A Comparison of the Flora as a Whole and the Weed Flora of Indiana as to Polyploidy and Growth Habits

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Cytological surveys of floras as a whole have become increasingly popular in recent years, but few accounts have appeared which have placed particular emphasis upon weedy floras. With T. W. Whitaker (9), I recently surveyed the chromosome numbers and growth habits of the most wide-spread weeds of California. The conclusion reached was that, with certain exceptions, polyploidy is not a significant factor in the formation of weeds. In the study of the weeds of California, no comparison was made between the amount of polyploidy in the flora as a whole and that of the weed flora, and in the present paper such a comparison is made.

Procedure

Deam's "Flora" (4) has been used throughout this study for the species found in the Indiana flora. Chromosome numbers have been taken from the lists of Gaiser, Tischler, Maude, Rutland, and Darlington and Janaki-Ammal, and from the more recent works of Bowden (2) and Löve and Löve (10). Special monographs were consulted for a number of families and genera, chief among them being those by Senn (17), Wahl (21), Gregory (6), Perry (14), Myers (13), and Brown (3). Information regarding the growth habits have been secured for the most part from MacDonald's (11) special study. Species designated as weeds have been determined from the notes given in Deam's "Flora," from Muenscher's (12) "Weeds," and from the author's own field experience.¹ Those weeds which have a purely local distribution or are known only from a very few localities have not been included, and hybrids have been also omitted from the computations. The methods of scoring follow the procedure used in the study of the weeds of California (Heiser and Whitaker, 9). This report is obviously a compilation.

Results

The principal results of the present survey are given in Tables I, II, and III. Of a total of 2073 species given in Deam's "Flora," counts have been located for 867 (42%), excluding those introduced species

¹The definition that has been followed here is that weeds are plants which are adapted to areas which have been disturbed in some way by man (or his domestic animals) but are not intentionally cultivated by him. (Heiser 8).

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	Total No.	% of
	of Species	total flora
woody perennials	300	14.76
herbaceous perennials	1323	65.11
annuals (& biennials)	409	20.13
diploids	464	51.61
polyploids	435	48.39
diploid annuals	102	11.35
diploid perennials	362	40.27
polyploid annuals	76	8.45
polyploid perennials	359	39.93
woody diploids	110	64.71
woody polyploids	60	35.29
herbaceous perennial diploids	253	45.83
herbaceous perennial polyploids	299	54.17
species with counts available	867*	41.82
species with growth habits available	2032	98.02

TABLE I. Polyploidy and Growth Habit of the Indiana Flora

* Some species are reported with two counts.

of limited distribution and escapes from cultivation. Growth habits have been tabulated for 2032 (98%) species. Of these, 409 (20%) are annuals; 1623 (80%) are perennials. In the latter group there are 1323 herbaceous species as opposed to 300 woody species (Table I).

For the flora as a whole, including both weedy and non-weedy plants, 52% of the species are diploid (Table I). It has been estimated that approximately half of the species of angiosperms are polyploids and the flora of Indiana does not fall far short of this mark. The amount of polyploidy in the Indiana flora is slightly less than that reported for the Scandanavian countries (see Löve and Löve, 10).

If the diploids and polyploids are broken down into annual and perennial categories, one finds a total of approximately 11% diploid annuals, 40% diploid perennials, 8% polyploid annuals, and 40% polyploid perennials. These figures would tend to suggest that among the angiosperms of Indiana, polyploidy is not significantly higher among the perennials than among the annuals. As one would expect, the perennials significantly outnumber the annuals at both the diploid and polyploid level.

Slight differences between diploidy and polyploidy are evident, if the perennial species for which chromosome counts are available are subdivided into herbaceous and woody categories. Thirty-five per cent of the woody species are polyploid as compared to 54% for the herbaceous perennial species. Approximately 43% of the annuals are polyploid. These figures lend support to Stebbins' (19) contention that the tendency toward polyploidy in the angiosperms is more pronounced in the herbaceous perennials than in woody plants and annuals.

