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## POLYPLOIDY AND THE EVOLUTION OF DOMESTICATED PLANTS<sup>1</sup>

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Polyploidy and domestication are common features of plant evolution. A number of selective advantages conferred by polyploidy appear relevant to domestication. Surprisingly, the correlation between the two has not previously been examined. Anderson (Plants, man and life. University of California Press, Berkeley, CA, 1969) asserted that we do not yet know exactly what percentage of cultivated plants and weeds are polyploid, but it must be high. Heiser (Seeds to civilization, the story of food, 2d ed., W. H. Freeman, San Francisco, CA, 1981) stated that a large number of the major food crops are polyploids, giving wheat, sugar cane, potatoes, sweet potatoes, and bananas as examples. In this study, the distribution of polyploidy in 244 crop species was compared to the estimates of polyploidy in their respective higher categories. The proportion of polyploidy in crop plants was considered in relation to taxonomic origin, habitat, and reproductive strategies of the crops. The study showed that the crop species were a random selection as far as ploidy level is concerned and that domestication did not appear to have favored polyploid over diploid genomes or vice versa. Vegetative, seed, and tree crops were statistically homogenous in their polyploid composition. The distribution of polyploidy in annual and perennial crops did not differ statistically. The data imply that polyploid genomic constitution neither facilitated nor hindered the ability of wild species for domestication.

Polyploidy and plant domestication are two common features in plant evolution. Surprisingly, there are no data available on the frequencies of polyploidy in crop plants and its role in the domestication process. It has been proposed that chromosome doubling tends to shift populations toward the *K* end of the *r-K* selection continuum or convey greater stress tolerance by fostering slower development, delayed reproduction, longer life span, greater defense against pathogens and herbivores, larger seeds, and lower reproductive effort with greater emphasis on vegetative reproduction (reviewed in Lewis, 1980a; Levin, 1983). Some of these traits are important in plant domestication. Polyploids have also been considered to have greater ability to colonize new or disturbed habitats than their diploid ancestors (Ehrendorfer, 1980), explaining the wider geographic distribution of the polyploids (Reese, 1958; Stebbins, 1972). Wild races of domesticated cereals are aggressive colonizers (deWet and Harlan, 1975), and thus polyploidy seems to be advantageous in domestication. On the other hand, Stebbins (1971) suggested that the processes of mutation and gene recombination are more effective in the evolution of diploids than polyploids, and consequently, radically new changes are more likely to evolve at the diploid than polyploid level. If this is true for plant domestication, then one would expect diploids to be at a selective advantage.

**Polyploidy**—Latest estimates of the frequency of polyploidy in flowering plants range between 47% to over 70% (Grant, 1963; Goldblatt, 1980; Lewis, 1980b). Although the estimates vary according to the criteria used to des-

ignate levels of polyploidy, the numbers are a clear indication of the significant role of polyploidy in the evolution of flowering plants. Surveys made by Goldblatt (1980) and Lewis (1980b) suggested that polyploid frequency and role in flowering plant evolution have been underestimated. The incidence of polyploidy in flowering plants also varies considerably among plant families and genera. For instance, 80% of the species in the grass family (Poaceae) are estimated to be polyploid (deWett, 1987), whereas only 19% of the lily family (Liliaceae) and 18% of the pulse family (Fabaceae) are polyploid (Goldblatt, 1980, 1981).

The high incidence of polyploidy in plants has been attributed to the success it confers under various ecological conditions due to chromosome multiplicity and genome hybridity (Tal, 1980; Levin, 1983). Levin (1983) presented evidence from biochemical, physiological, developmental, and genetic sources to show that genome doubling could bring populations to new adaptive spheres. Stebbins (1985) attributed the variation in polyploid frequency in plant groups to frequent opportunities for secondary contact and hybridization between different diploid populations rather than to the inherent nature of the genome. He stated that those contacts generate highly adapted, aggressive gene combinations that have been buffered and maintained largely by the effect of polyploidy in favoring tetrasomic inheritance and preferential pairing of homologous, as compared with partially homologous (homeologous), chromosomes.

