mechanism for increase in basic number. More intensive studies of the origin and behavior of centric fragments in the forage grasses are needed.

POLYPLOIDY

Occurrence

Polyploidy occurs frequently in most families of the angiosperms, particularly in the Gramineae, Polygonaceae, Nymphaeaceae, Rosaceae and Malvaceae (521). Among the species and chromosome races summarized in Table 1, more than two-thirds are polyploid or have one or more polyploid races. Polyploid species or chromo-

some races are found in almost every genus, the two principal exceptions being *Melica* (524, 525) and *Lolium.*

A striking feature of polyploidy in the Gramineae is the occurrence, within species, of races differing in chromosome number. Müntzing (279) has considered this phenomenon in detail. In 1936 he (279) estimated that the number of cases of intraspecific chromosome races known in the plant kingdom was something over one hundred. In Table 1 there are recorded 99 species with chromosome races, not including *Poa pratensis* and others in which the persistence of aneuploid forms is attributable to apomixis. Included among the species with intraspecific chromosome races are several of the important forage grasses. An extreme example of polyploid races within species is *Panicum virgatum.* In 59 collections, Nielsen (328) found $2n$ numbers of 18, 36, 54, 72, 90 and 108 chromosomes ($2x$, $4x$, $6x$, $8x$, $10x$ and $12x$). Among 17 collections (isolates) obtained from an area of not more than ten acres near Chippewa Falls, Wisconsin, $2x$, $4x$, $6x$, $8x$ and $10x$ forms were found.

Chromosome races occur in some species known to be highly variable. *Festuca elatior,* for example, is separated taxonomically into several varieties (242, 516) that have been given specific rank by some authorities. In other species, such as *Bromus inermis,* taxonomic varieties are not recognized (150). Müntzing (279) concluded that intraspecific chromosome races are always more or less different morphologically, but Nielsen's (328) results were contrary. In an intensive study of variation in *Panicum virgatum,* Nielsen (328) measured several characters that might prove useful in the morphological separation of the chromosome races. Considering all possible comparisons among isolates with different chromosome numbers, 66.4% showed statistically significant differences, while among isolates of the same chromosome numbers, 58.6% of the differences were significant. Thus differences were found among isolates of the same chromosome number almost as frequently as among those from different chromosome races.

Types of Polyploids

Cytologists have agreed generally upon classification of polyploids as autopolyploids and allopolyploids. This classification may be based either upon origin of the polyploid or upon degree of

differentiation of the genomes of the polyploid. On the former basis, autopolyploid refers to derivatives of chromosome doubling within a fertile species, whereas allopolyploid refers to derivatives of doubling in interspecific hybrids. On the second basis of classification, the autopolyploid has three or more genomes that are structurally identical (although they may be genetically different), while the allopolyploid has two or more different genomes. Neither system of classification is entirely satisfactory, the basic difficulty being that polyploids are not differentiated naturally into two discrete classes. At one extreme there may be polyploids derived by repeated chromosome doubling from the haploid (247), while at the other extreme are types derived from species hybrids in which chromosome pairing does not occur (193). Most naturally occurring polyploids probably occupy an intermediate position with regard to chromosomal differentiation.

There is no universal agreement on what constitutes a valid species, and the sterility of species hybrids varies within wide limits. Furthermore, in the analysis of established species it is impossible in many cases to postulate with certainty the mode of origin, whether by doubling of the fertile species or by doubling in the hybrid between two closely related species in which chromosomal differentiation has not proceeded very far. From the standpoint of application to existing polyploids a classification based upon differential affinity of the chromosomes of different genomes seems most appropriate, for it is this characteristic that is basic to the cytogenetical behavior of the species. For the purposes of this classification, however, observations of multivalent frequency in meiosis will be inadequate. There will be required a careful cytological and genetical analysis of the species and, in many cases, of species hybrids, polyploids and nullo- and polysomics.

Information on type of poylploidy is available for relatively few forage grasses, the most completely investigated being *Dactylis glomerata* and *Phleum pratense*. In *D. glomerata,* Müntzing (275, 281) reported the regular occurrence of quadrivalents in meiosis, the maximum number of 7 having been observed in some sporocytes. In F_1 of *D. glomerata* × *D. aschersoniana* meiotic behavior was of the type expected in an autotriploid (281). On the basis of these cytological data he (275, 281) concluded that *D. glomerata* is an autotetraploid derived by chromosome doubling from *D. ascher-*

soniana. Confirmatory evidence was provided by studies of polyhaploid plants ($2n = 14$) of *D. glomerata* (285). These plants resembled *D. aschersoniana* morphologically and had a regular meiosis with seven bivalents. The above reports (281) of meiotic behavior in *D. glomerata* have been substantiated (296, 297, 307–310). Furthermore, the assumption of autopolyploid behavior has been verified genetically (290, 293, 304).

Phleum pratense was originally considered an allohexaploid (278). From chromosome doubling in the hybrid *P. pratense* ($2n = 14$) $\times$ *P. alpinum* ($2n = 28$), fertile hexaploid plants were obtained that produced fertile offspring when crossed with hexaploid *P. pratense* (132, 134). This was one of the early instances of synthesis by hybridization and chromosome doubling of an existing polyploid species. Additional cytological evidence supporting the hypothesis of allohexaploidy was the reported absence of multivalents at metaphase I (278, 287, 349). There were rather limited genetical data available. Typical monohybrid ratios were reported for resistance to rust (25, 78, 306). Clarke (78) explained the occurrence of chlorophyll-deficient seedlings among inbred progenies by the assumption of triplicate factors. In similar material Wexelsen (587) obtained results interpreted on the basis of single, duplicate and triplicate factors, assuming that the species was an allohexaploid. In two families, however, the results suggested the possibility of tetrasomic inheritance.

In contrast with the cytological results previously obtained, 14 bivalents were found (347) in F_1 of *Phleum pratense* ($2n = 14$) $\times$ *P. pratense* ($2n = 42$), 28 bivalents were found (287) in 63-chromosome timothy plants obtained from twin seedlings, and a maximum of 12 bivalents were observed (292) in F_1 of *P. pratense* ($2n = 42$) $\times$ *P. subulatum* ($2n = 14$). In polyhaploid ($2n = 21$) plants obtained from twin seedlings there was variable pairing from seven bivalents plus seven univalents to 21 univalents, the former being the most common condition (237, 349). In addition, occasional trivalents were observed. In *P. pratense* ($2n = 14$) $\times$ *P. alpinum* ($2n = 28$), the frequency of trivalents, bivalents and univalents was similar to that found in autotriploid *P. pratense* ($2n = 14$). Diploid *P. pratense* and tetraploid *P. alpinum* are the putative parents of hexaploid *P. pratense* (132, 134). Thus, the

results (349) suggest homology between chromosomes of the genomes of *P. pratense* ($2n = 42$).

Consistent with these results, further studies (302) of meiosis in plants of hexaploid *Phleum pratense* revealed a frequency of quadrivalents ranging from 0 to 7 per sporocyte, the average being 2.9 to 4.9 for the seven plants. Also sexivalents occurred in about one-third of the sporocytes, the frequency varying from 1 to 3. Genetic data (302) from first and second generation inbred progenies of five unrelated plants confirmed the cytological evidence that this species is not an allohexaploid. It was impossible from the cytological and genetical data available to determine whether there were six homologous genomes or four genomes of one kind and two of another.

On the basis of the regular and frequent occurrence of quadrivalents in meiosis, autopolyploidy has been postulated for *Arrhenatherum elatius* (203, 307, 308), tetraploid *Agropyron cristatum* (307, 308), *Anthoxanthum odoratum* (203, 355, 359), *Hordeum bulbosum* (31, 70) and *Poa palustris* (212). In *Agropyron cristatum* and *Anthoxanthum odoratum* there are related diploid forms from which the tetraploid races presumably arose by chromosome doubling. No critical genetical data have been reported for any of these species.

Other reports of autopolyploidy, based, however, upon rather meager evidence, include *Eleusine coracana* (224), *Phippsia algida, P. concinna, Puccinellia angustata, Dupontia fisheri, Trisetum spicatum* (120), *Festuca ovina* (558), *Briza media* and *Agrostis trinii* (478). Müntzing (279) considered that most of the polyploid intraspecific chromosome races were autopolyploid, and developed several lines of evidence to support his assumption. Contrary to the report (224), based upon limited cytological evidence, of autopolyploidy in *Eleusine coracana,* the genetic ratios (387–390, 397, 398, 400–404, 580) agree more closely with those expected in an allopolyploid.

In the 72 chromosome race of *Tripsacum dactyloides,* 6_{IV} were formed commonly in meiosis, whereas 18_{II} were always found in the 36-chromosome race. From these results Anderson (12) concluded that the latter race is an allopolyploid with two highly differentiated genomes. The 72-chromosome race arose from

chromosome doubling in the hybrid of this race with another allotetraploid with one common genome.

Multivalents have been observed at meiosis in a few other polyploid species. The occurrence of quadrivalents and sexivalents at meiosis in *Sorghum vulgare* and of quadrivalents, sexivalents and octavalents in *S. halepense* has been reported (158). Occasional quadrivalents and other multivalents were found in *Brachypodium pinnatum* (202), *Bromus erectus* var. *eu-erectus* (203), *Alopecurus alpinus, Calamagrostis neglecta, Festuca rubra* and *Puccinellia phryganodes* (120), *Phalaris minor* and *Ehrharta calycina* (359), *Agropyron junceum* and *A. repens* (352), *Festuca elatior* var. *arundinacea* (312), *Agropyron glaucum* and *A. elongatum* (367), and *Lygeum spartum* (376). Multivalents were not observed at meiosis in *Bromus inermis* (217), *B. mollis* (219) and *Alopecurus pratensis* (377).

More critical cytological and genetical studies are needed in many species before a reliable evaluation of the incidence of auto- and allopolyploidy can be made. These data are not available at present, even for a majority of the most important forage grasses.

On the assumption of monophyletic origin of the Gramineae, a large part of the species must be secondary diploids and polyploids. Evidence for secondary polyploidy usually is based on the occurrence of secondary association at metaphase of meiosis which is presumed to result from relic homologies (235). This hypothesis has been criticized (144) and discussed (68). Secondary association has been observed in several grass species (120, 317, 359, 484).

