

Polyploidy among plant species extraneous in Indiana

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Butler University
Botanical Studies
(1929-1964)

Edited by

Ray C. Friesner

The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana's vegetation in past decades. Authors were Butler faculty, current and former master's degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler's first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daudenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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POLYPLOIDY AMONG PLANT SPECIES EXTRANEOUS IN INDIANA¹

By FRANCES I. SCOTT

This study was undertaken for the purpose of determining whether there is any relationship between polyploidy and geographic distribution with special reference to species extraneous in a given area. It has been maintained that a more rigorous habitat tends to produce polyploids, that plants which are on the limits of their geographic distribution in a given area should exhibit a high degree of polyploidy since they are on one of the extremes of their habitat range, (4). Since polyploids (particularly tetraploids) usually exhibit a greater vigor and adaptability than do diploids, it has seemed a natural deduction that diploid species might tend to give rise to polyploid races where the habitat had become more rigorous than the optimum for that species. To determine whether or not such a relationship exists among extraneous Indiana species, all such extraneous species which have been studied cytologically were tabulated.

MATERIAL

The material for this study was taken from various sources. The extraneous species were determined from distributions given in Deam's *Flora of Indiana* (8) and from the State Flora Index maintained by the Botany Department of Butler University. The chromosome numbers were chiefly obtained from the following published sources: Tischler's *Tabulae Biologicae*, (22, 23), Gaiser's *List of Chromosome Numbers in Angiosperms* (12), Darlington's *Chromosome Atlas of Cultivated Plants* (6), and the *Merton Catalogue* (17, 19). Chromosome numbers of additional species were found in the current botanical literature. Material covering the fields of cytogeography, cytology and genetics was taken from the literature which is cited in the bibliography.

¹ A portion of a thesis submitted in partial fulfillment of the requirements for the graduation honor Magna cum Laude, Department of Botany, Butler University.

Only those extraneous species of the Indiana flora for which chromosome numbers could be found in the literature are included in this study. In some cases, the particular species has not been studied cytologically, but if the other related species of that genus showed a consistent polyploid condition, the species was tabulated as polyploid. Such species are listed in Table I as probably polyploid by the symbol "p.p." The data utilized in this study are summarized in the following tables.

TABLE I
Indiana extraneous species and polyploidy

Species	General distribution outside Indiana							Ploidy	
	W	NW	N	NE	E	SE	S		
<i>Agave virginica</i>				x	x	x	x	x	2n
<i>Hymenocallis occidentalis</i>							x	x	p.p.
<i>Asclepias meadii</i>	x	x	x						2n
<i>variegata</i>				x	x	x	x		2n
<i>Myosotis laxa</i>			x	x			x		4n
<i>micrantha</i>			x	x					4n
<i>virginica</i> v. <i>macrosperma</i>					x	x	x		4n
<i>Campanula uliginosa</i>			x	x					2-4-6n
<i>Lonicera canadensis</i>		x	x	x	x				2-4n
<i>japonica</i>				x	x	x	x		2n
<i>Viburnum affine</i>		x						x	2n
<i>molle</i>	x	x					x	x	2n
<i>pubescens</i> v. <i>deamii</i>							x	x	2n
<i>Stellaria pubera</i>				x	x	x	x		p.p.
<i>Ambrosia bidentata</i>	x						x	x	2n
<i>Antennaria fallax</i>			x			x	x	x	12n
<i>solitaria</i>			x	x	x	x	x		2n
<i>Aster furcatus</i>							x	x	2n
<i>macrophyllus</i>			x	x	x	x			2n
<i>missouriensis</i> v. <i>thyrsoidea</i>	x						x	x	2n
<i>ptarmicoides</i>	x		x	x				x	2n
<i>sericeus</i>			x	x		x	x	x	2n
<i>vimineus</i>			x	x	x	x	x	x	2n
<i>Crepis capillaris</i>				x	x				2n
<i>Hieracium longipilum</i>			x	x				x	3-4-5n
<i>Senecio glabellus</i>						x	x	x	4n
<i>vulgaris</i>		x	x	x	x				4n
<i>Silphium laciniatum</i> v. <i>robinsonii</i>						x	x		2n
<i>Solidago erecta</i>			x	x	x	x	x	x	2n
<i>graminifolia</i> v. <i>media</i>		x	x					x	2n
<i>graminifolia</i> v. <i>remota</i>		x							2n