In terms of time of origin, polyploids can be classified into neopolyploids and paleopolyploids. Neopolyploid species are those having gametic chromosome numbers that are multiples of the basic diploid chromosome number found in their respective genera. Paleopolyploid species are ancient, rediploidized polyploids, with large basic chromosome numbers (Grant, 1963; Goldblatt, 1980). Grant (1963) postulated that species with haploid chro-

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TABLE 1. Species and genera of crops studied, their designated plant families, basic chromosome numbers, and percent of polyploidy. Haploid chromosome numbers are for the crop genera examined. Sources of information cited in Materials and Methods.

Family	# Of genera	# Of species	Chromosome numbers	% Poly-ploidy $x = 11$	% Poly-ploidy $x = 13$
Agavaceae	3	7	9, 10, 11	100	100
Araceae	3	6	13, 14	100	100
Arecaceae	5	5	16	100	100
Bromeliaceae	1	1	25	100	100
Cannaceae	1	1	9	100	100
Dioscoreaceae	1	10	10	100	100
Liliaceae	2	8	8, 10	38	38
Marantaceae	1	1	6	100	100
Musaceae	2	2	9, 11	50	50
Orchidaceae	1	1	16	100	100
Poaceae	18	27	5, 7, 9, 10, 12	74	67
Zingiberaceae	3	3	11, 12, 21	100	67
Amaranthaceae	1	1	16	100	100
Anacardiaceae	3	3	10, 14, 15	100	100
Annonaceae	1	1	7	0	0
Apiaceae	4	4	9, 11	75	0
Bombacaceae	1	1	7	0	0
Brassicaceae	5	12	8, 9, 10	58	58
Cannabaceae	1	1	10	0	0
Caricaceae	1	1	9	0	0
Chenopodiaceae	3	3	6, 9	67	67
Compositae	7	7	9, 10, 12	57	43
Convolvulaceae	1	1	15	100	100
Corylaceae	1	1	14	100	100
Cucurbitaceae	8	14	7, 10, 11, 12, 13	71	43
Ebenaceae	1	1	15	100	100
Ericaceae	1	4	12	100	50
Erythroxylaceae	1	1	12	100	0
Euphorbiaceae	4	4	9, 10, 11	75	50
Fabaceae	21	32	6, 7, 8, 10, 11, 12	78	16
Fagaceae	1	1	12	100	0
Clusiaceae	1	1	?	100	100
Juglandaceae	2	2	16	100	100
Lauraceae	2	2	12	100	0
Lecythidaceae	1	1	17	100	100
Linaceae	1	1	10, 15, 15, 16	100	100
Malvaceae	2	4	9, 13	100	100
Moraceae	3	5	13, 14	100	100
Myristicaceae	1	1	7	100	100
Myrtaceae	4	5	11	100	20
Oleaceae	1	1	23	100	100
Oxalidaceae	1	1	11, 12	100	0
Passifloraceae	1	2	9	0	0
Pedaliaceae	1	1	13	100	100
Piperaceae	1	2	16	100	100
Papaveraceae	1	1	11	100	100
Polygonaceae	2	2	8, 11	50	50
Proteaceae	1	1	14	100	100
Punicaceae	1	1	8, 9	0	0
Saxifragaceae	1	1	8	0	0
Rosaceae	7	17	7, 8, 16, 17	71	71
Rubiaceae	1	3	11	100	33
Rutaceae	1	8	9	0	0
Sapindaceae	1	2	11, 15	100	50
Sapotaceae	1	1	13	100	100
Solanaceae	4	6	12, 16	100	33
Sterculiaceae	2	3	10	67	67
Theaceae	1	1	15	100	100
Tiliaceae	1	2	7	0	0
Vitaceae	1	1	19	100	100

mosome numbers larger than  $n = 13$  are paleopolyploid, whereas species having  $n = 13$  or lower are predominantly diploid. Goldblatt (1980) maintained that almost all species with haploid chromosome numbers above  $n = 9$  or

10 probably have polyploidy in their evolutionary history, those with  $n = 11$  or more are almost certainly of polyploid origin, while even some plants having lower than  $n = 9$  are derived via polyploidy.