Characteristics of Natural Polyploids

Polyploids are known to differ morphologically and physiologically from related diploids. These differences have been summarized by others (36, 101, 279, 521). In general, they may be attributed, to a considerable extent, to the larger nucleus and cell resulting from chromosome doubling. Differences due to recombination of genes from different species (in allopolyploids) would not be constant features of polyploids in general. Stählin (516) reported that with an increase in chromosome number in the grasses from diploidy to tetra- and hexaploidy there was generally an increase in plant size and organ size. With further increase in

chromosome number to octo- or decaploidy there was no further increase in plant size; there was in some instances, in fact, a decrease. Müntzing (279) likewise postulated a maximum favorable chromosome number (which differs from one genus to another) above which there was no beneficial effect of increased numbers. In *Dactylis,* pentaploid derivatives of *D. aschersoniana* × *D. glomerata* may be more vigorous than the tetraploid, but an octoploid ($2n = 56$) plant was dwarf and could not be kept alive (281).

Hagerup (137) was one of the first to recognize the relationship of polyploidy in plants to their ecological adaptation and geographical distribution. In this connection he stated that polyploids have acquired new genetical and morphological characters whereby they are enabled to grow in other localities, so they can have a new ecological and phyto-geographical value. Among the flora of Timbuktu, one grass genus was studied. *Eragrostis cambessediana* ($2n = 20$) was annual and limited to the seashore where soil and atmosphere were always moist. *E. albida* ($2n = 40$) was very similar but was perennial and occurred in places of intermediate moisture, while *E. pallescens* ($2n = 80$) was a complete xerophyte. Later, Hagerup (138) reported that the tetraploid and octoploid species of *Deschampsia* have a wider ecological and geographical range than the diploid. Similar results were obtained by Tischler (551). In the flora of Schleswig-Holstein, among the species of which the chromosome numbers are known, 44% are polyploid. The frequency of polyploids varied, however, from 60% in the north to 27% in the south. The percentage of polyploidy is higher in the Faroe Islands but lower in Sicily than in Schleswig-Holstein. Studies of the flora of Schleswig-Holstein were extended by Rohweder (477). In the ditches of certain marshes flooded daily with the lime-bearing tidal waters of the Elbe, 95% of the species were polyploid. Likewise, in the Great Wapelfeld Moor with marl sub-soil, 79% of the species were polyploid, while in more recent land formations, the Island of Amrum, only 38% of polyploids are found.

In the high mountain regions of Pamir and Altai about 150 and 200 species, respectively, mostly Gramineae, were studied. Of these, 85% and 65%, respectively, were polyploids (512). The genera *Poa* and *Alopecurus* were represented in the highlands by polyploids (*P. alpina, P. altaica, P. tibetica, A. vaginatus, A.*

mucronatus, etc.), but migration into the highlands was not always concomitant with increased polyploidy. Apparently migration to the north usually was accompanied also by increased incidence of polyploidy. A similar correlation between high polyploidy and extremes of climate was observed in *Alopecurus* (534) and *Agrostis* (511). In the latter genus, the polyploid species occur on the eastern and northern limits of the range of distribution and in alpine regions.

Most of the arctic grasses studied by Flovik (120) were polyploids, some (*Alopecurus alpinus*—$2n = 112$ and 114) with very high chromosome numbers. Among 68 species and varieties from Spitzbergen (some of them grasses), 80% were polyploids (121). The only diploid grass found was *Puccinellia vahliana* ($2n = 14$). This represented an exception to the general rule that polyploid species had a more northern distribution; polyploid species of *Puccinellia* occur to the south. Increase in percentage of polyploids with increased latitude has been reported also by Löve and Löve (255). A high frequency of polyploids was found among the forage grasses of California where tolerance to heat and drouth is essential for survival (525). Polyploidy and tolerance were correlated. For example, five grasses were collected in the Mohave Desert. Three of these, *Poa secunda, Elymus condensatus* and *Sporobolus airoides,* are high polyploids; *Oryzopsis hymenoides* is the only polyploid yet known in the genus, while *Stipa speciosa* has one of the higher chromosome numbers of its genus (525).

In addition to variations in distribution and adaptation between diploid and polyploid species, there have been reported also numerous instances of differences among intraspecific chromosome races in this respect. Müntzing (279) summarized 38 cases for which data on ecology and distribution were available and concluded that intraspecific chromosome races are probably almost always different ecologically.

The two races of *Phleum pratense* ($2x$ and $6x$), although occurring in the same locality, occupied ecologically different habitats (132). Diploid *P. alpinum* was obtained from Switzerland, the tetraploid forms from Scotland and northern Scandinavia (279). According to Gregor and Sansome (134), the tetraploid forms were decidedly more vigorous than the diploid. The distribution of *Dactylis aschersoniana* is limited, whereas the autotetraploid *D.*

glomerata has spread throughout the temperate zones of the world as an important forage grass (279). In *Festuca,* polyploid races had contributed to the extension and distribution of the genus (178, 180). As forage plants, tall fescue (*F. elatior* var. *arundinacea,* $2n = 42$) is known to be adapted to drier and more impoverished soils than meadow fescue (*F. elatior,* $2n = 14$).

To these examples may be added several others including *Glyceria fluitans* (75), *Poa annua* (250), *Agropyron junceum* (502, 503, 504, 356) and *A. elongatum* (503). Tetraploid ($2n = 20$) plants of *Anthoxanthum odoratum* have been reported several times but diploids only once (355), indicating a wider distribution of the tetraploid.

It is apparent that an imposing array of evidence has been accumulated indicating that polyploid species of the Gramineae tend to be adapted to a wider range of ecological conditions and to occupy wider geographical distributions than their diploid relatives. Exceptions have been noted, however. The case of *Puccinellia vahliana* (120) has been cited. Stebbins and Love (525) found that differences in drouth and heat tolerance in California grasses apparently were limited to allopolyploids; in their material intraspecific chromosome races (autopolyploids) did not show differences in distribution. Likewise, Nielsen (328) did not find evidence of regional segregation on the basis of chromosome number of races of *Panicum virgatum.* Bowden (39) compared the winterhardiness of 100 species and varieties of angiosperm (none of them a grass, however) with their chromosome numbers and was unable to find a relationship between degree of polyploidy and winterhardiness.

Origin of Polyploids in Experiments

In the forage grasses, polyploids have been obtained experimentally from three sources: (*a*) induction by colchicine or heat treatment, (*b*) twin seedlings, and (*c*) sporadic occurrence in genetic and breeding stocks.

Heat treatment was shown (378) to be effective in causing chromosome doubling in early mitoses of the young embryo of maize. This method has been applied successfully also to some other species but has not been used extensively in the forage grasses. Peto (368), in attempts to produce amphidiploid hybrids of *Triticum vulgare* × *Agropyron glaucum,* applied a variety of heat treatments

to wheat florets following pollination with *A. glaucum*. Only one plant from over 13,000 treated florets showed chromosome doubling.

Discovery of the efficacy of colchicine in inducing chromosome doubling (34, 35, 322, 323) provided a generally and easily applicable method for production of polyploids. By use of colchicine, autotetraploids have been produced in *Lolium perenne* and *L. multiflorum* (147, 289, 495), *Sorghum vulgare* var. *sudanese* (*cf.* 289, 485), *Panicum miliaceum* (16), *Stipa lepida* (523), *Dactylis aschersoniana* and *Festuca elatior* var. *pratensis* (312). A 12-ploid ($2n = 84$) plant of *Phleum pratense* was also produced (284). Chromosome doubling was induced in *L. perenne, F. elatior, D. aschersoniana* and *S. lepida* by treatment of germinating seeds. Most of the plants were mixoploid, and, in *L. perenne*, $2x$ and $4x$ clones were established by repeated vegetative propagation with single tiller isolates (147). Colchicine treatment has been used also in production of fertile amphidiploids from sterile hybrids of *Agropyron glaucum* with varieties of *Triticum vulgare, T. durum, T. turgidum, T. dicoccum* and *T. pyramidale* (19, 370).

Polyembryony (586), resulting in twin seedlings, occurs relatively frequently in some grasses, *Poa pratensis* for example, and occasionally in other species. In most of the twins, the two seedlings are similar morphologically and have the same chromosome number; in some cases the twin plants differ phenotypically but have the same chromosome number; in other pairs the twin plants differ both phenotypically and in chromosome number. Ordinarily the deviating plants have one-half as many as or more than the normal number (termed haploids and triploids for convenience, although where a polyploid species is involved these terms are not strictly correct). Müntzing (280, 282) examined twin seedlings from species of 11 genera, including nine forage grasses. The frequency of plants with deviating chromosome numbers varied from 0 to 9% in the different species. Müntzing (282) concluded that the plant with the deviating number was almost invariably smaller and weaker as a seedling than the normal twin. On the other hand, Skovsted (508) found in some instances differences in chromosome number that were not associated with differences in size of seedlings. Also, he reported a higher frequency of twins with deviating number than Müntzing (282) found. Triploid and haploid plants of *P. pratense* and a haploid plant of *D. glomerata*

have been obtained from twin seedlings (346). It is evident that twin seedlings provide, in the grasses, a less fertile source of polyploids than colchicine treatment.

Ordinarily polyploids do not occur in sufficient frequency in untreated material to be of significance experimentally. Nevertheless, a few have been obtained, including autotriploid plants of *Pennisetum typhoides* (228) and *Phleum nodosum* (349) and autohexaploid plants of *Alopecurus pratensis* (188) and *Dactylis glomerata* (312). Occasionally, functioning of unreduced gametes has resulted in polyploids in crosses between species—a triploid F_1 from *Lolium loliaceum* × *L. rigidum* (184) and a triploid ($2n = 66$) from *Saccharum spontaneum* ($2n = 56$) × *Sorghum durra* (161). In *Paspalum urvillei* ($2n = 40$) × *P. malacophyllum* ($2n = 40$) the F_1 had 40 chromosomes. In F_1 × *P. dilatatum* ($2n = 40$) the plants had 60 chromosomes (61). In the hybrid *Festuca arundinacea* ($2n = 42$) × *F. pratensis* ($2n = 14$) the F_1 had 28 chromosomes. Progeny were obtained only from seed produced with open-pollination. Among these were plants with 35, 42, ± 49, 63 and 77 chromosomes (342). Likewise, a 35-chromosome plant was obtained (335) from a seed produced by open-pollination on the F_1 of hexaploid *Festuca rubra* × *Lolium perenne*.

