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Polyploidy is the duplication of an entire nuclear genome, whether diploid or higher level (Stebbins, 1971; Thompson & Lumaret, 1992) and a frequent occurrence in plants. Stebbins (1971) estimated that 30–35% of flowering plant species are polyploid, and that many more had a polyploid event in their evolutionary history, including all members of such important families as the Magnoliaceae, Salicaceae, and Ericaceae. Goldblatt (1980) estimated 55%, but probably up to 75%, of monocotyledons had at least one polyploid event in their history, using the criterion that if the species has a base number higher than $n=13$ it is derived from a polyploid. Using the same criterion, Grant (1981) estimated that 52% of angiosperms, 49% of dicotyledon species and 60% of monocotyledons are polyploid. Masterson (1994) supports high frequencies of ancestral polyploidy using fossil evidence. Clearly, polyploids have been fixed in many lineages.

Within many genera of higher plants, individual species often have different, but uniform, ploidy levels (e.g. *Draba*, Brassicaceae, Brockman & Elven, 1992), the grasses being no exception, e.g. *Bromus*, *Elymus* (Seberg & von Bothmer, 1991; Ainouche, Misset & Huon, 1995). Intrageneric polyploid series provide another indicator of frequent polyploid events. For example, of a miscellaneous collection of 87 grass genera for which I had chromosome numbers for two or more species, 65 (75%) formed a polyploid series in relation to other members of the genus (Table 7.1).

Stebbins (1947) distinguished the forms of polyploidy based on whether the duplicated genomes are derived from one species (autopolyploidy) or two (allopolyploidy) or both (segmental allopolyploidy). Recent detailed genetic analysis has made it possible to distinguish these based on homology of the genomes: the same genomes in multiple copies (autopolyploidy), or several different genomes in the same individual (allopolyploidy) (Jackson, 1982).

Table 7.1. *Polyploid series within some grass genera*

Plants entered only if cytotype is available for two or more species. Taxonomy is that of the author and not necessarily modern.

Genus	Cytotypes of selected members	
Aegilops	28, 56	Hickman, 1993
Agropyron	14, 28, 42, 56	Bowden, 1965
Agrostis	14, 28, 42, 56	Bowden, 1965; Hickman, 1993
Aira	14, 28	Myers, 1947
Alopecurus	14, 28, 56, 70, 98, 112–116	Myers, 1947
Ammophila	28	Myers, 1947
Andropogon	20, 30, 40, 45, 50, 60, 80, 120, 180	Myers, 1947; Norrmann & Quarín, 1987
Anthoxanthum	10, 20, 80	Myers, 1947; Hedberg, 1967
Aristida	22, 44	Hickman, 1993
Arrhenatherum	28, 40	Myers, 1947
Arthraxon	36	Myers, 1947
Arundinaria	48, 54	Myers, 1947
Avena	14, 28, 42	Hickman, 1993
Bambusa	68, 72	Myers, 1947
Bouteloua	20, 21, 22, 35, 40, 42	Myers, 1947
Brachypodium	14, 18	Myers, 1947
Briza	10, 14	Myers, 1947
Bromus	14, 28, 42, 56, 70	Myers, 1947; Sutherland, 1986; Ainouche *et al.*, 1995
Calamagrostis	28, 42, 56, 79, 84	Myers, 1947; Sutherland, 1986
Calamovilfa	40	Sutherland, 1986
Catabrossa	20	Sutherland, 1986
Cenchrus	34, 70	Myers, 1947; Sutherland, 1986
Chimonobambusa	48	Myers, 1947
Chloris	20, 30, 40, 50, 80	Myers, 1947
Cinna	28	Myers, 1947
Coix	10, 20	Myers, 1947
Cymbopogon	20, 40	Myers, 1947
Cynodon	18, 36, 54	Sutherland, 1986
Cynosurus	14	Myers, 1947
Dactylis	14, 28, 42	Lumaret, 1988*b*
Dactylocteniaum	34, 48	Myers, 1947
Danthonia	18, 24, 36, 42, 48	Myers, 1947; Hickman, 1993
Deschampsia	14, 26, 28, 42	Myers, 1947; Rothera & Davy, 1986
Dichanthelium	18	Sutherland, 1988
Digitaria	16, 24, 28, 30, 36, 54, 72	Myers, 1947; Sutherland, 1986
Distichlis	40	Myers, 1947
Echinochloa	36, 54, 130	Myers, 1947; Sutherland, 1986
Ehrharta	24, 48	Myers, 1947
Eleusine	18, 36, 45	Myers, 1947
Elymus	14, 28, 42, 56	Myers, 1947
Eragrostis	20, 40, 42, 50, 60, 80, 100, 120	Myers, 1947; Sutherland, 1986
Erianthus	20, 60	Myers, 1947
Euchlaena	20, 40	Myers, 1947
Festuca	14, 28, 42, 56, 63, 70	Seal, 1983
Gastridium	14, 28	Myers, 1947

Table 7.1. (*cont.*)

Plants entered only if cytotype is available for two or more species. Taxonomy is that of the author and not necessarily modern.