**Plant domestication**—Domestication is a relatively recent event in plant evolution. The oldest available records for phenotypic changes associated with plant domestication date back to about 10,000 B.C. (Higgs, 1972; Harlan, 1992). Thus, during most of human history, harvesting of wild plants as a source of food was the only practice. People harvested a large number of wild species and attempted to domesticate many of them, but only a small fraction of those species succeeded as crops. For instance, among the hundreds of species of grasses that were harvested in the wild, only about 34 species were domesticated (deWett, 1979). Positive responses to the attempts of genetic fixation of characteristics associated with plant domestication appear to have been unique features of a limited number of species.

Various morphological changes have been associated with plant domestication (deWett, 1979). Some changes were fundamental to the domestication process, whereas others were either secondary or the result of postdomestication selection for more desirable agronomic traits or superior cultivars. Examples of fundamental changes are the genetic switch from shattering to nonshattering seeds (or fruits) or from dehiscent to indehiscent fruits, dormant or nondormant seeds, and nonuniform to uniform growth. Nonshattering, uniform growth and synchronized maturity are basic for optimal crop harvesting and adequate yield. Adaptation to man-made habitat was an ecological prerequisite for domestication. de Wet and Harlan (1975) indicated that the wild races of domesticated cereals are aggressive colonizers but never true weeds, and thus, they rarely if ever successfully invade permanently disturbed habitats. Therefore, adaptation to permanently disturbed habitats was essential. Postdomestication traits include increase in size of the desired plant part, restoration of fertility in sterile flowers, dwarfness of cultivars, reduction in certain plant parts to facilitate harvesting of the crop, and adaptation to infraspecific competition for the emerging monoculture agricultural populations.

The questions posed here are: did polyploidy play a role in plant domestication by conferring some selective advantages or would polyploidy constitute a handicap? Does genome buffering in any way facilitate the domestication process and provide a basis for further diversity? If the answer to the last question is yes, then one would expect polyploidy to be significantly more frequent than diploidy among crop plants. To address these interrelated questions, the frequency and distribution of polyploidy in various crop species were surveyed from the literature and compared with those in the plant groups to which the crops belong. The distribution of polyploidy in crop plants was considered in relation to the taxonomic origin, habitat, and reproductive strategies of the crops.

## MATERIALS AND METHODS

The study focused on angiosperm food crops since the vast majority of our crops comes from this group. Chro-

mosome numbers from 244 crop species, belonging to 155 genera (Tables 1, 2) were obtained from the literature. The species represent 11 monocot and 48 dicot families. The sources of information were Darlington and Wylie (1956), Purseglove (1969, 1972), Simmonds (1976), Goldblatt (1980), Lewis (1980b), Simpson and Conner-Ogorzaly (1986), and Harlan (1992). Cross references were used whenever possible to check on the validity of the chromosome counts. Due to the large number of species examined, the list of crop species is reduced to the family level with information on number of species and genera summarized (Table 1).

Determination of neopolyploids was done by comparing the chromosome number of the crop with the smallest basic chromosome number of the species in its respective genus. A species was considered paleopolyploid if it has a gametic number larger than  $n = 11$  in one analysis and larger than  $n = 13$  in the other, following the criteria proposed by Goldblatt (1980) and Grant (1963), respectively. The frequency of polyploidy in the crops was compared with the estimates available for angiosperms in general, monocots, dicots, and some plant families.

Stebbins (1980) indicated that chromosome doubling tends to shift populations toward the  $K$  end of the  $r$ - $K$  selection continuum. Also, polyploidy generates the *gigas* effect which is commonly found in organs with determinate growth such as flowers and seeds, and in many instances, polyploidy has been associated with change in shape and texture (Stebbins, 1971). The crop species were, therefore, divided into three categories: 1) seed crops such as cereals and legumes; 2) vegetable crops; and 3) shrub-tree fruit crops. The division is based on selection for sexual reproduction compared with selection for vegetative vigor. The three groups of crops represent different points on the  $r$ - $K$  scale ranging from seed crops to shrub-tree fruit crops to vegetable crops. The distribution of polyploidy in these subgroups was statistically analyzed with the Brandt-Snedecor  $\chi^2$  test for homogeneity (Snedecor, 1946).