Amphidiploids have been discovered in *Phleum pratense* ($2n = 14$) × *P. alpinum* ($2n = 28$) (132, 134, 350), in *Festuca arundinacea* ($2n = 42$) × *F. gigantea* ($2n = 42$)—in the fertile derived polyploid $2n = 84$—(339), and in hybrids between species of *Triticum* and *Agropyron* (208–211).

Characteristics of Experimental Polyploids

Most determinations of effects of chromosomal reduplication are complicated by gene differences that may accentuate or obscure differences between the diploids and the induced polyploids. This difficulty may be obviated by use of genetically homozygous material or by vegetative propagation from plants that are sectorial chimeras or mixoploids of diploid and polyploid tissue. The latter method was used in *Lolium perenne* (147). Morphologically the autotetraploids were distinguishable from the related diploids in having somewhat wider, thicker and longer leaves, thicker but fewer tillers, longer leaf sheaths, and larger florets, spikelets, pollen grains and seeds. The stomata also were slightly larger, but the two types

could not be distinguished on that basis. Under favorable cultural conditions the $2x$ and $4x$ clones could, in most cases, be identified readily by appearance. There was, however, evidence of a differential response to chromosome doubling; in some pairs the morphological differences were slight (304). These effects of chromosome doubling on morphology are similar to those reported generally (36, 279, 521). Autotetraploids of *Stipa lepida,* likewise, had larger floral parts but differed in showing no evidence of broader and thicker leaves (523). In *Panicum miliaceum,* autotetraploids had larger spikelets and seeds (16).

A striking effect of chromosome doubling in *Lolium perenne* was the greater sensitivity to winter injury of the autotetraploids (304). This behavior was unexpected in view of the generally more northerly distribution of polyploids in the grasses, but is consistent with results obtained with tetraploid rape and tomatoes (482, 493). Also contrary to the usual effect of chromosome doubling, no differences were found between related $2x$ and $4x$ clones of *L. perenne* in maturity nor in growth rate, except in rapidity of production of new tillers (304). On the other hand, the tetraploids of *Stipa lepida* were all slower in growth and later in maturity than their diploid relatives (523).

In greenhouse experiments, relative yields were determined in eight pairs of diploid and tetraploid clones of *Lolium perenne* grown in soil and in gravel and subjected to different frequencies of defoliation by clipping (513, 514). Statistical analysis of the data showed an effect upon plant yield of chromosome doubling and that the effect was significantly altered by the genotype involved (pairs of clones from different original seeds), the medium in which the plants were grown, and the clipping treatment used for evaluation. In yield of tops the tetraploids did not differ significantly from the diploids when all clones and treatments were averaged. On the other hand, average yield of stubble and of roots of the diploids significantly exceeded that of the tetraploids. Variation in response to chromosome doubling was reported also in *Stipa lepida* (523). Some autotetraploids were more vigorous and others less vigorous than their related diploids. Triploids ($2n = 63$) of *Phleum pratense* and their seed progenies ($2n = 56$ to 64) were more vigorous and higher yielding than normal 42-chromosome plants (284, 286, 287). Of these, plants with $2n = 56$ (exactly $8x$) were most vigor-

ous of all. A 12-ploid plant ($2n = 84$) produced by colchicine proved to be inferior; its chromosome number was above the optimum for the genus (287).

In general, the effects of chromosomal reduplication in *Lolium perenne* on chemical composition were of small magnitude (535, 536). The tetraploids were higher in moisture, sucrose, total sugar and percentage of dry matter soluble in 80% alcohol. No difference was found in nitrogen content. The genotypes responded in a differential manner to chromosomal reduplication in regard to cellulose and lignin content. There have been reports of differences in chemical composition resulting from chromosome doubling in several other species, none of them forage grasses, however (*cf.* 26 for recent literature).

Autopolyploids obtained in experiments have been reduced in fertility compared with related diploid species, and autopolyploids in the forage grasses are not exceptional in that regard. Reduced fertility has been found in *Lolium perenne* and *L. multiflorum* (495), *Panicum miliaceum* (16) and *Stipa lepida* (523).

Evolutionary Significance of Polyploidy

The importance of polyploidy in the formation of new species and in extending the range of ecological adaptation and geographical distribution of genera and species is now generally recognized (101, 107, 279, 521, *et al.*). Stebbins (521) stated that of the many processes which have been active in plant evolution, only polyploidy is well enough understood from the cytological point of view to permit a safe estimate of its rôle in species formation.

With reference to the Gramineae, Avdulov (21) concluded that polyploidy played little or no part in the evolution of major groups, even genera. Its effect has been confined to evolution within the genus and frequently within a section of the genus. Even within *Festuca,* evolution from the Bovinae to the Ovinae has occurred without change in chromosome number (242). The present viewpoint of the functions of polyploidy has been adequately summarized by Stebbins (521) whose views are in agreement with those expressed by Avdulov (21) and several other investigators. Stebbins (521) attributed to polyploidy a major rôle in the formation of new species and races of plants. These new forms owe their characteristics, in part, to effects of chromosome doubling, but more par-

ticularly to the bringing together and recombination of genes from diverse forms. Stebbins (521) distinguished between the origin of species and evolution itself, and concluded that polyploids have not been and could not be expected to be the starting point of a new evolutionary line. Compared with diploids, a polyploid complex tends to be a closed system. Huskins (156) expressed agreement with this hypothesis.

The dominant rôle of polyploidy in speciation usually has been attributed to allopolyploids (107, *et al.*), but Müntzing (279), although recognizing the importance of allopolyploidy, presented considerable evidence of the importance of autopolyploidy. Stebbins (521) concluded that the relative importance of chromosome doubling alone compared with allopolyploidy varies with different genera. Thus allopolyploidy is the important factor in *Crepis* (24, 521), whereas in *Tradescantia* autopolyploidy has assumed the dominant rôle (13).

Abundant evidence of the importance of polyploidy is found in the Gramineae. Included among the polyploids are most of the widely distributed and economically important forage grasses (294). In fact, relatively few of the important forage species are diploid—*Lolium perenne, Festuca elatoir* var. *pratensis, Agropyron cristatum* (the Fairway strain but not the commercial forage strains which are autotetraploid), *Pennisetum glaucum* and *Setaria italica.*

MONOHAPLOIDS AND POLYHAPLOIDS

Haploids were divided by Katayama (*cf.* 159) into monohaploids (from diploid species) and polyhaploids (from polyploid species). Monohaploid (polyhaploid ?) plants of *Sorghum vulgare* occur relatively frequently and are characterized by being smaller than normal and highly sterile (51). At midprophase, synapsis of the chromosomes was nearly complete. Bivalents were observed at metaphase I, and dicentric bridges occurred at anaphase I.

Two polyploid plants of *Dactylis glomerata* were less than half the size of normal tetraploids and showed some resemblance to *D. aschersoniana,* the putative parent of *D. glomerata* (285). In one plant the anthers degenerated prior to meiosis. In the other, seven bivalents were formed regularly in meiosis, but no functional pollen was produced (285).

Polyhaploid plants (somatic number = 21) of *Phleum pratense*

were smaller and weaker than the hexaploids and were kept alive only with difficulty (349). The heads and spikelets especially were smaller, and the plants were both male and female sterile. Microsporogenesis was very irregular; the most frequent pairing in meiosis was seven bivalents plus seven univalents (349), but variations from seven bivalents plus seven univalents to 21 univalents occurred (237). The most striking irregularity was cell fusion in meiotic prophase, from two to 30 pollen mother cells fusing to form one large syncytium. At metaphase I, these large cells formed a single bipolar spindle with all bivalents on one regular equatorial plate (237).

Polyhaploids of *Poa pratensis* have been obtained several times (329, 533) from twin seedlings. One polyhaploid (329) was markedly different in size and vigor from its normal twin. The plant had 28 chromosomes plus a fragment, and produced a high frequency of aposporous embryo sacs, but the seed was not viable. A polyhaploid of *Stipa cernua* was shorter than normal but relatively vigorous, and was completely sterile. At meiosis, 35_I occurred in about one-third of the sporocytes, with one or two bivalents plus univalents in the remainder (256).

ANEUPLOIDS

Variable and aneuploid chromosome numbers have been reported commonly in some of the species of *Poa*, particularly *P. pratensis* and *P. alpina*. In these species, the aneuploid numbers are perpetuated by apomixis. This subject will be considered in more detail later. Variable numbers have been found also in *Alopecurus alpinus* (120, 188) and *A. antarcticus* (188). Flovik (120) concluded that there was no constant number for *A. alpinus*, the variation being conditioned by autopolyploidy and by viability of aneuploids due to the very high chromosome number ($2n = 112$, 114, 119 to 122). A similar situation probably obtains also in *A. antarcticus* ($2n \doteq 112$ to 116).

Aneuploid plants have been found occurring naturally or among the progenies of euploid parents in *Lolium perenne* (304), *Agropyron cristatum* (288, 308, 365), *Arrhenatherum elatius* (308), *Festuca arundinacea* (366), *Phleum pratense* (304) and *Dactylis glomerata* (275, 281, 308). Of these species, only *L. perenne* is diploid. The remaining species except *F. arundinacea* have meiotic

behavior characteristic of autopolyploids, and, hence, aneuploidy is expected.