The total number of species considered as weeds in the present investigation is 287. Fifty-seven per cent of these weedy species are annuals in contrast to 23% annuals for the herbaceous flora as a whole (Table II). This result might be interpreted as indicating that there is a greater tendency for annuals than for perennials to behave as weeds. This tendency, except for specialized areas, may well be a general phenomenon and not applicable only to the Indiana flora. The number

	Total No. of Species	% of total flora
perennials	123	42.86
annuals (& biennials)	164	57.14
diploids	135	54.66
polyploids	112	45.34
diploid annuals		32.79
diploid perennials	54	21.86
polyploid annuals	56	22.67
polyploid perennials	56	22.67
species with counts available	232*	80.84
species with growth habits available	287	100.00

TABLE II.	Polyploidy	and	Growth	Habit	\mathbf{of}	Indiana	Weeds
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* Some species are reported with two counts.

of annual weeds in the California flora is even more pronounced. For the 175 weeds of California analyzed as to chromosome number, 56%were annuals (Heiser and Whitaker, 9). If, however, all of the species in the "Weeds of California" (Robbins, Bellue, and Ball, 15) are included, it is found that over 80% of the species are annuals. However, in the California flora, no comparison between the weedy annuals and the annuals in the flora as a whole has yet been made; the annuals of California may be considerably more numerous than for the Indiana flora because of the great number of desert annuals.

The total number of introduced species among the 287 weeds of Indiana treated in the present work is 53%, the great majority of the aliens coming from Europe or Eurasia. It is of interest to note that Blatchley, in 1912, records 51% aliens among the 150 weeds "most harmful to the farmers" of Indiana. Muenscher (12) analyzed 500 weeds of the northern United States and found that 61% of the species were introduced. The reason for the large number of introduced weeds in the eastern United States has been discussed by Gray (5).

Chromosome numbers have been located for 232 of the weedy species, of which 55% are found to be diploid (Table II). The percentage of polyploidy among the weeds (45%) is actually slightly lower than that

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for the flora as a whole (48%), but this difference is probably not significant. The data presented here would certainly seem to verify the conclusion that polyploidy, *per se*, has not been an important factor in the formation of weeds. This last statement, however, should not be taken to mean that polyploidy may not have been of importance in the development of some weedy species.

When the weeds are subdivided into the various categories of growth habit and ploidy, the greatest number are found in the diploid annual group (33%) and the remaining species are about evenly distributed among the other categories (22% diploid perennials, 23% polyploid annuals, and 23% polyploid perennials). These figures are similar to those for the California weeds.

Although it does not seem desirable to make detailed comparisons of the weedy and the non-weedy species, for many of the native species may fall into both classes, the following figures are of interest: 79%of all the diploid annuals and 74% of all the polyploid annuals are weeds, whereas only 21% of the diploid perennials and 19% of the polyploid perennials are weeds; very few woody species behave as weeds and hence the woody members have been excluded from the perennial groups for the above percentages. The above figures indicate that the diploid annuals are the most successful weeds in Indiana and are followed closely by the polyploid annuals.

A comparison of the total number of introduced and native weeds in the various categories of growth habits and ploidy is shown in Table III. There are approximately equal numbers of native species in the four different categories, but among the introduced species by far the greatest number is found in the diploid annual category. The great preponderance of introduced diploid annuals among the weeds of Indiana seems to indicate that as a class they are the most successful weeds.