Polyploidy is considered to be more frequent in perennial than annual plants (Stebbins, 1971). The distribution of polyploidy in annual crops compared with the perennials was calculated for monocots, dicots, and angiosperm crops species in general. Biennial crops are classified as annuals. Crops that have a perennial habit but are grown as annuals were treated as perennials since the annual habit was artificially enforced. The data were treated with the  $\chi^2$  statistical test.

## RESULTS

Among the 244 crop species surveyed, 55% and 75% were found to be polyploids based on  $n = 13$  and  $n = 11$ , respectively (Table 2). The 75% value falls within the 70%–80% polyploidy in angiosperms obtained from the estimates of Goldblatt (1980) and Lewis (1980b), and the 55% is not statistically different from the 47% proposed by Grant (1963). In monocots, the frequency of polyploidy in domesticated plants was 78% ( $n = 13$ ) and 82% ( $n = 11$ ). The former value is higher than the 58% estimate of Grant (1963) obtained from chromosome counts available by 1955 and based on gametic numbers higher than

TABLE 2. Monocot and dicot crops and their subdivisions along with the percentages of polyploidy in each group using both  $n = 11$  and  $n = 13$  genetic chromosome numbers for delimiting polyploidy.

Type of plants	# Of species counted	% Polyploidy $n = 13$	% Polyploidy $n = 11$
<b>Monocots</b>			
Total monocots		58	75
Crops	72	78	82
Seed crops	24	65	73
Vegetable crops	40	83	85
Fruit crops	6	100	100
Crop annuals	28	68	71
Crop perennials	43	84	86
<b>Dicots</b>			
Total dicots		43	75
Crops	172	45	73
Seed crops	49	45	80
Vegetable crops	44	50	70
Fruit crops	79	43	70
Crop annuals	48	33	67
Crop perennials	103	50	72
<b>Angiosperms</b>			
Total angiosperms <sup>a</sup>	—	47	75
Total crops	244	55	75
Total seed crops	75	52	77
Total vegetable crops	84	65	77
Total fruit crops	85	47	72
Total crop annuals	76	46	68
Total crop perennials	146	60	76

<sup>a</sup> Number of angiosperm species surveyed was not available in some of the references.

$n = 13$ . The 82% frequency is similar to the estimated 70%–80% polyploidy in monocots based on similar criteria (Goldblatt, 1980).

In dicotyledonous crops, the proportions of polyploidy were 45% and 73% on the basis of  $n = 13$  and  $n = 11$ , respectively. The 45% value is quite similar to the 43% estimate of Grant (1963) using the same basis for the determination of polyploidy (Table 2). Similarly, the 72% found in dicots crops is within the range given by Lewis (1980b) for dicotyledonous plants using similar gametic chromosome numbers for defining polyploidy. Lewis (1980b) stated that the frequency of polyploidy in dicotyledons closely approximates 70% and may reach 80%.

The frequency of polyploid crop species in the monocot families Poaceae, Liliaceae, Araceae, and Arecaceae and the dicot families Fabaceae and Brassicaceae were compared with the estimates of polyploidy frequencies in the families. The data are summarized in Fig. 2. The frequency of polyploidy in the crops was not statistically different from the estimates provided for their respective families, except for the Dioscoreaceae.