Genus	Cytotypes of selected members	
Glyceria	10, 14, 20, 28, 40, 56	Myers, 1947; Hickman, 1993
Hilaria	18, 36	Sutherland, 1986
Holcus	14, 28	Jones, 1958; Richard *et al.*, 1995
Hordeum	14, 28, 42	von Bothmer & Jacobsen, 1986; Kankanpää *et al*, 1996
Hystrix	28, 56	Myers, 1947
Koeleria	14, 28	Myers, 1947
Leersia	48, 96	Myers, 1947
Leptochloa	20, 40	Sutherland, 1986
Lepturus	14, 26, 36	Myers, 1947
Lolium	14, 28	Sutherland, 1986
Melica	18	Myers, 1947
Milium	18, 28	Myers, 1947
Miscanthus	36, 42, 64	Myers, 1947
Muhlenbergia	18, 20, 40, 42, 60, 80	Myers, 1947; Hickman, 1993
Munroa	16	Sutherland, 1947
Oplismenus	54, 72	Myers, 1947
Oryza	24, 48	Myers, 1947
Oryzopsis	22, 24, 46, 48	Sutherland, 1988
Panicum	18, 20, 36, 40, 54, 72, 90, 108	Myers, 1947; Sutherland, 1986
Paspalum	20, 25, 40, 45, 55, 60, 80, 120, 160	Burton, 1942; Myers, 1947; Quarín *et al.*, 1982
Pennisetum	14, 27, 28, 36, 45, 54	Burton, 1942
Phalaris	12, 14, 28, 42	Myers, 1947
Phippsia	28	Myers, 1947
Phleioblastus	48	Myers, 1947
Phleum	14, 28, 42	Myers, 1947
Phyllostachys	48, 54	Myers, 1947
Poa	14, 28, 35, 42, 54, 56, 62, 64, 70, 76, 84, 106	Myers, 1947; Sutherland, 1986
Polypogon	14, 28, 42	Hickman, 1993
Puccinellia	14, 28, 42, 56	Myers, 1947; Sutherland, 1986
Saccharum	40, 80, 112	Myers, 1947
Sasa	48	Myers, 1947
Setaria	18, 36, 54, 72	Sutherland, 1986
Sitanion	28	Myers, 1947
Sorghastrum	20, 40	Myers, 1947
Sorghum	10, 20, 40	Gu *et al.*, 1984
Spartina	28, 40, 42, 56, 80, 84, 112, 128	Myers, 1947; Hickman, 1993
Sporobolus	18, 24, 36, 45, 46, 54, 72, 82, 108	Sutherland, 1986
Stipa	24, 28, 34, 36, 40, 42, 44, 46, 48, 64, 68, 70, 82	Myers, 1947
Tridens	16, 32, 40, 60	Sutherland, 1986
Triodia	28, 48	Myers, 1947
Trisetum	14, 24, 26, 28, 42	Myers, 1947
Zizania	30	Myers, 1947

In many taxa the current genome is a complex product of multiple occurrences of both allo- and autopolyploidy. Allopolyploids begin with a hybrid. The doubling of the two genomes solves pairing problems between its component genomes. Sometimes doubling occurs after the production of a relatively sterile hybrid (e.g. *Spartina anglica*, Guenegou, Citharel & Levasseur, 1988), sometimes allopolyploidy is the result of direct combination of unreduced gametes (Bretagnolle & Thompson, 1995). Allopolyploidy can occur multiple times in the history of a species as in *Triticum aestivum* (Sears, 1969). Autopolyploidy occurs when, within a single lineage, the genome duplicates, usually by production of an unreduced gamete that successfully forms an embryo, either combined with a normal (reduced) gamete or another unreduced gamete (Bretagnolle & Thompson, 1995). Historically, more attention has been paid to allopolyploidy than autopolyploidy and it has been considered to be by far the most important form of polyploidy (Stebbins, 1971; Grant, 1981). Recent work, however, finds autopolyploidy to be relatively common (Thompson & Lumaret, 1992; Bretagnolle & Thompson, 1995).

Stebbins (1947, 1971) proposed a widely accepted sequence for the development of polyploidy within lineages. First tetraploidy occurs, then the tetraploids spread and replace the diploids. The diploids become geographically restricted, rare, and then extinct, and the process repeats as hexaploids and octoploids are formed from the tetraploids and expand at the expense of the tetraploids. Although Stebbins considered autopolyploidy rare, the model needs little modification to incorporate autopolyploidy.

In an allopolyploid complex, when the ploidy levels are incompatible, there is a tight relationship between ploidy level and taxonomy, i.e. different ploidy levels belong in different species. Such polyploid series occur in many grass genera (Table 7.1). Although it has not been studied, polyploid series within genera should also result from autopolyploids becoming fixed in one derived species, but not in another. During this process, populations containing a mixture of ploidy levels might persist for long periods of time. Indeed, it appears that derived species may carry intraspecific polyploid variation with them, as in the case of *Andropogon hallii*, which is clearly derived from *A. gerardii*, and has similar intraspecific polyploidy (Sutherland, 1986; Table 7.3). In these cases ploidy level need not correlate with taxonomic divisions (see below). Little is known about the relative frequency of these processes.

This paper discusses polyploidy within species of grasses. For more general reviews of polyploidy, see Stebbins (1971), Lewis (1980), Grant (1981), Lumaret (1988*a*), and Thompson & Lumaret (1992).

Distribution of intraspecific polyploidy

Species that are composed of individuals and populations with differing ploidy levels are known from many families, including the Chenopodiaceae (Dunford, 1985; Freeman & McArthur, 1989), Fabaceae (Grant, Brown & Grace, 1984; Hymowitz, Parker & Singh, 1991), Rosaceae (Campbell, Greene & Bergquist, 1987), reviewed in Lewis (1980).

Variation in ploidy level occurs within many grass species (Federov, 1974; Lewis, 1980; Keeler & Kwankin, 1989; Table 7.2). Of the grass species listed in the floras of the Great Plains (Sutherland, 1986) and California (Hickman, 1993) about 21% of the species were reported to have intraspecific polyploidy (Table 7.3). It is difficult to evaluate the quality of this value: (a) Some old counts produced with untrustworthy methods are probably still being cited (see discussion in Church, 1936). (b) With higher numbers of chromosomes, accurate counting is more difficult and so less accurate. (c) Some reports of intraspecific polyploidy may be the result of taxonomic confusion: certainly taxonomic revision can greatly simplify the cytogenetics of some genera. (d) On the other hand, for some species, the cytotype is known from a single count, therefore it is not known whether the species is chromosomally variable. (e) Other species are only very sketchily sampled or from only part of an extensive range, likewise making undetected intraspecific polyploidy possible. I think it is premature to analyse patterns of intraspecific polyploidy within the Poaceae, although it is obvious that a substantial number of species have been reported to possess intraspecific polyploidy.