TABLE I—(Continued)

Indiana extraneous species and polyploidy

Species	General distribution outside Indiana								Ploidy
	W	NW	Compass N	Directions NE	E	SE	S	SW	
<i>rugosa</i> v. <i>celtidifolia</i>						x	x	x	2n
<i>sphacelata</i>						x	x	x	2n
<i>squarrosa</i>			x	x	x	x			2n
<i>Arabis patens</i>			x	x	x	x	x	x	4n
<i>Dentaria heterophylla</i>			x	x	x	x	x		2n
<i>multifida</i>				x	x	x	x		2n
<i>Leavenworthia uniflora</i>						x	x	x	6n
<i>Carex canescens</i> v. <i>disjuncta</i>			x	x					6n
<i>canescens</i> v. <i>sublobiacea</i>		x	x	x					8n
<i>gravida</i> v. <i>lunelliana</i>	x	x							p-p.
<i>howei</i>			x			x	x	x	6n
<i>incomperta</i>			x	x	x	x	x	x	5n
<i>laricina</i>			x	x	x				p-p.
<i>mesochorea</i>			x	x	x	x	x		p-p.
<i>richii</i>			x	x	x	x			8n
<i>seorsa</i>			x	x	x	x	x		p-p.
<i>Carex tonsa</i>	x	x	x	x	x	x	x		p-p.
<i>Cyperus dentatus</i>			x	x	x	x			4n
<i>acuminatus</i>	x	x				x	x	x	4n
<i>Eleocharis robbinsii</i>			x	x	x				p-p.
<i>Eriophorum spissum</i>			x	x	x				2n
<i>Dipsacus sylvestris</i>			x	x	x	x			2n
<i>Vaccinium aboreum</i>				x	x	x	x	x	2-4n
<i>stamineum</i>			x	x	x	x	x		2n
<i>Euphorbia heterophylla</i>	x	x				x	x	x	8n
<i>Agropyron pauciflorum</i>	x	x	x	x	x				4n
<i>repens</i>	x	x	x	x	x			x	4-6n
<i>subsecundum</i>	x	x	x	x	x				4n
<i>Agrostis elliottiana</i>				x	x	x	x	x	p-p.
<i>palustris</i>	x	x	x	x	x				p-p.
<i>Alopercurus aequalis</i>	x	x	x	x	x				2n
<i>pratensis</i>	x	x	x	x	x	x			4n
<i>Ammophila breviligulata</i>			x	x	x				4n
<i>Andropogon elliottii</i>					x	x	x	x	4n
<i>virginicus</i>				x	x	x	x	x	4n
<i>Anthoxanthum odoratus</i>			x	x	x	x	x	x	2-4n
<i>Arrhenatherum elatius</i>	x	x	x	x	x	x	x		4n
<i>Bromus brizaeformis</i>	x	x	x	x	x				2n
<i>ciliatus</i>	x	x	x	x	x	x		x	2-4n
<i>kalmii</i>		x	x	x					2n
<i>mollis</i>	x	x	x	x	x				4n

TABLE I—(Continued)