The most extensive studies of the occurrence of aneuploids have dealt with *Dactylis glomerata.* Müntzing (275, 281) found 10% of aneuploids on the basis of "accurate values" and 19% on the basis of "total values" among the plants of eight progenies, all the parents of which were probably euploid. Among plants from open-pollinated populations, Myers and Hill (308) reported about 40% aneuploids, while in progenies of euploid plants, aneuploids occurred in frequencies varying from 5% to 27% (312). The incidence of aneuploidy is particularly high among the progenies of aneuploids. Among 76 plants of the progeny of a 29-chromosome plant, 29 had 28 chromosomes, two had 27, 30 had 29, 14 had 30, and one had 31 (275). Among the offspring of 27-chromosome plants, 26-chromosome plants were expected but none was obtained. Part of the plants were $2n = 27$ and part $2n = 28$. In all cases investigated there was a tendency for progenies of aneuploid plants to revert to the normal number of 28. In types with less than 28 chromosomes, gametic and zygotic selection are important factors, while in plants with more than 28, the extra chromosomes are lost frequently during meiosis (281).

From backcrosses of *Dactylis aschersoniana* × *D. glomerata* to *D. aschersoniana,* Mün' g (281) obtained plants with chromosome numbers from 14 to 20. In backcrosses of the F_1 to *D. glomerata,* the chromosome numbers of the progeny varied from 22 to 41 and one plant had 56 chromosomes. Thus there was established an almost continuous series of numbers from 14 to 41. Selfed progenies of pentaploid plants ($2n = 35$) likewise contained plants with somatic numbers varying from 28 to 41.

Among 119 plants from seed produced by open-pollination (pollen from diploid plants) on an autotriploid plant of *Lolium perenne,* 25% had $2n = 14$, and the remainder had 15 to 18 chromosomes (300). In progenies of various trisomic plants pollinated with pollen from diploids, the incidence of trisomics varied from almost 50% to less than 5% (304).

An aneuploid series was established in *Phleum* (349) from triploid *P. nodosum* ($2n = 21$) × *P. pratense* ($2n = 42$) and in the progeny of 63-chromosome plants of *P. pratense* obtained from twin seedlings (287). In the former case the chromosome numbers varied from 33 to 44 and in the latter from 56 to 64.

In the euploid and aneuploid plants of *Dactylis,* Müntzing (281) found a progressive increase in vigor through the series 14, 21, 28 and 35. Plants with chromosome numbers between these euploids showed reduced vigor, the reduction being greatest in each case approximately at the mid-point, *i.e.,* the greatest deviation from a multiple of 7. The 56-chromosome plant was weak and died before flowering. In *Phleum* the entire group of plants with chromosome numbers from 56 to 64 were more vigorous than normal hexaploids, while plants with 56 to 58 chromosomes were more vigorous than those with 59 to 61 (287).

It is well known from the investigations of *Datura* that different trisomics frequently may be recognized from the phenotypes of the plants. Similar but less complete results have been obtained for the pentasomics of *Dactylis glomerata* (281) and the trisomics of *Lolium perenne* (304). In the latter case, however, one of the trisomics had no observable effect upon the phenotype, at least when the plants were grown in the greenhouse.

MEIOSIS

Normal Meiosis

Meiosis has been observed in more than 80 species of grass (exclusive of *Triticum, Aegilops, Secale, Avena, Oryza* and *Zea*). In most reports only general statements were made; details of the extent of observations and the frequency of various irregularities have been given only in relatively few cases. Furthermore, the investigations frequently were limited to one or a few plants of the species. Thus more complete studies of larger numbers of plants may reveal in many species features of meiotic behavior not now known.

Meiosis has been reported to be regular in *Phalaris coerulescens, P. paradoxa* (359), *P. canariensis* (202, 359), *Zizania aquatica* (376), *Bromus mollis* (219), *B. carinatus* and *B. catharticus* (526), *B. arizonicus* (527), *Puccinellia angustata* (120), *Andropogon furcatus, A. scoparius, A. virginicus, A. glomeratus, Festuca capillata, F. elatior* var. *pratensis, Spartina patens* var. *juncea* and *S. cynosuroides* (71, 72, 74), *Hordeum* spp. (14), *Eleusine indica* (224), *Agropyron tenerum* (=*A. trachycaulum*), *A. richardsonii, A. caninum* and *A. dasystachyum* (365), *Paspalum gayanus* and *Poa resinulosa* (490), and *Oryzopsis hymenoides* and *Stipa viridula* (185).

Irregularities of Meiosis

Quadrivalents and other multivalents occur with such regularity in certain instances that the species are considered to be autopolyploids. The meiotic behavior of such species will be discussed later (*cf.* Meiosis in Autopolyploids). Low frequencies of quadrivalents, resulting presumably from autosyndesis, have been reported in several other species (*cf.* Types of Polyploids).

Aside from multivalent formation, the most commonly reported irregularity of meiosis has been the occurrence of univalents at metaphase I and lagging chromosomes at anaphase I. Unpaired chromosomes at metaphase I have been reported in *Calamagrostis neglecta, Puccinellia phryganodes, Trisetum spicatum* (120), *Agrostis nebulosa* (546) and *Dactylis aschersoniana* (202). In these cases the behavior of the univalents was not reported. The occurrence and behavior of univalents at metaphase I were investigated in *Lolium perenne* (291). The univalents usually became oriented on the equatorial plate somewhat later than the bivalents and divided equationally at anaphase I. The daughter half chromosomes were sometimes left in the cytoplasm at telophase I, but, more commonly, they were included in the daughter nuclei and lagged and were lost in the second division. This type of univalent behavior in meiosis occurs frequently and had been reported among forage grasses in *Festuca elatior* (312), *Dactylis aschersoniana* (281), in the interspecific hybrids *Phleum pratense* ($2n = 42$) × *P. subulatum* (292), *P. pratense* ($2n = 14$) × tetraploid *P. alpinum* (349), *Agropyron junceum* × *A. repens* (352), *Dactylis aschersoniana* × *D. glomerata* (281), and *Festuca elatior* ($2n = 42$) × *Lolium perenne* (312). (*cf.* also Meiosis in Autopolyploids.) In contrast, the univalents of polyhaploid *P. pratense* ($2n = 21$) passed at random to the poles and split only rarely, while in triploid *P. nodosum* ($2n = 21$) an average of 4.68 univalents was observed at metaphase I and only 1.81 univalents were seen to divide at anaphase I (349). Univalents at metaphase I and laggards at anaphase I have been reported also in *Bromus inermis* (217), *B. villosus* (27), *Deschampsia alpina* (120), *Agropyron junceum, A. repens* (352), *Poa pratensis* (18), *P. caesia, Alopecurus fulvus* and *A. myosuroides* (84). The quantitative relationship of metaphase I univalents and anaphase I laggards was not reported in these cases. Church (71, 72) reported univalents and laggards in several spe-

cies. In the species reported in one paper, however, he (71) made an effort to select for study plants that produced poor pollen. Therefore, the meiotic behavior may not be typical for normal plants of the species.

Lagging chromosomes at anaphase I were observed in *Pennisetum typhoideum* (381), *Bromus marginatus* and *B. rubens* (27). Presumably these laggards resulted from unpaired chromosomes at metaphase I. Relatively high frequencies of laggards at anaphase I were found in *Agropyron amurense, A. intermedium, A. repens* and *A. trichophorum* (9). Irregularities of meiosis (not described) and considerable sterility occur in *Paspalum intermedium* (490). A case of complete asynapsis that was heritable was found in *Alopecurus myosuroides,* and some plants of *A. pratensis* were partially asynaptic (188). In addition to plants of *Lolium perenne* with low frequencies of metaphase I univalents, a type of asynapsis, conditioned by a single gene, has been studied in which two or rarely four univalents occur in from 20% to over 80% of the sporocytes (304).

Two cases of failure of the spindle mechanism to function properly have been reported in forage grasses. In a derivative of *Lolium perenne* × *Festuca elatior,* Darlington and Thomas (103) reported lack of spindle compactness and failure of the spindle to converge on the poles. Krishnaswamy (224) described a type of spindle abnormality in *Eleusine coracana* in which the bivalents did not orient regularly at metaphase nor disjoin in an orderly manner at anaphase I. The non-orientation of bivalents in *L. perenne* (291) may be a manifestation of the same phenomenon.

Non-homologous pairing was first reported in midprophase of maize (258). In the forage grasses this phenomenon has been observed in a triploid F_1 plant of *Lolium loliaceum* × *L. rigidum* (184) and in autotriploid *L. perenne* (300). Likewise, in haploid *Sorghum vulgare* there was nearly complete synapsis at midprophase that was attributed largely to non-homologous pairing (51).

The random distribution of chromosomes of bivalents to the two poles at anaphase I is one of the cardinal principles in cytogenetics. This assumption of random distribution has been extended also to the third set of chromosomes of triploids (101) and the extra chromosomes of aneuploids. When this hypothesis was tested in triploid *Datura,* however, an excess of sporocytes with a majority

of extra chromosomes passing to one pole and a deficiency of the more nearly equal distributions was found (487, 488). On the other hand, in plants of *Lolium perenne* with two extra chromosomes ($2x + 1 + 1$), the observed ratio of 7–9 and 8–8 distributions at anaphase I did not deviate significantly from the expected 1 : 1 (300). Likewise, in the autotriploid (301) the distribution of extra chromosomes gave a satisfactory fit to the binomial $(a + b)^7$, expected on the hypothesis of randomness.

Meiosis in Autopolyploids

Studies of meiotic behavior in autopolyploids have dealt most commonly with frequency of multivalents at diakinesis and metaphase I. In *Dactylis glomerata* the number of quadrivalents varied from zero to seven among sporocytes with an average of 3.5 to 3.8 for the species (275, 281, 307, 308). Similar results were obtained in *Arrhenatherum elatius* (307, 308), tetraploid *Agropyron cristatum* (307, 308), *Hordeum bulbosum* (31) and autotetraploid *Lolium perenne* (303). Kattermann (203) reported four to seven quadrivalents per sporocyte in *Arrhenatherum elatius.* Variations among plants in average quadrivalent frequency have been reported in *Arrhenatherum elatius, Dactylis glomerata, Agropyron cristatum, Phleum pratense* and autotetraploid *Lolium perenne* (307–311, 297, 302, 303). In *D. glomerata* the extremes among plants were 2.62 and 4.91 (311). Multivalent formation in *Anthoxanthum odoratum* varies widely in different sporocytes. Trivalents, quadrivalents, sexivalents, octavalents and rings of 10 and 12 chromosomes were observed (203), the associations varying from 10 bivalents to $1_{XII} + 1_{IV} + 2_{II}$ in 50 sporocytes. Similar behavior was reported by others (355, 359).