Discussion

It is worth while to list some of the reasons why some of the conclusions reached above, particularly those regarding polyploidy, are of a very tentative nature. (1) Not all of the species for which chromosome counts are reported can be scored definitely as diploids or polyploids since the basic number in many genera has not been established with certainty. (2) Two counts are recorded for some "species" and scoring these in both diploid and polyploid categories may introduce some error. However, probably no greater accuracy would be gained by giving such species one-half value in each category or by omitting them entirely. At least one species-Claytonia virginica-(Heiser, unpubl.) is known to have both diploid and tetraploid forms in Indiana. This may well be true of other species. (3) Many of the chromosome counts used in preparing this report may be inaccurate for Indiana materials. Only a small fraction of the counts have been made or verified from the Indiana flora, and, moreover, a large portion have not even been made upon North American material. (4) Inaccurate taxonomic determinations of some of the early workers or various other nomenclatorial difficulties may have led to mistakes in the present tabulation. (5) As may be seen from Table I, less than half of the species represented in Indiana are reported with chromosome counts, and the conclusions regarding the polyploidy in the flora as a whole may have to be altered somewhat when our knowledge becomes more complete. However, over 80% of the species regarded as weeds (Table II) have known chromosome counts, so that the figures for them are somewhat more reliable. Since chromosome numbers of so few of the non-weedy species are known, comparisons have been made between the whole flora (including the weeds) and the weeds alone. This is also necessary because many of the native species may behave both as weeds and non-weeds. (6) Mc-Donald's (11) list of growth habits has been found to contain some mistakes, and additional ones may have been overlooked. (7) Exactly what species to admit among the weeds has offered difficulties. Opinions as to what constitutes a weed vary greatly and the likelihood of two people compiling exactly the same list of weeds for the Indiana flora is remote.

With the foregoing limitations in mind, however, I would still be inclined to conclude that apparently polyploidy has had no greater effect in producing successful weeds than it has had in producing successful wild species, and, secondly, that as a class the diploid annuals seem to be particularly successful as weeds. These studies fail to corroborate Gustafsson's (7) conclusion that presumably diploid predecessors of weeds were not able to create successful "(agro-)ecotypes."

The annual species, both diploid and polyploid, seem to have provided us with a greater number of weeds than the perennials. Bews (1) has stated that annuals are characteristic of the most adverse conditions and points out that they are particularly suited to habitats brought about by man's disturbance, but he advances no reasons to account for these characteristics. Salisbury (16, p. 25) has suggested that "in so far as the small seed and annual habit go together, they are both features which probably alike have survival value in habitats which are subject to recurrent adverse conditions." The total seed output of the annuals might appear to be an important factor in the success of annuals under such conditions, but Salisbury (16, p. 231) in a comparison of annual and perennial species of the same genus, finds that the latter have the higher seed output. A more rapid reproduction rate (Heiser and Whitaker, 9) and the ability to produce seed under adverse conditions (see Muenscher, 12, p. 4) are probably more effective than is total seed output. Wulff (22) drawing particularly from the work of Thellung, has suggested that there is an involuntary selection for the annual habit among weeds through the annual plowing of fields.

The small seed, a rapid reproduction rate, the ability to seed under adverse conditions, and involuntary selection by man have probably been responsible for the great proportion of annuals among weeds; and polyploidy apparently has not played an important role. As So5 (18) has pointed out, gene content is more important than chromosome number in the ecological adaptation of plants. The future approach BOTANY

to the study of the origin and evolution of weeds should probably be through combined ecological and genetical studies rather than a mere analysis of chromosome numbers.

Summary

A compilation of chromosome numbers and growth habits of Indiana plants has been undertaken, and the principal results in regard to polyploidy and growth habits of the flora as a whole are presented in Table 1. An analysis of polyploidy and growth habits in weedy species has also been attempted and the results are shown in Tables 2 and 3. It is pointed out that many of the conclusions drawn must be of a tentative nature, but it is apparent that polyploidy has been of no greater importance in the formation of weeds than it has in the formation of wild species and that the annual species, particularly diploid annuals, are the most successful weeds.

	NA	TIVE	INTRODUCED		
	Total No. of species	% of total flora	Total No. of species	% of total flora	
diploid annuals	22	24.18	59	37.82	
diploid perennials	26	28.57	28	17.95	
polyploid annuals	21	23.08	35	22.44	
polyploid perennials	22	24.18	34	21.79	
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TABLE III. A Comparison of the Polyploidy and Growth Habits of the Native and Introduced Weeds of Indiana

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