The data for the distribution of polyploidy in the seed, vegetable, and fruit crop categories are summarized in Table 2 and illustrated in Fig. 1 for both  $n = 11$  and  $n = 13$  gametic chromosome numbers. In monocots, using  $n = 11$  as a criterion, all of the six shrub-tree fruit crops were polyploid (100%), whereas 73% of seed crops and 85% of vegetative crops were polyploid (Table 2; Fig. 1). The sample size in the latter two categories was larger than that of the shrub-tree fruit crops (Table 2). The use of  $n = 13$  slightly changed the proportions of polyploidy in seed and vegetable crops while the proportion of poly-

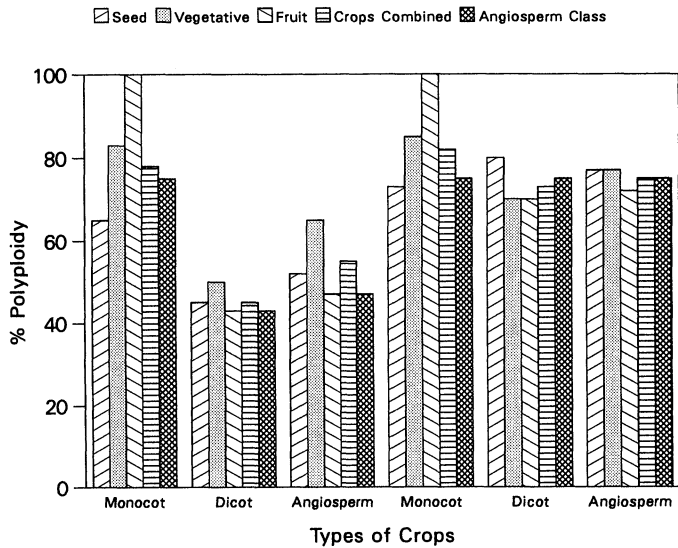


Fig. 1. The proportion of polyploidy in crop species and their respective monocot and dicot classes based on chromosome number of  $n = 13$  (three categories on the left) and  $n = 11$  (three categories on the right). The proportion of polyploidy in seed, vegetative, and fruit crops is also presented and contrasted with that in their respective angiosperm class.

polyploidy in shrub-tree crops remains 100% (Table 2). Among the three categories of dicot crops, the vegetative crops were only slightly higher in the percentage of polyploids (50%) than the other two categories (45% and 43%; Table 2; Fig. 1). Compared with the 100% polyploidy in shrub-tree fruit crops in monocots ( $n = 11$  or 13), the dicot group displayed polyploid proportions of 43% for  $n = 13$  and 70% for  $n = 11$ . The number of shrub-tree fruit species surveyed in dicots was 79 compared with six species in monocots.

The differences in proportions of polyploids among the three categories of crops within monocots and within dicots were subjected to the Brandt-Snedecor  $\chi^2$  test for homogeneity (Snedecor, 1946). The differences among the three groups in monocots and in dicots were not statistically significant for the  $n = 13$  ( $P > 0.05$  and  $P > 0.50$ , respectively) or the  $n = 11$  ( $P > 0.10$  and  $P > 0.30$ , respectively) gametic chromosome number calculations. Thus, the distribution of polyploidy appears to be homogeneous within both monocot and dicot crops.

The distribution of polyploid in annual and perennial crops is reported in Table 2. This analysis shows slightly higher frequency of polyploidy in perennial crops compared with annuals. However, the difference is not statistically significant for  $n = 11$  ( $P > 0.20$ ) or  $n = 13$  ( $P > 0.70$ ). Similarly, the proportions of polyploidy in the perennial crops were not statistically significant in monocots ( $P > 0.05$  for both  $n = 11$  and 13) or dicots ( $P > 0.30$  for  $n = 11$  and 13).

## DISCUSSION

Did selection pressure for the various traits associated with domestication favor polyploid genomes over diploid ones among the scores of wild species harvested and subjected to the domestication process? The frequencies of