Genetics of polyploids

Polyploidy usually produces profound changes in the genetics of the species. These changes can include change in Mendelian inheritance patterns and modification of dominance relationships, declines in fertility, loss of incompatibility, greater retention of genetic diversity under selfing and loss of interfertility with other members of the (former) species (Haldane, 1930; Mather, 1936; Fisher, 1949; Levin, 1983; Fowler & Levin, 1984; reviewed in Bever & Felber, 1993). There is a rich literature on the genetics of polyploids of agricultural importance, such as *Solanum* and *Triticum* (e.g. Simmonds, 1976; Tsuchiye & Gupta, 1991). Theoretical studies of polyploid genetics go back 60 years (Haldane, 1930; Mather, 1936), and there is a growing body of more recent population genetics theory (Ehlke & Hill, 1988; Bever & Felber, 1993, Rodríguez, 1996*a*,*b*). Only a brief review relevant to intraspecific polyploid variation will be given here.

Table 7.2. *Grasses reported to have within-species polyploidy*

Genus and species	Ploidy	Chromosome numbers	Reference
Distribution studied			
Agropyron dasystachyum	2*n*, 6*n*	14, 42	Sadasivaiah & Weijer, 1981
Agrostis stolonifera		28, 35, 42	Björkman, 1984; Kik *et al.*, 1992
Andropogon gerardii	6*n*, 9*n*	60, 90	Norrmann *et al.*, 1997
Anthoxanthum odoratum	2*n*, 3*n*, 4*n*	10, 15, 20	Hedberg, 1967
Bouteloua curtipendula	3*n*, 4*n*, 5*n*, 6*n*, 8*n*, 10*n*, 14*n*	21, 28, 35, 40, 42, 45, 50, 52, 56, 70, 98	Harlan, 1949; Gould & Kapadia, 1962; Kapadia & Gould, 1964
Dactylis glomerata	2*n*, 4*n*, 6*n*	14, 28, 42	Müntzing, 1937; Stebbins & Zohary, 1959; Zohary & Nur, 1959; Lumaret, 1988*b*
Deschampsia caespitosa	2*n*, 4*n*	26,52	Rothera and Davy, 1986
Holcus mollis	4*n*, 5*n*, 6*n*, 7*n*	28, 35, 42, 49	Jones, 1958; Jones & Carroll, 1962
Panicum virgatum	2*n*, 4*n*, 6*n*, 8*n*, 10*n*, 12*n*	18, 21, 25, 30, 32, 36, 54, 56–65, 70, 72, 90, 108	Nielsen, 1944; McMillan & Weiler, 1959
Paspalum brunneum	2*n*, 4*n*	20, 40	Norrmann *et al.*, 1989
P. cromyorrhizon	2*n*, 4*n*	20, 40	Quarín *et al.*, 1982
P. haumanii	2*n*, 4*n*	20, 40	Norrmann *et al.*, 1989
P. hexastachyum	2*n*, 4*n*, 6*n*	20, 40, 60	Quarín & Hanna, 1980
P. intermedium	2*n*, 4*n*	20, 40	Norrmann *et al.*, 1989
P. maculosum	2*n*, 4*n*	20, 40	Norrmann *et al.*, 1989
P. quadrifarium	2*n*, 3*n*, 4*n*	20, 30, 40	Norrmann *et al.*, 1989
P. rufum	2*n*, 4*n*	20, 40	Norrmann *et al.*, 1989

Intraspecific polyploidy reported			
Andropogon hallii	6*n*, 7*n*, 10*n*	60, 70, 100	Nielsen, 1939; Brown, 1950
Aristida purpurea	2*n*, 4*n*, 6*n*, 8*n*	22, 44, 66, 88	Hickman, 1993
Arrhenatherum elatius	2*n*, 4*n*, 6*n*	14, 28, 42	Hickman, 1993
Bouteloua gracilis	2*n*, 4*n*, 6*n*	20, 29, 35, 40, 42, 60, 61, 77, 84	Fults, 1942; Snyder & Harlan, 1953
B. hirsuta		12, 20, 21, 28, 37, 42, 46	Fults, 1942; Gould, 1958
Buchloe dactyloides	2*n*, 4*n*, 6*n*	20, 40, 60	Sutherland, 1986
Elymus canadensis	2*n*, 4*n*	28, 42	Nielsen & Humphrey, 1937
Festuca elatior	2*n*, 4*n*, 6*n*,	14, 28, 42	Myers, 1947; Myers & Hill, 1947
Koeleria pyramidata	2*n*, 4*n*, 8*n*, 10*n*, 12*n*	14, 28, 56, 70, 84	Hickman, 1993
Phalaris arundinacea	2*n*, 4*n*, 5*n*, 6*n*	14, 27, 28, 29, 30, 31, 35, 42, 48	Hansen & Hill, 1953
Phleum alpinum	2*n*, 4*n*	14, 28	Hickman, 1993
P. pratense	2*n*, 3*n*, 4*n*	14, 21, 28	Hickman, 1993
Phragmites australis	4*n*, 6*n*	36, 44, 46, 48, 49–52, 72, 84, 96	Hickman, 1993
Saccharum spontaneum	not certain 2*n* (=8*x*=64), 4*n* ?	40, 48, 54, 56, 60, 64, 72, 80, 96, 104, 112, 128	Panje & Babu, 1960; Al-Janabi *et al.*, 1993
Spartina pectinata	4*n*, 6*n*, 12*n*	28, 40, 42, 80, 84	Myers, 1947; Sutherland, 1986
Sporobolus cryptandrus	2*n*, 4*n*, 6*n*, 8*n*	18, 36, 38, 72	Hickman, 1993
Trisetum canescens	2*n*, 4*n*	14, 28	Hickman, 1993
T. flavescens	2*n*, 4*n*	14 28	Hickman, 1993
T. spicatum	2*n*, 4*n*, 6*n*	14 28 42	Hickman, 1993