Indiana extraneous species and polyploidy

Species	General distribution outside Indiana								Ploidy
	W	NW	N	NE	E	SE	S	SW	
<i>Calamagrostis canadensis</i>	x	x	x	x	x	x			4-6-8n
<i>inexpansa</i>	x	x	x	x					4-6n
<i>longifolia</i>	x	x	x						4-6n
<i>Cynodon dactylon</i>			x	x	x	x	x	x	4n
<i>Elymus riparius</i>			x	x	x				4n
<i>virginicus v. australis</i>	x			x	x	x	x	x	4n
<i>virginicus v. glabriflorus</i>	x			x	x	x	x	x	4n
<i>virginicus v. submuticus</i>			x	x	x	x	x	x	4n
<i>Festuca ovina</i>	x	x	x	x	x				2-8-10n
<i>Glyceria acutiflora</i>				x	x	x			4n
<i>borealis</i>	x	x	x	x					4n
<i>canadensis</i>		x	x	x	x				4n
<i>grandis</i>	x	x	x	x	x	x			4n
<i>pallida</i>	x	x	x	x	x				4n
<i>Hierochloa odorata</i>	x	x	x	x					4n
<i>Holcus lanatus</i>	x	x		x	x	x	x	x	2n
<i>Hordeum jubatum</i>	x	x	x	x	x	x	x		2-4n
<i>nodosum</i>	x	x		x			x		2-4-6n
<i>Hystrix patula v. bigeloviana</i>	x	x	x	x				x	4n
<i>Koeleria cristata</i>	x	x	x	x				x	4n
<i>Leptochloa filiformis</i>				x	x	x	x	x	2n
<i>panicoides</i>							x	x	2n
<i>Leptoloma cognatum</i>	x	x		x	x	x	x	x	4n
<i>Lolium perenne</i>	x	x	x	x	x				2-3-4n
<i>Melica mutica</i>	x				x	x	x	x	2n
<i>nitens</i>	x	x		x	x			x	2n
<i>Milium effusum</i>		x	x	x					4n
<i>Muhlenbergia mexicana</i>	x	x	x	x	x	x		x	4n
<i>Panicum anceps</i>				x	x	x	x	x	4n
<i>ashei</i>			x	x	x	x	x	x	2n
<i>bicknellii</i>			x	x	x	x		x	2n
<i>boscii</i>	x	x		x	x	x	x	x	2n
<i>boscii v. molle</i>	x	x		x	x	x	x	x	4n
<i>commutatum</i>	x		x	x	x	x	x	x	2n
<i>depauperatum v. psilophyllum</i>		x	x	x	x				2n
<i>mattamuskeetense</i>				x	x	x			2n
<i>microcarpon</i>	x		x	x	x	x	x	x	2n
<i>oligosanthes</i>	x	x		x	x	x	x	x	2n
<i>pseudopubescens</i>	x	x	x	x	x	x	x		2n
<i>sphaerocarpon</i>	x		x	x	x	x	x	x	2n
<i>subvillosum</i>	x	x	x	x					2n

TABLE I—(Continued)

Indiana extraneous species and polyploidy

Species	General distribution outside Indiana							Ploidy
	W	NW	N	NE	E	SE	S	
<i>tsugetorum</i>		x	x	x	x	x		2n
<i>verrucosum</i>				x	x	x	x	2n
<i>xalapense</i>	x					x	x	2n
<i>yadkinense</i>					x	x	x	2n
<i>Paspalum circulare</i>					x	x	x	2-4n
<i>fluitans</i>						x	x	2-4n
<i>stramineum</i>	x	x	x					2-4n
<i>Phalaris arundinacea</i>	x	x	x	x	x	x		2n
<i>Phragmites communis</i>	x	x	x	x		x		4-8n
<i>Poa alsodes</i>		x	x	x	x			4n up
<i>autumnalis</i>	x		x	x	x	x	x	4n up
<i>chapmaniana</i>	x	x			x	x	x	4n up
<i>cuspidata</i>				x		x		4n
<i>languida</i>		x	x	x	x			4n up
<i>Poa nemoralis</i>		x	x	x	x			4-6-8n
<i>paludigena</i>		x	x	x				4n up
<i>palustris</i>	x	x	x	x	x	x		4-6n
<i>wolfii</i>	x	x	x	x				4n
<i>Setaria verticillata</i>	x	x	x	x	x		x	2n
<i>Sorghum halapense</i>	x	x		x	x	x	x	4-8n
<i>vulgaris</i> v. <i>drummondii</i>	x	x		x	x	x	x	4n
<i>Spartina pectinata</i>	x	x	x	x	x			4n
<i>Stipa comata</i>	x	x						4n
<i>Uniola latifolia</i>	x			x	x	x	x	2n
<i>Zizania aquatica</i>	x	x	x	x	x	x	x	2n
<i>Hydrangea aborescens</i> v. <i>deamii</i>				x	x		x	4n
<i>sedum acre</i>			x	x	x	x		4n
<i>thelephioides</i>				x	x	x	x	p.p.
<i>Hypericum virginicum</i>			x	x		x		4n
<i>Scutellaria australis</i>	x	x				x	x	4n
<i>Teucrium canadense</i>				x	x	x		2n
<i>Cassia hebecarpa</i>			x	x	x	x	x	2n
<i>Comptonia peregrina</i>		x	x	x	x	x		4n
<i>Hibiscus lasiocarpus</i>						x	x	p.p.
<i>Forestiera acuminata</i>			x					2n
<i>Fraxinus tomentosa</i>	x	x					x	2n
<i>Styrax americana</i>						x	x	2n
<i>Cypripedium acaule</i>			x	x	x	x		2n
<i>Plantago pusilla</i>		x	x	x				2n
<i>Phlox amplifolia</i>						x	x	2n
<i>Phlox carolina</i> v. <i>triflora</i>						x	x	2n