polyploidy in crop species are strikingly similar to those of their respective taxonomic categories (Table 2; Fig. 1). The frequency of polyploidy in the 244 crops was not statistically different from the estimates provided for angiosperms regardless of the basic chromosome number used. In dicots, the 45% polyploidy in crops is compared with 43% in the whole class for  $n = 13$ , and the 73% polyploid crops is contrasted with the about 75% for  $n = 11$ . Applying the Binomial One-Tailed statistical test (Zar, 1984) to the data revealed that the differences are not statistically significant ( $P = 0.85$  for  $n = 11$  and  $P = 0.27$  for  $n = 13$ ). The proportion of polyploid monocot crops was not statistically significant from the estimated percentage of polyploids in the monocot class based on  $n = 11$  ( $P > 0.12$ ), while the differences on the basis of  $n = 13$  were statistically significant ( $P = 0.0002$ ). However, the 58% frequency of polyploidy in monocots based on  $n = 13$  is considered by Goldblatt (1980) and Lewis (1980b) to be very conservative and an underestimation of the frequency of polyploidy in the group. Therefore, the data in this study show that crop species in general were a random selection from their respective classes as far as the polyploid level is concerned and demonstrate that domestication does not appear to have favored diploid over polyploid genomes or vice versa.

The randomness of the sample was also evident in the three groups of crops designated within monocots and dicots. The Brandt-Snedecor  $\chi^2$  for homogeneity showed the three groups within both monocots and dicots to be highly homogeneous. The results imply that vegetative crops did not harbor polyploidy and seed crops did not foster diploidy as one would expect from the proposed position of diploid-polyploid species on the  $r$ - $K$  continuum (Levin, 1983). Fitness in crop plants is not a population survival aspect as we know it in wild populations. Crop plants are primarily monospecific populations now and very likely had similar composition at the early stages of plant domestication. Thus, interspecific competition was either minimal or lacking in cases where the wild species were cultivated and subjected to the selection pressure of domestication. In addition, the amount and type of seed that will establish the next population in plants under domestication are selected and maintained by the domesticator. Therefore, wild populations undergoing domestication were subjected to strong artificial selection that is not parallel in principle to the natural selection normally operating in wild populations devoid of such human disturbance. Consequently, in selecting for vegetative vigor or high seed set, it seems that diploids and polyploids were stretched to desirable limits of yield under the artificial selection conditions despite the genome number.

The percentages of polyploidy in annual vs. perennial crops were statistically similar. This finding is in contrast with the proposed higher proportion of polyploidy in perennial plants since the perennial habit confers a selective advantage to polyploidy. Perenniality, with its inherent lack of a prerequisite for immediate fitness, provides a better chance for autopolyploids and allopolyploids to recover from the sterility problems associated with chromosome pairing and interaction between new cytoplasmic genomes. Stebbins (1971) indicated that it is not surprising that polyploidy is much less common among annuals than

perennials. The statistically insignificant difference in distribution of polyploidy between annual and perennial crops implies that polyploids and diploids are equally domesticable regardless of their habit.

Since polyploidy varies among families and genera, its proportion in crop species was examined and compared at that taxonomic level whenever reliable estimates were found. The families chosen in this case are the ones that contain six species or more for appropriate statistical sampling. Polyploidy in the grass family is well studied and has been estimated to be about 80% (deWett, 1987; Hunziker and Stebbins, 1987). Goldblatt (1980) provided estimates for polyploidy in Liliaceae (23%), Araceae (82%), and Araceae (Palmae 93%). The data on the frequency of polyploidy in dicot families are scanty. Polyploid frequency has been estimated for the Fabaceae (18%; Goldblatt 1981) and Brassicaceae (37%; Al-Shehbaz, 1984). When the percentages of polyploidy in these families are compared with those of their respective crop species, a pronounced deviation toward diploidy or polyploidy is not apparent (Fig. 2). Since the sample size of the crops in some families was relatively small, the data were analyzed with the Binomial One-Tailed statistical test (Zar, 1984), which is especially useful when expected frequencies are small. The difference between the frequencies of polyploid crops and those of their respective families was not statistically significant ( $P > 0.05$ ) except for the family Dioscoreaceae. These results imply that there was no selection for or against polyploidy in species that underwent domestication. The predominantly polyploid families such as the Poaceae did not show disproportionately high frequency of diploidy among its crops. Neither did the Fabaceae, a family with a low frequency of polyploidy, show a higher proportion of polyploidy among the pulse crops.