The occurrence and behavior of unpaired chromosomes at metaphase I were investigated in tetraploid *Agropyron cristatum, Arrhenatherum elatius* (307, 308), *Phleum pratense* (302), *Dactylis glomerata* (297, 307–311), and autotetraploid and autotriploid *Lolium perenne* (300, 303). In each species the percentage of sporocytes with one or more univalents varied among plants. The greatest variation was among 84 first inbred generation plants of *D. glomerata;* the percentages of metaphase I sporocytes with univalents ranged from 0.8% to 97% (311).

The orientation of the univalents was variable in each species.

Some were oriented on the equatorial plate along with the bivalents and multivalents prior to the initiation of anaphase I; others were scattered through the sporocyte during metaphase I but became oriented some time before the completion of anaphase I. The univalents, upon orientation, divided equationally, and the daughter half chromosomes reached the poles in a majority of cases in time to be included in the interphase nuclei. Some, however, were left in the cytoplasm where they were seen at interphase as chromatin clumps. The daughter half chromosomes behaved abnormally in the second division. Some were scattered in the cytoplasm near the poles and probably were included in the microspore nuclei at telophase II. Others were oriented on the plate at metaphase II, lagged at anaphase II and occurred as chromatin clumps or micronuclei in the quartets.

The interrelationships of chiasma frequency, quadrivalent frequency, percentage of metaphase I sporocytes with univalents, percentage of anaphase I with laggards, and percentage of quartets with micronuclei and chromatin clumps have been investigated by correlation and covariance analysis in *D. glomerata* and autotetraploid *L. perenne*. Chiasma frequency was positively correlated with quadrivalent frequency but negatively correlated with percentage of metaphase I univalents in both species. Metaphase I univalent frequency was not correlated with quadrivalent frequency in either species when unrelated plants were studied (*297*, 303, 309, 310). By the analysis of covariance it was shown that variations in chiasma frequency did not account for all differences in quadrivalent frequency and incidence of metaphase I univalents (*297*). Among inbred plants of *D. glomerata* (within inbred families), however, there was a significant negative correlation between quadrivalent frequency and incidence of metaphase I univalents (311). The nature of the interrelation of chiasma, quadrivalent, and metaphase I univalent frequency has been discussed (*297*, 311).

As expected from behavior of the metaphase I univalents, their frequency was positively correlated with frequency of anaphase I laggards and of micronuclei in the quartets. Likewise, there was a positive correlation between the latter two characters. In *D. glomerata,* quadrivalent frequency was not correlated with frequency of laggards at anaphase I, indicating that quadrivalents were not a source of anaphase I laggards (*297*, 309–311). Furthermore,

the analysis of covariance showed that variations in metaphase I univalents were sufficient to account for all significant differences in anaphase I laggards (297). In *Lolium perenne,* however, frequency of anaphase I laggards was positively correlated with frequency of quadrivalents, indicating that some of the laggards in this species may have resulted from improper disjunction of the quadrivalents (303).

The irregularities of meiosis and, consequently, the low fertility of autopolyploids have been attributed to multivalent association of chromosomes during synapsis and the tendency of multivalents to disjoin unequally at anaphase I (101, 221, 222, *et al.*). Consequently, there has been a general tendency to accept multivalent frequency as a criterion of the relative meiotic irregularity of autopolyploids. On the other hand, Müntzing (279) attributed much of the infertility of autopolyploids to physiological disturbances and upsets in genic balance accompanying chromosomal reduplication. Randolph (379) recognized that meiotic irregularities cause some sterility but agreed that physiological and genic disturbances are the important causes. In *Antirrhinum* (515) and maize (119), differences were found in fertility of autotetraploids of different origin that were not associated with variations in quadrivalent frequency. Similar results were obtained in inbred progenies of *Dactylis glomerata,* but in this species quadrivalent frequency is not a reliable criterion of regularity (297, 311). Only 2.5% of the anaphase I sporocytes had 13–15 distribution, while the remainder were normal, indicating that regular disjunction of the quadrivalents was the rule. Furthermore, quadrivalents did not contribute significantly to lagging at anaphase I in *D. glomerata* (297, 311).

Unequal disjunction of quadrivalents occurs commonly in *Lolium perenne,* however. Only 52% of the anaphase I sporocytes had a 14–14 distribution, while 40% had 13–15 and 8% had 12–16 (303). Similar results have been obtained in several other autopolyploids (see 303 for literature). Quadrivalent frequency also contributed in *L. perenne* to the incidence of laggards at anaphase I.

The importance of unpaired chromosomes at metaphase I, with their subsequent loss or random inclusion in daughter nuclei, as a source of aneuploid gametes has been stressed (297, 311). In *D. glomerata,* frequency of metaphase I univalents was negatively correlated with fertility among plants of inbred progenies (311).

Metaphase I univalents also occurred commonly in autotetraploid *L. perenne* and probably were an important factor in causing aneuploidy and reduced fertility in that species (303).

There are at least three major types of meiotic irregularity in autopolyploids, namely: (*a*) unequal disjunction of members of the multivalents, (*b*) incomplete disjunction of the multivalents, resulting in lagging and dividing univalents at anaphase I, and (*c*) unpaired chromosomes at metaphase I. Of these, the first type has been recognized most commonly. The feature of meiotic irregularity of greatest importance varies with the species, and multivalent frequency alone will not always be a reliable criterion of fertility and stability of the autopolyploid (297, 303).

Kostoff (221, 222) concluded that in species with short chromosomes autopolyploids would tend to be more regular in meiosis because of lower chiasma frequency and hence fewer quadrivalents. This hypothesis was adopted to account for fertility of autotetraploid sea plantains allied to *Plantago maritima* (109). In *Dactylis glomerata* and *Lolium perenne,* however, chiasma frequency was negatively correlated with incidence of metaphase I univalents. Hence, decrease in chiasma frequency, although it would tend to reduce the number of quadrivalents, would, in these species, result in greater irregularity of meiosis because of the greater frequency of univalents at metaphase I (297).

The relation of meiotic behavior in autotetraploids to behavior in the related diploid was studied in *Lolium perenne,* using pairs of diploid and tetraploid clones isolated from single seedlings (147). In some pairs the chiasma frequency per chromosome of diploid and autotetraploid was not different, but in others the tetraploid had a lower frequency than the related diploid (303). In this regard Upcott (566) postulated that chiasma frequency per chromosome might be lower in polyploids than in comparable diploids due to a delay of pairing resulting from the larger nucleus of the polyploid. From the literature on this problem (303) it is evident that the relationship varies with different species and even among clones of the same species, as in *L. perenne.*

In *L. perenne* there was no significant correlation between diploid and autotetraploid in chiasma frequency, percentage of metaphase I with univalents, percentage of anaphase I with laggards, and percentage of quartets with micronuclei. There was evidence in one

clone of an upset in timing balance in meiosis resulting from chromosome doubling. The meiotic regularity of an autotetraploid in *L. perenne* could not be predicted from the behavior of the diploid from which it was produced (303).

Statistically significant differences among clones in regularity of meiosis must generally result from heritable differences. The progeny test provides, however, the only critical proof of such heritable differences. From progeny tests in *Dactylis glomerata* (311), heritable variations among plants were found for chiasma frequency, average number of quadrivalents per sporocyte, percentage of metaphase I with univalents, percentage of anaphase I with laggards and percentage of quartets with micronuclei. The existence of heritable variations in these characters indicates the possibility of selecting for greater regularity of meiosis in autopolyploids.

Comparative studies of meiotic behavior of parental clones and their first inbred generation progenies of *Dactylis glomerata* have been reported (311). Among eight comparisons, the average quadrivalent frequency of the inbred did not differ significantly from that of the parent in six cases but was significantly higher in two cases. The most striking effect of inbreeding was on incidence of univalents at metaphase I. On the average, inbred progenies had two to three times as many unpaired chromosomes at metaphase I as their respective parents. Similar increases were found in frequencies of laggards at anaphase I and micronuclei in the quartets. The greater incidence of asynapsis in the inbreds could not be attributed to decreased chiasma frequency. The behavior of second inbred generation progenies (299) was similar throughout to that in the first generation.

It has been suggested that some species which behave cytologically as allopolyploids have developed from autopolyploids by a process of chromosomal differentiation (101, 279). According to Darlington (101), gene rearrangements rather than intragenic changes would be the principal factor in such differentiation. There is a dearth of experimental evidence on the effectiveness of various amounts and kinds of rearrangements in inhibiting random pairing among the four or more homologues of the autopolyploid. Skirm (507) reported an autotetraploid form of *Tradescantia* with predominantly bivalent pairing attributed to structural heterozygosity and to doubling after fertilization. Because of their interference

with regularity of synapsis, inversions might be expected to play an important part in limiting synapsis to particular pairs in an autopolyploid. From comparisons of bridge and fragment frequencies at anaphase I in pairs of diploid and autotetraploid clones of *Lolium perenne,* it was evident, however, that single inversions of the size dealt with had no very appreciable effect on random pairing between the four homologues (303).

CHROMOSOMAL REARRANGEMENTS

Associations of four or more chromosomes at diakinesis and metaphase I have been reported in several diploid species, including *Briza media* (204 to 206), *Puccinellia vahliana* (120), *Agrostis nebulosa* (546), *Dactylis aschersoniana* (281) and *Festuca pratensis* (377). These have been attributed by the authors (except Flovik (120)) to structural hybridity. The most analyzed case is *Briza media.* From studies of the progenies of structurally heterozygous plants and of intercrosses between ring-forming and non-ring-forming plants it was established clearly that the ring of four chromosomes resulted from an interchange (205, 206). In a cross of two non-ring-forming plants the progeny plants had a ring of four chromosomes (206). Some of the quadrivalents reported in polyploid species (see Types of Polyploids) may also have resulted from reciprocal interchanges rather than homology between chromosomes of different genomes. *Anthoxanthum odoratum* behaves cytologically like an autotetraploid (203, 355, 359). Associations of more than four chromosomes occur frequently, and this has been attributed by the authors to structural hybridity. A more nearly complete cytogenetic analysis of this species seems warranted. Associations of more than three chromosomes were observed occasionally in autotriploid *Pennisetum typhoides* and were attributed to segmental interchanges (228). Reciprocal interchanges, resulting in semisterility, were produced in *Pennisetum typhoides* by treatment of resting seeds with X-rays (229).