Table 7.3. *Frequency of grass species with intraspecific polyploidy in two recent floras*

Flora	Intraspecific polyploid series reported	One chromosome number in the species	Variation but not a polyploid series	No value reported	Total grass species
Great Plains	84 (33.5%)	127 (50.6%)	19 (7.6 %)	21 (8.4%)	251
California	82 (16.6%)	307 (62.0%)	34 (6.9 %)	72 (14.5%)	495
Shared species	27	45	6	0	78
Combined	138 (20.7%)	390 (58.4%)	47 (7.0%)	93 (13.9%)	668

Note:
Taken from Sutherland (1986); Hickman (1993).

For ease of description I will outline the differences using diploids and tetraploids. Diploids are the basis on normal Mendelian genetics: each individual has two copies of each (non-duplicated) locus, and so can be heterozygous (a_1a_2) or homozygous (a_1a_1, or a_2a_2). If there is dominance, the heterozygote shows some phenotype other than one intermediate between the homozygotes. Under selfing, diploids approach two pure lines rapidly: half of the progeny are expected to be homozygotes and so frequency of heterozygotes drops by 50% each generation. Progeny receive just one of the two alleles of each parent.

In contrast, tetraploids have four copies of each locus, and normal terminology for heterozygosity immediately breaks down. While homozygous tetraploids are clear: $a_1a_1a_1a_1$ and $a_2a_2a_2a_2$, heterozygotes could be $a_1a_1a_1a_2$, $a_1a_1a_2a_2$ and $a_1a_2a_2a_2$. But of course they are not limited to just two alleles per individual the way diploids are, so additional forms of heterozygosity exist, to the extreme of $a_1a_2a_3a_4$. Dominance between the alleles is not *per se* affected by ploidy levels, but since so many more alleles can occur in the same individual, that dominant allele may mask a greater variety of different genetic combinations. In addition, the phenotypes produced by interactions between co-occurring alleles are far more complicated ($a_1a_1a_2a_3$ might be functionally distinguishable from $a_1a_2a_2a_3$ and $a_1a_2a_3a_3$). At the enzyme level, being tetraploid opens up the possibility for a wide array of dimeric enzymes produced by combinations of two allele products. Under selfing, a much lower percentage of the progeny will be homozygotes. Assume for simplicity we start with $a_1a_1a_2a_2$, selfed: 17% of the progeny will be homozygotes, so that 83% of the genetic variation is retained. After five generations, when 97% of the diploid population would

be expected to be homozygous under selfing (0.5^5), 60.6% of the tetraploid population will be homozygous (0.83^5), a much slower loss of genetic variation (Haldane, 1930). Finally, progeny receive two copies of the genome from each parent. This is more complex than it seems, because at meiosis, crossing over can recombine the alleles with respect to the centromere. Genetic exchange among the two chromosomes of diploids breaks up linkage groups. In tetraploids, since crossing over and segregation can result in double reduction, the same allele being twice included in a gamete, it is therefore possible for $a_1a_2a_2a_2$, selfed, to produce among its progeny $a_1a_1a_2a_2$. In some cases the frequency of double reduction could be 50% (Mather, 1936). Thus the genetic recombination of tetraploids is more than just a simple doubling of all the values of the diploid: much more variation is possible. For more detail see the review by Bever & Felber (1993).

The comments made for tetraploids relative to diploids apply likewise to hexaploids and octoploids and other higher multiples (summarized by Bever & Felber, 1993). The variety possible is a geometric, not linear, expansion.

One of the key observations about polyploidy is that where there is not strict control of meiotic segregation, there is significant loss of fitness due to production of gametes with incomplete or partially duplicated genomes. In addition, segregation in polyploids that are odd multiples of the basic number, i.e. triploids ($3n$), pentaploids ($5n$), etc., often results in gametes receiving partial genomes and, therefore, chromosome complements that function poorly or not at all. There is widespread documentation of reduced fertility of these odd-numbered ploidy levels although the situation is complex and species differ greatly (Stebbins, 1971; Grant 1981).

Chromosome combinations which produce few viable gametes are important in understanding the evolution of polyploidy because chromosome complements and crosses that result in unbalanced gametes are usually at a fitness disadvantage compared with conspecifics with even multiples of the genome. Where polyploidy confers an obvious decrease in fitness, it is clear that doubling the genome is not a neutral trait, and an explanation for maintenance or recurrent origin of the polyploids is required.

As emphasized by Bever & Felber (1993) much more work remains to be done on the genetics and population genetics of polyploids.

Implications of intraspecific polyploidy

Intraspecific polyploidy is not necessarily a result of poor taxonomy. Disparate ploidy levels are frequently both interfertile and morphologically

indistinguishable: the evolutionary unit in many grass species is a population of plants of diverse ploidy levels. Although historically plants with different ploidy levels have been held to be reproductively isolated from each other, this has proven to be an oversimplification.

First, gene flow can occur between ploidy levels. *Dactylis glomerata* and *Andropogon gerardii*, both autopolyploid complexes, show interploidy level fertility (i.e. gene flow) (Zohary & Nur, 1959; Lumaret, 1988*b*; Norrmann, Quarín & Keeler, 1997). In *Holcus*, allopentaploids produce fertile diploid progeny (Richard *et al.*, 1995).