TABLE I—(Continued)

Indiana extraneous species and polyploidy

Species	General distribution outside Indiana								Ploidy
	W	NW	N	NE	E	SE	S	SW	
<i>ovata</i>				x	x	x	x		2n
<i>Clematis pitcheri</i>	x	x						x	2n
<i>Ranunculus bulbosus</i>				x	x	x	x		2n
<i>Thalictrum perelegans</i>						x	x		p.p.
<i>Fragaria vesca</i>			x	x	x		x		2n
<i>Geum laciniatum</i>			x	x	x		x		6n
<i>virginianum</i>				x	x	x	x		6n
<i>Prunus lanata</i>						x	x	x	p.p.
<i>Galium labradoricum</i>			x	x	x				p.p.
<i>Penstemon canescens</i>				x	x	x	x		2n
<i>deamii</i>	x	x							2n
<i>tubaeflorus</i>	x	x						x	2n
<i>Veronica glandifera</i>				x	x				4n
<i>Valerianella chenopodifolia</i>			x	x	x	x			p.p.
<i>Viola missouriensis</i>	x	x					x	x	6n
<i>triloba</i>				x	x	x	x		6n
<i>Vitis labrusca</i>				x	x	x	x		2n

TABLE II

Polyploidy among di- and monocotyledons in Indiana extraneous species

Family—Dicotyledonae	Genera		Species	
	Polyploids	Diploids	Polyploids	Diploids
Asclepidaceae		1		1
Boraginaceae	1		3	2
Campanulaceae	1		1	
Caprifoliaceae	1	2	1	4
Caryophyllaceae	1		1	
Compositae	3	5	4	16
Cruciferae	2	1	2	2
Dipsacaceae		1		1
Ericaceae	1	1	1	1
Euphorbiaceae	1		1	
Grossulariaceae	2		3	
Hypericaceae	1		1	
Labiatae	1	1	1	1
Leguminosae		1		1
Malvaceae	1		1	
Myricaceae	1		1	

TABLE II—(Continued)

Polyploidy among di- and monocotyledons in Indiana extraneous species

Family—Dicotyledonae	Genera		Species	
	Polyploids	Diploids	Polyploids	Diploids
Oleaceae		3		3
Plantaginaceae		1		1
Polemoniaceae		1		3
Ranunculaceae	1	2	1	2
Rosaceae	2	1	3	1
Rubiaceae	1		1	
Scrophulariaceae	1	1	1	3
Valerianaceae	1		1	
Violaceae	1		2	
Vitaceae		1		1

Family—Monocotyledonae	Genera		Species	
	Polyploids	Diploids	Polyploids	Diploids
Amaryllidaceae	1	1	1	1
Cyperaceae	3	1	13	1
Gramineae	41	23	71	44
Orchidaceae		1		1