The presence of dicentric chromatid bridges and acentric fragments at anaphase I and, less frequently, at anaphase II has been shown to result from crossing over in heterozygous inversions (258, 260). Bridges and fragments have been observed in *Phalaris brachystachys* (359), *Bromus carinatus* (526), *Agropyron junceum* and *A. repens* (352), autotriploid *Pennisetum typhoides* (228),

Lolium perenne (291, 303), *Dactylis glomerata* (297, 308 to 311), *Phleum pratense* (302), *Festuca elatior*, $2n = 14$ and $2n = 42$ (312), *Anthoxanthum odoratum* (355), *Agropyron amurense, A. intermedium, A. repens* and *A. trichophorum* (9). One plant of *Pennisetum typhoides* obtained from X-ray-treated seed was heterozygous for an inversion (229).

INTERSPECIFIC AND INTERGENERIC HYBRIDIZATION

Natural and Controlled Hybrids

Interspecific and intergeneric hybrids and their cytogenetic characteristics have been reported commonly in the Gramineae. Investigations of this nature involving the cereals, particularly *Triticum* and the related genera *Aegilops, Secale* and *Haynaldia,* have been reviewed (1), and studies of hybrids of maize and maize relatives have been summarized (262). In the forage grasses, over 200 interspecific and intergeneric hybrids have been reported. Of these, 93 were naturally occurring, 119 artificial or controlled, and 17 both natural and controlled. Identification of natural hybrids and their parents is, at best, circumstantial and must be based upon proximity of the hybrids to the putative parents in nature, sterility of the hybrids, chromosome numbers and meiotic behavior, and comparative characters of the hybrids and the putative parents. Since not all of the data are available in many instances, it is probable that some of the reports of natural hybrids may be erroneous. Ullmann (565) tabulated most of the natural and controlled hybrids reported prior to 1936. Extensive lists of natural hybrids have been reported in the flora of Denmark (11) and New Zealand (81, 82). Cugnac (90) has discussed the high frequency of hybridization among grass species in nature.

Bromus. Most of the studies of interspecific hybrids in *Bromus* (especially in 65, 66, 88, 89, 92, 93, 95–98, 100), were for the purpose of elucidating problems of phylogeny and systematics in the genus. Cugnac (88) reported that between the species *B. sterilis* L. and *B. madritensis* L. there exists a series of intermediates formed by *B. rigidus* Roth., *B. gussonei* Parl and *B. macrantherus* Hack. The F_1 plants of *B. sterilis* × *B. madritensis* resembled *B. madritensis,* were irregular in meiosis and produced little pollen (89). In *B. sterilis* × *B. macrantherus* the F_1 resembled *B. sterilis* and meiosis was irregular. Apart from its sterility the F_1 of this

cross resembled *B. gussonei* in every respect (89). Later, chromosome number determinations supported the assumption of the hybrid origin of *B. gussonei* (100). In hybrids involving *B. grossus, B. secalinus* and *B. arduennensis* the F_1 was completely fertile in each case. Cugnac (96) concluded that these three species should be considered varieties of one collective species. Hybrids of members of this collective species with the closely related *B. arvensis* and *B. macrostachys* were sterile.

B. arduennensis and *B. grossus* differ in pubescence of spikelets and in several other characters. The *B. grossus* characters were completely dominant in F_1 and a dihybrid segregation occurred in F_2. Pubescence was conditioned by a single factor, and all other differential characters segregated *en bloc* as if determined by a single gene (93, 95).

The characters of *B. arduennensis* were completely recessive in crosses with *B. arvensis, B. macrostachys, B. secalinus, B. grossus* and *B. grossus nitidus.* In contrast, the characters of *B. macrostachys* were completely dominant in crosses with *B. arduennensis, B. grossus nitidus, B. arvensis* and *B. squarrosus.* In *B. grossus* × *B. arvensis* the F_1 was sterile and resembled *B. grossus* morphologically (97).

Knowles (220) attempted to cross *Bromus mollis* with 13 species representing five sections of *Bromus.* Hybrids were produced with *B. racemosus, B. arenarius, B. rubens, B. madritensis* and *B. carinatus.* The chromosome pairing in F_1 paralleled the morphological similarities of the parents. In the hybrid with the morphologically similar *B. racemosus,* bivalent pairing was nearly complete. On the other hand, in the F_1 with *B. carinatus,* which is distinct morphologically and geographically from *B. mollis,* bivalent formation was rare.

The F_1 plants of *Bromus hordeaceus* × *B. mollis* (334, 341) were intermediate between the parents in morphology and fertility. The fertility of the hybrids indicates a close relationship between these species.

Stebbins and Tobgy (526) reported $21_{II} + 7_I$ in the F_1 of *B. carinatus* ($2n = 56$) × *B. catharticus* ($2n = 42$). The univalents appeared to be the chromosomes of seven long bivalents observed in *B. carinatus.* The F_1 plants were completely sterile despite relatively regular meiosis. The authors suggested that *B. carinatus*

was an amphipolyploid derived from a hybrid of *B. catharticus* with some diploid species of the Bromopsis section. In *B. arizonicus* × *B. carinatus,* F_1 plants showed a maximum pairing of seven medium sized trivalents, 14 medium sized bivalents, 14 medium sized univalents, and seven large univalents, the latter coming from *B. carinatus* (527). In this hybrid extensive inversion hybridity was indicated by the high frequency of bridge-fragment configurations.

Festuca and Lolium. Interspecific and intergeneric hybrids of *Festuca* and *Lolium* have been found in nature (11, 58, 82, 335, 339, 483, 539, 589, also *cf.* 565) and have been produced by controlled cross pollination (88, 146, 168, 175, 178, 179, 183, 184, 218, 312, 332, 333, 342, 553, 591, 592). Meiotic behavior in F_1 of *Festuca elatior* var. *arundinacea* × *F. gigantea* has been investigated (339, 366). Bivalents and univalents, with occasional quadrivalents and trivalents were observed at metaphase I. Peto (366) reported an average of 13.9 univalents (range from 10 to 19) per sporocyte, while Nilsson (339) found a maximum of 14 univalents. The F_1 was pollen sterile and rarely produced seeds with open-pollination. One such seed produced a plant with 84 chromosomes, an amphipolyploid (338).

Among the six species of *Lolium* recognized by Jenkin and Thomas (183), 11 interspecific hybrids have been investigated (178, 179, 183, 184). In general, seven bivalents were formed in meiosis in each hybrid, although as many as 40% of the sporocytes in certain crosses had two, or rarely four or more, univalents at metaphase I. Dicentric bridges and acentric fragments at anaphase I in six of the hybrids might be interpreted to indicate chromosomal differentiation among species, although such inversion bridges occur commonly in plants of *L. perenne* (291, 303). The anthers dehisced and 20% to 25% good pollen was produced in *L. perenne* × *L. italicum* (= *L. multiflorum*), *L. perenne* × *L. rigidum* and *L. rigidum* × *L. loliaceum* (triploid plant). In the remaining crosses the anthers did not dehisce (179, 183).

Hybrids of *Lolium* spp. × *Festuca* spp. (178) are particularly interesting, since these genera have been placed in different tribes on morphological characters. In *L. perenne* × *F. elatior* var. *pratensis* the 14 chromosomes of the F_1 occurred regularly as seven bivalents at metaphase I, with a chiasma frequency only slightly

lower than in the parents (366). Despite the regularity of meiosis, the F_1 plants were completely male sterile (the anthers did not dehisce) but produced some seed from backcrosses to the parents. Sterility of the hybrids was attributed to genic causes.

In F_1 *L. perenne* × *F. elatior* var. *arundinacea* an average of 32.4% of the 28 chromosomes occurred as univalents, 55.2% as bivalents, 4.3% as trivalents, 5.7% as quadrivalents, and 2.4% as quinquevalents (366). In another study the number of univalents varied from zero to three, the number of bivalents from five to 12, and the number of quadrivalents from zero to four (312). The results indicate considerable homology between *L. perenne* and *F. elatior* chromosomes, and between chromosomes of the genomes of *F. elatior*. Consistent with these results, one to five quadrivalents were observed at diakinesis and metaphase I in *F. elatior* var. *arundinacea* (312). Similarly in F_1 of *L. perenne* × *F. rubra* the frequency of bivalents varied in different sporocytes from seven to 12, indicating pairing between *Lolium* and *Festuca* chromosomes and between chromosomes of different *Festuca* genomes (335).

Poa. *P. arachnifera* × *P. pratensis* was one of the first controlled hybrids recorded among the forage grasses. According to Vinall and Hein (582), the cross was made by Oliver in 1908, and was repeated later by Brown. The primary objective was to combine the heat and drouth tolerance of *P. arachnifera* (Texas bluegrass) with good forage quality of *P. pratensis*. Some selections from this cross have appeared promising in preliminary trials, but no new commercial variety has yet been developed from the material.

The hybrids of *P. pratensis* × *P. alpina* (4, 7, 283) and *P. compressa* × *P. pratensis* (48, 49) are of interest primarily for their contribution to analysis of the problem of apomixis in *Poa* (see Apomixis). In the latter cross, an unreduced gamete of *P. compressa* was fertilized by an approximately reduced gamete of *P. pratensis*. The F_1 plant was intermediate between the parents in several characters, but in other respects, particularly retention of green leaves during midsummer, it appeared to be superior to either parent. Furthermore, the hybrid was rather highly fertile (49). Despite the fact that both parents were highly apomictic, the hybrid was completely or nearly completely sexual; the F_2 showed extreme segregation, plants occurring with various combinations of the characters of the parents. In extensive F_2 and F_3 populations, not a

single plant appeared to be superior to either parent, a majority being distinctly inferior in vigor, leafiness and other important characters (304).