In general, fertility is greater in even multiples of the genome, and intraploidy level hybrids such as triploids and pentaploids are of significantly lowered fertility (Zohary & Nur, 1959; Stebbins, 1971; Grant, 1981; Richard *et al.*, 1995; Norrmann *et al.*, 1997). However, in a surprising number of species, some individuals with odd-numbered ploidy levels, e.g. pentaploids in *Holcus mollis* (Jones, 1958; Jones & Carroll, 1962), triploids in *Dactylis glomerata* (Zohary & Nur, 1959; Borrill, 1978), enneaploids ($9x$) in *Andropogon gerardii* (Norrmann *et al.*, 1997) have good fertility, linking the ploidy series into an evolutionary whole (Jackson, 1976; Lumaret, 1988*a*; Thompson & Lumaret, 1992).

Secondly, from a pragmatic identification standpoint, many ploidy levels are not recognizable as distinguishable separate taxa. So long as polyploids are recurrently created as multiple events, whether allo- or autopolyploid, there is going to be a range of characters that do not lend themselves to distinguishing ploidy levels easily. In some cases this has been carefully studied, e.g. *Dactylis* (Stebbins & Zohary, 1959), *Anthoxanthum odoratum*, (Hedberg, 1967), and *Deschampsia* (Rothera & Davy, 1986).

Stebbins & Zohary (1959) summarize the problem succinctly:

> . . . the evolutionary relationships within *Dactylis* would be reasonably well expressed by only two ways of recognizing species. One would be to recognize a single tetraploid and one or two diploid species . . . [but] . . . the only absolute criterion which separates all diploids from all tetraploids is the chromosome number. The separation of *Dactylis* into two such variable and similar species is not only impractical from a taxonomic point of view, but is also not altogether compatible with a species concept based upon reproductive isolation.

Thus, they reduce the diploid and tetraploid forms to subspecific status. It is a clear reflection on the reality of gene flow and morphological variation in the complex that the many subsequent workers have largely accepted the merging of eleven diploid taxa, two to five tetraploid taxa and one hexaploid taxon into one named species, *Dactylis glomerata* (e.g. references cited below).

Given that some polyploid complexes are considered intraspecific because the ploidy levels are neither morphologically nor genetically discrete, it is important to consider what this might tell us about the population ecology of grasses. I will describe two well-studied examples.

Dactylis glomerata L., cocksfoot, orchard grass, is a rhizomatous grass naturally distributed throughout Europe to northern Africa and Asia that has been widely introduced elsewhere in the world (Müntzing, 1937; Myers, 1941; Stebbins & Zohary, 1959; Zohary & Nur, 1959; Borrill, 1961, 1978; Parker & Borrill, 1968; Lumaret *et al.*, 1987; Lumaret, 1988*b*; Bretagnolle & Thompson, 1996). Diploid, tetraploid, and hexaploid plants and populations are known. The diploids are narrowly distributed and often readily distinguished from each other morphologically (Parker & Borrill, 1968; Lumaret, 1988*b*). They hybridize to some degree with each other and the diploid hybrids are fertile, although less so than the parents (Borrill, 1961, 1978). Tetraploids in this complex are more abundant and more widespread than the diploids. In many cases (Stebbins & Zohary, 1959; Borrill, 1961) they cannot be readily distinguished from diploids occurring in the same area. Furthermore, tetraploids are fully interfertile (Stebbins & Zohary, 1959). Where diploids and tetraploids occur together, natural triploids form. Triploids have about 1% fertility and are responsible for gene flow between the ploidy levels (Zohary & Nur, 1959). As noted above, the complexity of the group led Stebbins & Zohary (1959) to classify all the recognizable types as simply subspecies of *Dactylis glomerata*.

A detailed study looking for microhabitat differences in northern Spain found local tetraploids to be distributed more broadly than diploids, but particularly they inhabited open and disturbed habitats, whereas the corresponding diploids were confined to shaded areas (Lumaret *et al.*, 1987). Experimental studies indicated that the correlation with shade resulted from the moister conditions under the trees, rather than shade tolerance (Lumaret *et al.*, 1987). The picture was complicated by the presence of tetraploids of subspecies *Dactylis glomerata glomerata* which escapes from cultivation and had hybridized with local (Galician) tetraploids. Plants of subspecies *glomerata* and Galacian tetraploids were concentrated in different habitats and their hybrid was found in between them (Lumaret *et al.* 1987; Fig. 7.1*A*). The outcome of the extensive study of *Dactylis* is a picture of a taxon in which local plants form autopolyploids fairly frequently, but diploids can form interspecific hybrids occasionally, the tetraploids are interfertile, and triploids hybridize with tetraploids and other triploids. Thus gene flow links the complex at many points. The variation in the tetraploids matches that of diploids in their areas of origin, but