Totals and percentages:				
Dicotyledonae	24	23	30	42
	51%	49%	42%	58%
Monocotyledonae	45	26	85	47
	63%	37%	64%	36%

TABLE III

Summarized relations of polyploids and diploids

	Polyploids		Diploids	
	Number	Percentage	Number	Percentage
Dicot Species	30	42%	42	58%
Dicot Genera	24	51	23	49
Monocot Species	85	64	47	36
Monocot Genera	45	63	26	37
Total Species	115	56.5	89	43.5
Total Genera	69	58.5	49	41.5
Species on northern limits of range	40	50	40	50
Species on southern limits of range	59	69	26	31

DISCUSSION

According to Friesner (10) 45% of the species of fern and seed plants occurring in Indiana are on the borders of their present-day range and are therefore on critical ground. Their survival depends upon their ability to adapt themselves to a habitat which is more rigorous than the optimum since it represents the limit of distribution. (For this study, all plants which are on the limit of their range in Indiana are considered as extraneous species).

It has long been known that most plants show greater vigor if present in polyploid form. In most cases the tetraploid is the optimum ploidy and such plants are larger, stronger, and more viable than the diploids. In other cases octoploids are the optimum. At any rate, experimental evidence has shown that in cases where diploid species develop tetraploid races, the tetraploids are more often stronger and able to withstand more extreme habitat conditions (4). Often when diploid races from a mild climate are transplanted into a very cold or alpine environment they develop into polyploid types. Thus it has been found that an increase in rigor of habitat tends to increase ploidy.

Gustafsson (13) gives the credit to polyploids for survival following glaciation and climatic changes. He holds that the isolated communities which result from climatic change cross-breed and result in stuffing the species with lethals of different strength. These isolated communities, which have been cut down from original populations by the climate change, successively homozygotize, giving lethal recessives a chance to function. The strong heterozygotes disappear and the species is faced with degeneration. However, if a polyploid arises, the lethals immediately lose most of their fatal effect; inbreeding is thus not so dangerous, and the cross-breeding populations tend to become self-fertilizing to a high degree. The resulting polyploid populations now possess a double number of favorable genes (double if tetraploid, triple if hexaploid, etc.), but do not have the destructive effects of the lethals. These plants cover the area and initiate a new and vigorous community.

Gustafsson (13) holds that the polyploids are produced in such cases of change in climate in the following way: If a species continues to grow at a temperature below its optimum, its meiosis is subjected to repeated cold shocks which prevent reduction-division and result in the formation of unreduced gametes. The union of two such

gametes, of course, results in offspring containing exactly twice the chromosome complement of the parents . . . a tetraploid in the case of diploid parents. These will be continuously fed into the species and for this reason many diploids will automatically give rise to tetraploids, then hexaploids, then octoploids, if further unreduced gametes of polyploids are involved. When polyploids arise in this manner, it is not because of any inherent lack of viability in the diploids; it is simply a response to the colds. Such polyploids are invariably hardier than the original diploids. In cases where the species is adapted by special physiological properties to withstand the increased cold, the species remains diploid.

Several explanations for the increased vigor of polyploids have been advanced. The most logical, however, is propounded by Melchers (18) who says, "Better adaptability of polyploids as compared with diploids lies in the fact that genes for selection-worthy characters may be accumulated in a greater quantity than in diploids." This seems particularly true in cases of multiple factors in which the greater the number of genes present, the greater the effect, the genes being cumulative in effect. An example of this type of character is cold hardiness.

Among the genera represented, 58.5% are polyploid, while only 41.5% are diploid. Of the species studied, 56.5% are polyploid, while 43.5% are diploid. Of course, since there are about 800 extraneous species in Indiana (9) and only 172 were utilized for this study, it cannot be stated with complete certainty that the above percentages hold for the entire collection of extraneous species. However, since thirty families and 118 genera are included in the number studied, it seems that a fairly representative idea of the ploidy of these extraneous species in general can be obtained from the 172 used. Thus it would appear that over half of the species extraneous to Indiana are found in polyploid, usually the tetraploid, form.