Controlled hybrids of *P. nemoralis* × *P. pratensis* (*cf.* 565) and *P. pratensis* × *P. glauca* (7) have been obtained, but their characteristics were not reported. In addition, several natural interspecific hybrids have been recorded (11, 82, 251, 565).

Dactylis. *Dactylis aschersoniana* × *D. glomerata* has been recorded several times in nature (11, 152, 281, 538, 565) and has been produced by controlled hybridization (146). Meiosis in the F_1 is characteristic of an autotriploid, trivalents, bivalents and univalents occurring at metaphase I (281). The F_1 plants were male sterile but produced seed in backcrosses with either parent. According to Ullmann (565), Vogt produced the intergeneric hybrid *Cynosurus cristatus* × *D. glomerata.*

Melica. In F_1 of *Melica imperfecta* × *M. torreyana* pairing is normally as bivalent; univalents occur only rarely, yet the plants are nearly 95% seed sterile (189). Allotetraploids, from chromosome doubling in the F_1 were vigorous, high in pollen fertility, variable but exceeding the hybrid in seed fertility, and formed two to five multivalents at diakinesis. Behavior of the F_1 is similar to that reported in *Lolium* × *Festuca* hybrids (see page 357). Increased fertility and meiosis in the allotetraploids resembles the condition in *Primula kewensis* (565). Many of the naturally occurring polyploid grasses, in which multivalents occur at meiosis, may prove to have arisen in a similar manner.

Agropyron, Elymus, Triticum, Aegilops, Secale. Several interspecific hybrids in *Agropyron* have been reported (11, 146, 352, 353, 501, 502, 565, 575). Only one of them, *A. junceum* × *A. repens* (352), has been studied in detail. In four hybrid plants the average pairing at metaphase I varied from $13_{II} + 9_I$ to $9_{II} + 17_I$, and, in addition, a few trivalents were observed. The hybrids were male sterile and failed to produce seed with open pollination.

The intergeneric hybrids of *Triticum* × *Agropyron* have been investigated more extensively than any others among the forage grasses. Excellent reviews of the literature, particularly pertaining to crossing relationships, have been published recently (509, 510, 564, 588). Much of the work with these hybrids has been done in Russia where the primary objective has been production

of a perennial wheat. The possibility of producing new forage plants was recognized, however (209–211, 233, 560). Likewise, the work in Canada, particularly in Saskatchewan, has been directed towards the production of a large-seeded, perennial forage plant, combining some of the winterhardiness, disease resistance and perenniality of *Agropyron* with the seed size and better forage quality of *Triticum* (588).

Among numerous species of *Agropyron, A. elongatum* and *A. glaucum* have been used most extensively and successfully in crosses with *Triticum* (17, 19, 20, 37, 186, 187, 209, 233, 324, 367–370, 372, 486, 506, 561–564, 567–579). Successful crosses have been reported also with *A. intermedium, A. trichophorum* and *A. junceum* (20, 208–211, 324, 355, 509, 510, 562, 563, 572, 574–579). Smith (509, 510) obtained one hybrid plant of *T. aestivum* × *A. cristatum* that died before flowering, and several hybrid seeds of *T. durum* × *A. amurense* and *T. aestivum* × *A. amurense.* The *"A. amurense"* may have been mislabeled and actually have been a strain closely allied to *A. intermedium* (510).

Crosses using several other species of *Agropyron* have been attempted without success. These include *A. caninum, A. tenerum* (*A. trachycaulum*), *A. sibiricum, A. loliodes, A. repens, A. turczaninovii, A. desertorum, A. prostratum, A. orientale, A. subsecundum, A. smithii, A. inerme, A. dasystachyum, A. ciliare, A. semicostatum* and *A. spicatum* (509, 510, 562, 575, 588).

For the *Triticum* parent, varieties of *T. aestivum* and *T. durum* have been used most extensively in hybrids with *Agropyron.* Verushkin (575) reported, however, that some *Agropyron* species will cross with forms in all three sections of *Triticum.* White (588) succeeded in crosses with *A. elongatum* and *A. glaucum* using *T. dicoccoides, T. dicoccum, T. durum, T. turgidum, T. polonicum, T. timopheevi, T. pyramidale* and *T. vulgare* (*T. aestivum*) as female parents. Östergren (354) reported the hybrid *T. turgidum* × *A. junceum,* and Popowa (372) reported *T. timopheevi* × *A. elongatum.*

Greater success has been attained in crosses using *Triticum* as the female parent (560, 579, 588), and the seed set was better on the average with *T. durum* × *Agropyron* spp. than with *T. aestivum* × *Agropyron* spp. (17, 510, 588). Furthermore, the crossing results varied with different varieties of *Triticum* and different strains of *Agropyron* (186, 211, 510, 560, 575, 579, 588).

Investigations of meiotic behavior in *Triticum* × *Agropyron* hybrids were reported by Vakar (567–572). In F_1 of *T. vulgare* × *A. elongatum* the maximum association of chromosomes varied in different hybrids—28_{II}, $21_{II}+14_I$ and $14_{II}+28_I$. On the basis of the pairing behavior, Vakar (568, 570) concluded that the genomes of *A. elongatum* were Aa, Ba, Da, X_1 and X_2 where Aa, Ba, and Da are *Agropyron* genomes homologous with the A, B, and D genomes of *T. vulgare*. One of these genomes was less homologous than the other two and failed to pair in some hybrids ($14_{II}+28_I$). In hybrids with 28_{II}, autosyndesis between X_1 and X_2 genomes was assumed. These conclusions were supported also by pairing observed in *T. durum* × *A. elongatum* (568); in these hybrids maximum associations of 14_{II} or occasionally 21_{II} occurred. Sapegin (486) observed $21_{II}+7_I$ as the maximum association in F_1 of *T. vulgare* × *A. elongatum*. Popowa (372) found a maximum pairing of $21_{II}+7_I$ in F_1 of *T. timopheevi* × *A. elongatum* which he attributed to pairing of A and G of *T. timopheevi* with Aa and Ba of *A. elongatum* and autosyndesis of X_1 with X_2. In *A. elongatum* an average of three quadrivalents with low frequencies also of quinquevalents, sexivalents and octavalents occurs (367). The occurrence of quadrivalents is consistent with Vakar's (569) postulation of homology between the X_1 and X_2 genomes. In the F_1 of *T. vulgare* × *A. elongatum*, Peto (367) reported very complex pairing including all of the types of association observed in *A. elongatum* but in different frequencies.

In F_1 *T. vulgare* × *A. glaucum*, Vakar (568) reported variations from 6_{II} to 14_{II} with an average of 10_{II}, while in *T. durum* × *A. glaucum* a maximum of 7_{II} was observed. He (568) concluded that *A. glaucum* had the genomes Aa, Da and X_2. Peto (367) found an average of 6.2_{II} in *T. dicoccum* (Vernal emmer) × *A. glaucum* and 5.5_{II} in *T. durum* × *A. glaucum*. On the other hand, Sapegin (486) observed only two or three, rarely four, bivalents in *T. vulgare* × *A. glaucum*. According to Sipkov (506), pairing varied in different hybrids of *T. durum melanopsis* × *A. glaucum* from 2_{II} or 3_{II} to $14_{II}+7_I$.

The behavior in crosses involving *A. intermedium* has been reported (208–211). In *T. durum* × *A. intermedium* ($2n = 28$) the frequency of bivalents varied from zero to two. In *T. durum* × *A. intermedium* ($2n = 42$) the F_1 plants produced unreduced (35 chro-

mosomes) gametes. In backcrosses to wheat, sesquidiploids were produced, while upon selfing of the F_1, amphidiploids resulted. In some crosses, 95 to 98% of the selfed progeny of the F_1 were amphidiploids. Some of the amphidiploids were reported to be exceedingly valuable forage plants (210, 211).

The fertility, particularly self-fertility (male fertility ?), of the F_1 plants varied widely among crosses of different species and even among different hybrids involving the same species. Verushkin (575) reported that (*a*) in *T. vulgare* × *A. elongatum* there was a tendency for fertility, (*b*) in *T. durum* × *A. intermedium* (*cf.* 211) and *T. durum* × *A. trichophorum* individual plants were self-fertile, (*c*) in *T. vulgare* × *A. intermedium* and *T. vulgare* × *A. trichophorum* the F_1 very rarely set seed following selfing, and (*d*) in *T. durum* × *A. elongatum* the F_1 was entirely self-sterile. Similar results were reported by others (20, 187, 561). In *T. vulgare* × *A. elongatum* the most fertile F_1 hybrids were obtained when varieties of soft wheat were used and the self-fertile forms were those with 21_{II} to 28_{II} whereas those with 14_{II} were self-sterile (568). On the other hand, there was no relation between fertility and meiotic behavior in hybrids involving *A. glaucum* (561, 569). In cases in which the F_1 has been self-sterile, it usually has been possible to obtain progenies by backcrossing to the parents.

In the F_1 the *Agropyron* characters tended to be dominant and in some cases heterosis was observed (561, 562, 575, 588). In F_2 and later generations from the self-fertile hybrids there was extreme segregation (most characters of both parents were recovered according to White, 588), an increase in fertility and self-fertility, and a decrease in percentage of perennial plants. Similar results were obtained in progenies of backcrosses of the F_1 to *Triticum,* but in these progenies there was a tendency to revert rapidly to the *Triticum* type, and, particularly, a rapid reduction of the percentage of perennial plants. The progenies of self-fertile hybrids tended to become stabilized with characteristics intermediate between the parents and with a chromosome number of 56 (568, 572). For satisfactory forage, types more wheat-like than any plants in the F_2 progenies were required (187). In general, the hybrids of *A. glaucum* were more suitable for forage than those of *A. elongatum* (186, 588).

Favorskii (118) reported successful crosses of *A. intermedium*

with three species of *Aegilops*. These hybrids are of interest primarily because of the relation of *Aegilops* to *Triticum* (1).