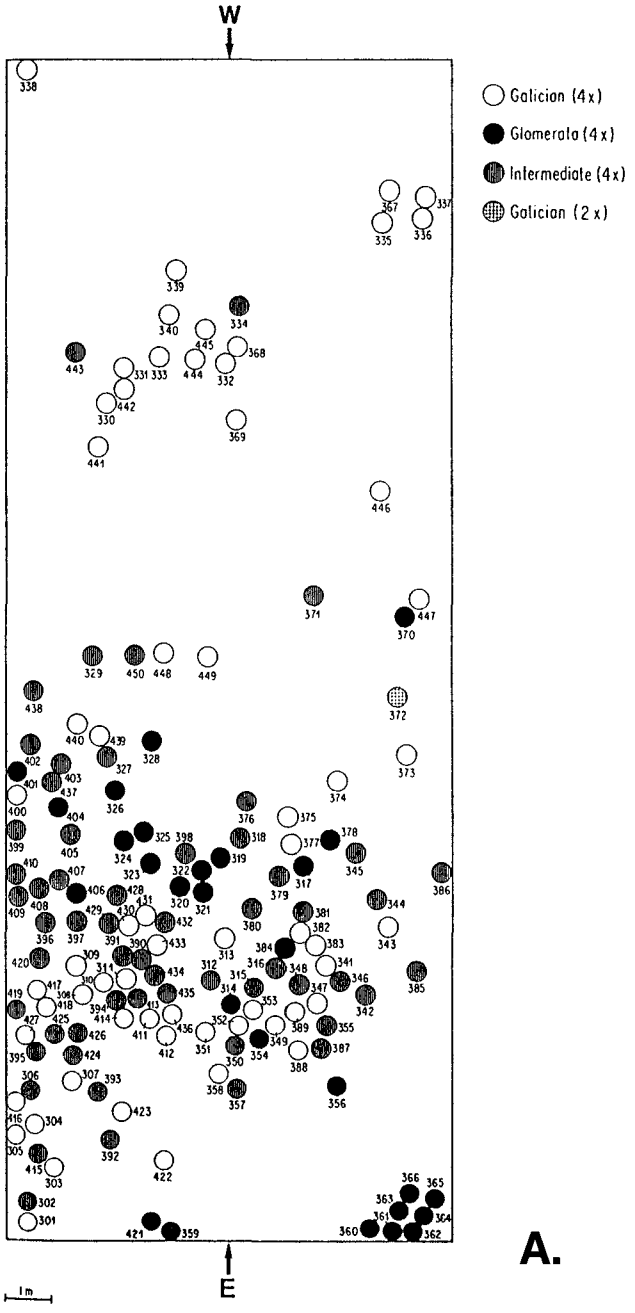

Fig. 7.1. Spatial distribution of polyploids within populations. (*A*) *Dactylis glomerata* (fig 5 from Lumaret *et al.*, 1987). The diploid and tetraploid morphs are mapped. (Reproduced with permission of Springer-Verlag.)

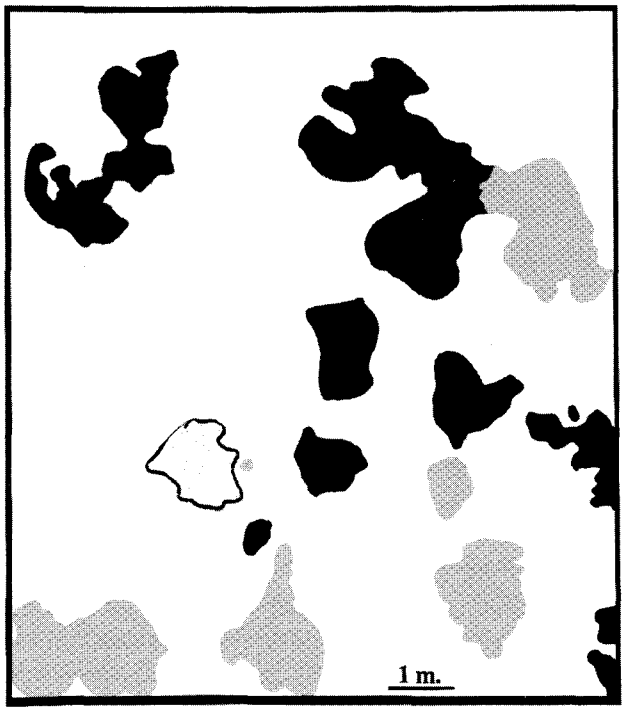

Fig. 7.1. (*cont.*)
(*B*) *Andropogon gerardii* (K. H. Keeler unpublished) population in Boulder Co., CO. Shaded are *A. gerardii* individuals: dark, 60 chromosomes; light, 90 chromosomes; outline intermediate value (probable aneuploid).

overall exceeds that of diploids, because although there is some increase in variation with chromosomal increase, the greater genetic variation is also a result of the multiple origins of tetraploids and their hybridization with each other (Lumaret, 1988*b*).

Panicum virgatum, switchgrass, is a tall rhizomatous perennial of central North America. A polyploid series was recognized by Nielsen (1944): $2n=18$, 36, 54, 72, 90, 108. He found no geographic patterns and in one population the complete range of cytotypes were present. Comparing the morphological characteristics of agronomic potential between the cytotypes, Nielsen (1944) found no consistent differences or any reason to prefer higher polyploids as forage grasses. McMillan & Weiler (1959) conducted a study of the central USA and again found multiple cytotypes within populations (although none with more than three cytotypes). They too found no consistent pattern for characters they compared between cytotypes (e.g. date of first flowering, height). They reported that clones from one region

were more similar to clones of the other ploidy levels found in that area, than to the same ploidy level found elsewhere. In Oklahoma and Kansas, *Panicum virgatum* has two distinct morphotypes that are described as 'lowland' and 'upland' forms. A series of studies (Porter, 1966; Barnett & Carver, 1967; Brunken & Estes,1975) found the lowland form, which is conspicuously taller, more robust and more clumped, to be tetraploid, while the upland form was both hexaploid or octoploid, often equally frequently. Recent studies indicate that this pattern does not hold across the range: upland forms from Nebraska included tetraploids (Hultquist, Vogel & Kaeppler, 1996; Hultquist *et al.*, 1997), which led Hultquist *et al.* (1997) to suggest separate origins of the two forms and an autopolyploid series within the upland race, something suggested by Brunken & Estes (1975) from much less detailed information. Hybridization between the upland and lowland races has not been reported in the literature but can occur (K. P. Vogel & J. Martinez Reyna, unpublished data).