To obtain additional insight into the role of polyploidy in plant domestication, it is useful to examine the proportion of polyploidy in genera and tribes that contain diploid and polyploid wild species. The tribe Triticeae (Poaceae, monocots) is composed of a large number of polyploid and diploid species that are based on the gametic number  $X = 7$ . The tribe also contains eight cereal crops. Both diploid crops (einkorn wheat, barley, and rye) and polyploid crops (emmer and bread wheats) were among the early important plant domesticates. The genus *Triticum*, *sensu stricto* or *sensu lato* including *Aegilops*, contains diploid, tetraploid, and hexaploid species including wheat. The domesticated wheats belong to diploid, tetraploid, and hexaploid species. The domesticated hexaploid species are the result of crosses between diploid wild taxa and tetraploid domesticated ones, and thus are not as relevant to the discussion. However, both diploid and tetraploid species were among the first crops to lend themselves to domestication. The superiority of the tetraploid species is not due to the degree of success of domestication but to traits such as the larger grains and postdomestication preference in the consumption of the crop. Thus, in the Triticeae, polyploidy does not seem to be a factor in promoting or hindering the domestication process.

The parallel domestication of the diploid and polyploid species can be further illustrated in a number of other plant genera. The situation in *Prunus* and *Allium* will be cited as examples. *Prunus* (Rosaceae) contains about 150

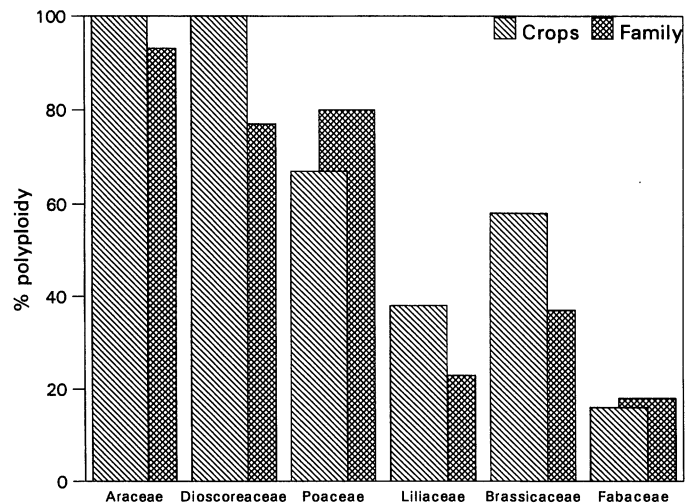


Fig. 2. The proportion of polyploidy in six angiosperm families and their crop species is illustrated. These families were selected because they are among those having the largest number of crop species and that information on the proportion of their polyploidy was available in the literature.

diploid and polyploid species based on  $X = 8$ . Among these species are about 45 fruit crops such as plums, cherries, peaches, and almonds. Domestication in the genus took place at both diploid and polyploid levels (Watkins, 1976). Similarly, among the about 500 species of *Allium* (Liliaceae) are over 20 vegetable crops such as onions, chives, garlic, and leeks. The genomic constitution of the crops and their wild ancestors range from diploid to up to hexaploid (reviewed by McCollum, 1976). Of special interest in the genus are the diploid and polyploid cytotypes of the wild species *A. schoenoprasum* L. and *A. tuberosum* Rottler that were all successfully domesticated into cultivars of corresponding diploid and polyploid forms.

In conclusion, the proportions of polyploid crop species in relation to the polyploid estimates for their respective higher categories did not show significant deviation from randomness. This implies that a polyploid genomic constitution and its proposed selective advantages neither facilitated nor hindered the ability of the species to be domesticated. Diploid and polyploid genomes seem to have similar responses to genetic alteration essential for domestication. The proportions of polyploidy in vegetative, seed, and tree crops were statistically homogeneous, indicating that polyploidy was not a significant factor in domestication when the position of the crop species along the  $r$ - $K$  continuum was taken into consideration. In addition, polyploidy was not significantly more prevalent in perennial crops than in annuals.

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