Using *Secale cereale* as the female parent, successful crosses have been made with *A. intermedium* (575), *A. cristatum* (223), *A. sibiricum, A. repens* and *A. trichophorum* (509). At meiosis in the F_1 of *Secale cereale* × *A. cristatum* ($2n = 28$), bivalents were almost always formed, a maximum of seven occurring (117). This was interpreted by the author to indicate pairing of *Secale* and *Agropyron* chromosomes. Since *A. cristatum* ($2n = 28$) behaves cytologically like an autotetraploid (308), Favorskii's (117) interpretation probably is questionable. Smith (509) used six other species of *Agropyron* in attempted crosses with *S. cereale* and none was successful.

Species of *Elymus* have been used successfully in intergeneric hybrids in three instances. Cugnac (91) and Cugnac and Belval (99) reported hybrids of *Elymus riparius* × *Agropyron caninum,* and TSitsin (561) obtained crosses of *Secale cereale* × *Elymus junceus.* Hertzsch (146) reported hybrids of *Melica ciliata* × *Elymus arenarius.* Poddubnaja-Arnoldi (371) attempted a number of *Triticum* × *Elymus* crosses and found neither embryo nor endosperm development. In *T. timopheevi* × *E. araliensis* and *T. vulgare* × *E. dahuricus,* however, the embryo and endosperm occasionally passed through early stages of development before aborting. Smith (509) pollinated *T. aestivum, Secale cereale* and *Hordeum vulgare* with several species of *Elymus* but none of the crosses was successful.

Danthonia. Seven natural interspecific hybrids of *Danthonia* were reported from the flora of New Zealand (82).

Calamagrostis. Six natural interspecific hybrids (11, 67) and two intergeneric hybrids—*Ammophila arenaria* × *Calamagrostis epigeios* (11) and *Calamagrostis tenella* × *Agrostis alba* (*cf.* 565)—have been recorded.

Agrostis. Numerous natural interspecific hybrids have been reported (11, 82, 122; *cf.* 565). The probability of extensive natural hybridization of *Agrostis tenuis, A. alba* and, possibly, *A. palustris* in New England is indicated by the work of Stuckey and Banfield (605). Single panicles, judged on morphological ground to be *A. tenuis,* were collected from old pastures and meadows, and spaced planted progeny plants were grown from the seed of each

panicle. In part of the progenies, morphological variations were within the limits expected of *A. tenuis,* but in others the plants showed varying combinations of vegetative and panicle characters of *A. tenuis, A. alba,* and, occasionally, *A. palustris.* Furthermore, the chromosome numbers were variable within progenies. Rarely plants were found with 28 or 42 chromosomes, but usually the numbers were intermediate. There was no evident relation between chromosome number and morphology. Further investigations of this interesting problem are in progress.

The possibility of an intergeneric hybrid involving *Agrostis* has been suggested. Sokolovskaya (511) postulated that *A. verticillata* may form a connecting link between *Agrostis* and *Polypogon* and that *P. litoralis* is possibly a hybrid of *P. monspeliensis* and an *Agrostis* species.

Alopecurus. Ten natural interspecific hybrids have been reported (11; *cf.* 565). In a review in Plant Breeding Abstracts, Johnsson (188) is credited with describing interspecific hybrids in *Alopecurus.* Only *A. antarcticus* × *A. pratensis* is mentioned specifically. Since this paper apparently is not available in libraries in this country, the additional hybrids could not be checked.

Phleum. Meiotic behavior in interspecific hybrids in *Phleum* have been discussed previously (see Types of Polyploids). The hybrids seem to offer little of practical value, but have been of particular importance in the analysis of the chromosomal relationships in hexaploid *P. pratense.*

Stipa. Six interspecific hybrids involving eight species of *Stipa* have been produced experimentally (256*a*). The hybrids include *S. lepida* × *S. pulchra, S. pulchra* × *S. cernua, S. cernua* × *S. lepida, S. cernua* × *S. leucotricha, S. comata* × *S. neomexicana,* and *S. californica* × *S. occidentalis.* All hybrids were completely sterile, but fertility was induced in *S. cernua* × *S. pulchra* by use of colchicine. In *S. lepida* × *S. pulchra* there were 14 to 18 bivalents, zero to two trivalents, and no or one quadrivalent at meiosis, while in *S. pulchra* × *S. cernua* there were 10 to 19 bivalents, no or one trivalent and no or one quadrivalent. No conclusions can yet be drawn regarding the chromosomal homologies in this genus.

Spartina. On the basis of chromosome numbers and the occurrence of the two species in the locality in which *S. townsendii* originated, it was assumed that *S. townsendii* arose by chromosome

doubling in the hybrid of *S. alterniflora* × *S. stricta* (154, 155). This explanation has been accepted generally. It was questioned, however, by Chevalier (69) who suggested that *S. townsendii* has affinities to *S. glabra pilosa* and *S. merrillii* (*S. glabra* × *S. polystachya*) which deserve consideration. *S. townsendii* is an outstanding example in the Gramineae of a species that has arisen, supposedly by polyploidy following interspecific hybridization, in comparatively recent times—it was discovered in 1870. Since that time it has spread widely, occupying the area formerly occupied by the putative parents and exceeding greatly the parents in distribution. Moreover, it is an important forage grass along coastal areas of northwestern Europe (56, 57, 154).

Phalaris. The F_1 plants of *P. arundinacea* × *P. tuberosa* were male sterile but fairly female fertile (2 to 4% of the florets set seed) in the presence of the parental species. In meiosis, $12_{II} + 4_I$ were regularly formed. In F_2 (open-pollinated seed, probably from *P. tuberosa* pollen) there was a great diversity of types, some different from either parent (182). Vogt (*cf.* 565) reported *P. arundinaceae* × *P. canariensis* but the hybrid was not described.

Paspalum. The hybrids of *P. urvillei* × *P. malacophyllum* were male sterile but produced seed when pollinated with pollen from *P. urvillei* or *P. dilatatum.* From these backcrosses plants of F_1 × *P. urvillei* and F_1 × *P. dilatatum* were obtained, in addition to plants identical with the F_1. Only unreduced gametes functioned in the F_1 plants and the unreduced eggs were capable of parthenogenetic development (61). *P. urvillei* and *P. malacophyllum* both produce uniform progeny, suggesting parthenogenesis, but the F_1 plants had $2n = 40$, indicating that reduced gametes functioned in production of the hybrids.

Setaria. In the F_1 of *S. italica* × *S. viridis* there were nine bivalents at metaphase I and otherwise regular meiosis (243). The plant produced 70% sterile pollen and 50% of the spikelets were empty. Plants of the F_2 segregated from very low fertility to as high as the parents. Li, Pao, and Li (246) found $9_{II} + 9_I$ usually in meiosis in F_1 *S. faberii* × *S. italica* and *S. faberii* × an F_2 plant of *S. italica* × *S. viridis.*

Sorghum. Hybrids of *S. vulgare* × *S. halepense* have been reported (30, 198, 270). Univalents, bivalents and quadrivalents were found at meiosis in the F_1 (198). The F_1 plants were fertile

and extreme segregation occurred in F_2, resulting in a complete range of intermediate types. Over one-fourth of the F_2 plants survived the winter. The F_3 plants were more fertile than F_2 and retained their hybrid vigor (30). Mikharlovskii (270) also found segregation in F_2 and reported that in most F_2 plants $2n = 30$ but in some $2n = 40$. *S. dimidiatum* and *S. purpureo-sericeum* hybridize easily. *S. dimidiatum* is characterized by the lower half of the lower glumes being coriaceous, the upper half papery. In hybrids with *S. purpureo-sericeum,* this character behaves as a simple recessive (443).

Saccharum and related genera. *Saccharum officinarum* and *S. spontaneum* have been crossed successfully with *Sorghum vulgare* (38, 165, 166, 167, 273, 505, 543) and *S. halepense* (165). In hybrids of sugar cane variety P.O.J. 2725 ($2n = 107$) with *Sorghum vulgare* (273) three types of F_1 plants were obtained: (*a*) normal or sugar cane type with $2n = 118$, (*b*) intermediate type with $2n = 64$, and (*c*) dwarf type with $2n = 64$, all plants of which died before flowering. One or both of these species of *Saccharum* have been crossed successfully also with *Narenga narenga, Erianthus sara, E. arundinaceus, E. ravennae, Zea mays, Imperata cylindrica* and *Bambusa arundinacea* (165, 166, 480). A majority of the hybrids were pollen-sterile; some failed to flower, but others were fertile (165).

Other hybrids. Additional hybrids that have been recorded are as follows:

Puccinellia distans × *P. maritima* (11)
P. distans × *P. retroflexa* (11)
P. maritima × *P. retroflexa* (11)
Arundo conspicua × *A. fulvida* (11)
Hordeum sativum × *H. bulbosum* (230)
H. jubatum × *H. vulgare* (375)
H. nodosum × *H. vulgare* (375)
H. jubatum × *Secale cereale* (46, 47, 85)
Arrhenatherum elatius × *Avena pubescens* (*cf.* 565)
Stipa viridula × *Oryzopsis hymenoides* (185)
Phippsia algida × *P. concinna* (120)
Anthoxanthum aristatum × *A. odoratum* (355)
Brachypodium pinnatum × *B. silvaticum* (11, 65)
Deschampsia chapmani × *D. tenella* (82)

Deyeuxia avenoides × *D. quadriseta* (82)
D. billardieri × *D. foisteri* (82)
D. foisteri × *D. pilosa* (82)
Dichelachne crinita × *D. sciurea* (82)
Hierochloe fraseri × *H. redolens* (82)
Microlaena avenacea × *M. stipoides* (82)
Trisetum antarcticum × *T. youngii* (82)
Glyceria fluitans × *G. plicata* (565)
G. fluitans × *L. perenne* (565)

Variations in Seed Set in Reciprocal Crosses

Variations in cross-compatibility in reciprocal interspecific and intergeneric hybridizations have been encountered commonly. Ordinarily, the cross has been most successful when the parent with higher chromosome number was used as the female. Explanations for this difference have been proposed (276, 544, 545, 585). In the forage grasses, exceptions to this general behavior have been encountered. In interspecific and intergeneric hybrids of *Lolium* and *Festuca* the cross most commonly succeeded best when the female parent had the lower chromosome number (178). Likewise, *Triticium* × *Agropyron* crosses were more successful when *Triticum* was the female parent (588, *et al.*).

(*To be concluded in next issue*)