Thus, in *Panicum virgatum* there is widespread and significant chromosomal and morphological variation, with a strong geographic component to both cytotype and morphology, but apparently with no simple relationship between them. Despite extensive study, however, there are many regions in which *P. virgatum* has not been analysed and which may clarify the situation. While the details of the polyploid complexes within *Dactylis glomerata* and *Panicum virgatum* differ greatly, one could conclude that both species show important and widespread cytotypic and morphological variation which are not related in any simple manner. Both taxa suggest that, whether or not intraspecific polyploidy is adaptive, it is evolving independently of morphology.

Population ecology of intraspecific polyploidy

As discussed above, there is usually gene flow between the cytotypes in a grass population with several ploidy levels. In *Dactylis glomerata*, for example, diploids and tetraploids produced viable hybrids at a frequency of at least 3 triploids per 2000 plants. While the triploids were largely pollen-sterile, they produced viable seeds, including tetraploids and pentaploids (Zohary & Nur, 1959; Lumaret & Barrientos, 1990). Thus, genes from the diploids could move via triploids into tetraploid populations. In the case of Zohary & Nur's study, this logical argument was supported by the presence of B chromosomes in the progeny of the triploids, because in the Israeli populations studied, B chromosomes were found only in diploid plants. Similarly inter-cytotype ($6x \times 9x$) hybrids of *Andropogon gerardii* form a

potential bridge between the ploidy levels of that species because they have some pollen and seed fertility, despite being largely aneuploid (Norrmann *et al.*, 1997).

The genetic complexity of some populations can hardly be overemphasized. Nielsen (1944) found five ploidy levels within a single population of *Panicum virgatum*, and populations with three cytotypes were common (McMillan & Weiler, 1959). Lumaret *et al.* (1987) mapped *Dactylis glomerata* plants with a plot of 10×80 m that had a local diploid and tetraploid cytotype and an agronomically introduced tetraploid cytotype and the tetraploid hybrids of the two tetraploid races (Fig. 7.1*A*). *Andropogon gerardii* also has populations with plants of different ploidy levels intermingling (Keeler 1992, Fig. 7.1*B*). Because these cytotypes are interfertile, all contribute to the evolutionary population.

When the species-wide variation is considered, many grass species are very complex indeed. Over its range, *D. glomerata* has a very wide variety of cytotypes, genotypes and phenotypes, occurring as single or multiple cytotype populations (Lumaret 1988*b*; Lumaret & Barrientos, 1990). The diploid:tetraploid:pentaploid complex of *Holcus mollis* × *H. lanatus* likewise has regional differences superimposed on the local populations that contain varying combinations of cytotypes (Jones, 1958; Richard *et al.*, 1995). Others that have not been as intensely studied are likely to be very complex as well, e.g. *Bouteloua curtipendula* (Gould & Kapadia, 1962; Kapadia & Gould, 1964), *Poa pratensis, Phragmites australis* (Table 7.2).

For most intraspecific polyploid complexes studied, ploidy levels cannot be distinguished at the individual level with sufficient accuracy for taxonomic distinctions (Hedberg, 1967; Rothera & Davy 1986; Norrmann *et al.*, 1997). Populations of different ploidy levels often differ, but there is such extensive overlap, especially by the higher ploidy levels, that individuals are difficult to categorize. Generally this is a result of the broader variation in the higher ploidy levels (Stebbins 1947, 1971; Hedberg, 1967; Rothera & Davy, 1986). To the degree that selection acts on the phenotype, not the genotype, such cytotypic variation is cryptic variation, invisible to selection.

Ecological and geographic differentiation

Except for their impact on speciation, the evolutionary and population biology consequences of polyploidy and intraspecific polyploidy are largely unexplored. Intraspecific polyploid complexes could, like any form of genetic variation, be, for example, adaptive, deleterious, neutral or transient.

Some differences between ploidy levels seem as if they should be subject to selection. Hedberg (1967) found that tetraploid plants of *Anthoxanthum odoratum* had hairier leaves, leaf sheaths and glumes than diploids, but the occasional glabrous tetraploid eliminated that for use as a distinguishing character. Diploids on the whole also had smaller spikelets and pollen, but the overlap again precluded using these characters diagnostically. Rothera & Davy (1986) found that tetraploid *Deschampsia caespitosa* often, but not always, had larger florets than diploids. This and other characters formed a general syndrome that distinguished diploids and tetraploids, but it broke down for individual plants. Enneaploid ($9x$) *Andropogon gerardii* are usually taller than hexaploids ($6x$), but there is so much phenotypic plasticity that the difference is detectable only statistically within populations, not for individuals (K. Keeler, unpublished). Differences in winter-hardiness and growth rate to flowering have been reported in *Dactylis* (e.g. Bretagnolle & Thompson, 1996). Other differences have been correlated with ploidy level (e.g. Stebbins, 1971; Lewis, 1980; Grant, 1981; Roy & Lumaret, 1987; Warner, Ku & Edwards, 1987, Masterson, 1994). Without a series of direct experiments, it is difficult to judge whether the ploidy levels respond differently enough to stresses in the environment to show different relative fitnesses: although the types of differences suggest they do, the lack of consistent responses within these polyploid complexes argue they do not.

Small-scale ecological differences occur between ploidy levels in *Dactylis glomerata* (Lumaret *et al.*, 1987; Bretagnolle & Thompson, 1996); the *Holcus lanatus – Holcus molis* complex (Richard *et al.*, 1995), *Paspalum hexastachyum* (Quarín & Hanna, 1980), *Agrostis stolonifera* (Kik, Linder & Bijlsma, 1992), and *Anthoxanthum odoratum* (Hedberg, 1967). Small-scale ecological differentiation was not found among cytotypes of *Deschampsia cespitosa* (Rothera & Davy, 1986) or *Andropogon gerardii* (Keeler, 1990, 1992). For *Panicum virgatum*, the situation appears to vary across its range (Nielsen, 1944; McMillan & Weiler, 1959; Porter, 1966; Barnett & Carver, 1967; Brunken & Estes, 1975; Hultquist *et al.*, 1996, 1997).

If the cytotypes cannot be morphologically distinguished in any reliable way, yet can be shown to have distributions correlated with environmental variables, the ecological patterns presumably stem from the fine differences resulting from doubling of the genome, although experiments are needed to eliminate the possibility that the pattern is a stochastic artifact. In *Dactylis glomerata* there is sufficient data to suggest that patterns are deterministic not random (Stebbins & Zohary, 1959; Lumaret *et al.*, 1987; Roy & Lumaret, 1987; Bretagnolle & Thompson, 1996), while for *Andropogon*

gerardii, the lack of match between patterns at different scales (Keeler *et al.*, 1987; Keeler, 1990, 1992) could reasonably result from stochastic effects.

Small-scale maps often reveal intimate mixing of cytotypes (Fig. 7.1*A,B*), whether or not the species shows ecological differentiation. For *Dactylis*, levels of mixing vary greatly across its range (Lumaret, 1988*b*). *Andropogon gerardii* is mainly hexaploid in the eastern part of its extensive range, but the populations in the west have roughly equal frequencies of 60 and 90 chromosome plants, thoroughly intermingled (Keeler *et al.*, 1987; Keeler, 1990, 1992, unpublished data, Fig. 7.1*B*). Mixing of the cytotypes of *Anthoxanthum odoratum* has been enhanced by human activities (Hedberg, 1967). *Panicum virgatum* populations are usually a mix of cytotypes (Nielsen, 1944; McMillan & Weiler, 1959), but there is ecological separation as well (e.g. Porter, 1966). *Holcus lanatus* in France shows both ecological and geographic differences among cytotypes (Richard *et al.*, 1995).

The simplest of the consequences of multiple cytotypes within populations is that a wide array of morphologies and ecological adaptations are available within the complex. Lumaret *et al.* (1987) demonstrate the power of cytotypic variation (Fig. 7.1*A*), in the sense that one evolutionary unit (*Dactylis glomerata sensu lato*) occupies three microhabitats. Given the ecological importance of grasses (they are after all the only plant family with a major ecosystem named for them, and that ecosystem occupies every continent except Antarctica), the ecological differentiation afforded by polyploid complexes deserves to be looked at as a potential adaptive strategy. Much work needs to be done to understand the implication of these consequences of polyploidy to mixed populations and to adaptive evolution of grasses. *Andropogon gerardii*, for example, is an ecosystem dominant despite cytotypic variation that should lower fitness (Keeler, 1990; Norrmann *et al.*, 1997) (Fig. 7.2). A frequently burned prairie in what is now the 'corn belt' was a virtual monoculture of *A. gerardii*, with more than 80% of the biomass from this single species (Weaver, 1954). In the face of arguments that 'nature abhors a monoculture' one is moved to ask whether ploidal variation may have helped ameliorate the disadvantages of a monoculture (e.g. lack of genetic variation to resist diseases), facilitating ecological dominance by a single lineage.

Other important points in the population ecology of intraspecific polyploidy are illustrated in *Holcus* (Jones, 1958; Richard *et al.*, 1995), *Anthoxanthum* (Hedberg, 1967), *Dactylis* (Lumaret 1988*b*), and *Panicum* (Hultquist *et al.*, 1996, 1997), where in all cases there are inconsistencies in the breeding relationships and behaviour of cytotypes (such as hybridization

Fig. 7.2. Photo of *A. gerardii* -dominated prairie (Konza Prairie, Manhattan, KS). Photo by K. H. Keeler

and genetic composition of populations) in different parts of the species' range. This is understandable given the recurrent formation of auto- and allopolyploids, and backcrossing within the complex. It does, however, mean that caution must be used in extrapolating experimental results across the geographic range of a polyploid complex.

The taxon cycle of Stebbins (1947) provides a description of reality but begs the question of causation. What are the forces that increase ploidy level and allow higher ploidy levels to survive (cf. Levin, 1983; Fowler & Levin, 1984; Rodríguez, 1996*a*, *b*)? Are taxa found at different places in Stebbins' progression simply because of different periods since they originated, or is polyploidy adaptive in some contexts but not in others?

Polyploids have been described as being more variable than diploids (see above). Their differences result from the hybrid origin of allopolyploids or the multiple origin of autopolyploids in different local populations, which must produce selective advantage under some conditions. Other differences ascribed to polyploidy include loss of the incompatibility systems of diploids or other means of greater reproductive promiscuity (Lumaret, 1988*a*,*b*; Bretagnolle & Thompson, 1995). In several *Paspalum* species, diploids are obligate outcrossers but autotetraploids are largely apomictic (Quarín & Hanna, 1980; Quarín, Hanna & Fernández, 1982).

It seems unlikely that all or even most grass species with intrapopulation polyploidy will have the same fitness relationships among the cytotypes, but it is reasonable to expect that there are a finite number of combinations of genetics and ecology which select for (or permit) the realized distribution of cytotypes. Given the importance of grasses, both ecologically and economically, and the frequency of intraspecific polyploidy (Tables 7.2, 7.3), the evolutionary forces underlying intraspecific polyploidy present a rich area for future research.

Summary

Polyploid series within local populations occur in many grass species. The evidence suggests recurring autopolyploidy is often the cause of the polyploid variation, but recurrent allopolyploidy is indicated in some cases. Often the different ploidy levels cannot be distinguished morphologically and they exchange genes at least occasionally; thus the evolutionary unit is a cytologically complex population. The implications of the presence of multiple cytotypes for local adaptation have scarcely begun to be investigated.

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