The grasses, because of their commercial value, have been studied cytologically to a greater extent than have the other families. According to Cook (5), 62% of the Indiana grasses are extraneous; thus about 16% of the total extraneous species here studied are grasses.

Love and Love (16) found that the percentage of polyploid monocots increased with latitude and extremes of climate. Dicotyledonous plants, on the other hand, decrease as the climate becomes more severe. The predominance of polyploids among monocots seems to be the

rule. From table II it may be seen that of the dicot species studied, the diploids exceed the polyploids, (58% diploids to 42% polyploids). Among the monocots, however, only 36% are diploids and 64% polyploids. Heiser (14), in a study of California weeds, found that of the monocots, 65% were polyploids and 35% were diploids, while among the dicots no great difference in percentages of polyploids and diploids was evident. His percentages of ploidy for monocots among California weeds are almost identical with the results of the present tabulation of Indiana extraneous species of monocots (64% to 36%).

In table III it will be seen that only 50% of the extraneous species reaching northern limits in Indiana are polyploid, while 69% of those reaching southern limits are polyploid. Since species reaching northern limits in Indiana have a general southern distribution and those reaching southern limits have a northern distribution, it appears that these results agree with those of Love and Love (16).

An interesting fact borne out in this study is that the genera which show polyploidy in their species are among the most hardy and persistent, e.g., such genera as *Hordeum*, *Sorghum*, *Thalictrum*, *Arabis*, *Prunus*, *Hypericum*, *Viola*, *Vaccinium*, *Veronica*, *Lonicera*, *Crepis*, and *Senecio*. Burton (3) has pointed out that the most promising pasture species of *Paspalum* are tetraploid.

There are many exceptions to the general rule that polyploidy tends to develop where the habitat is more rigorous. Some of these exceptions are found among the Indiana extraneous species. Among them are such genera as *Viburnum*, *Fragaria* and *Forestiera*. Members of the genus *Viburnum* are found in Asia, Europe, and North America over a great variety of habitats, yet the plants are always diploid, (6). *Fragaria vesca* shows the same characteristic, being found in Indiana and in Ecuador as a diploid (6). *Forestiera acuminata*, ranging from southwestern Indiana to Texas and South America, is diploid throughout its range, (6). The genus *Poa*, on the other hand, is world-wide in range with chromosome numbers varying from 14 to 106 and its ploidy from diploid to 15-ploid, (15). *Leavenworthia uniflora* is a hexaploid and is found the farthest north of any of the species of the genus, (1). As Gustafsson has pointed out, it is self-fertile and quickly invades and covers a new area.

Whatever the complete casual relations for the development of polyploids are, it is apparent that the percentage of polyploids increase as conditions for growth became more widely divergent from the op-

tinum for that particular species. The presence of a high percentage of polyploidy among the plants which are extraneous and which are therefore near the limit of their distribution range is in line with this observation. We must not make the error, however, of assuming that polyploids always develop where the climate is extreme or environment is unfavorable. Clausen, Keck and Hiesey (4) stress gene balance as determining adaptability to environment. They point out that not only change in chromosome number must be recognized in polyploids, but also change in numbers of genes. If large numbers of favorable genes are present, the polyploid form is more vigorous; however, if the increase in chromosome number results in the multiplication of large numbers of unfavorable genes, the polyploid form is less adaptable.

We cannot claim that polyploids develop as means of adaptation to more rigorous habitats among floras as a whole. The figures obtained from this study clearly indicate that only among the monocots is such a relationship shown. There is no such correlation between polyploidy and dicot species as a whole. Of course, there are many instances among individual dicots where the increased adaptability of the polyploid over the diploid is strikingly illustrated, (4).

SUMMARY AND CONCLUSIONS

1. Among 172 species extraneous to Indiana, 56.5% are polyploid, while 43.5% are diploid. Among 118 genera, 58.5% have polyploid species.

2. Of the dicot extraneous species studied, 58% are diploids and 42% polyploids. Among the monocots, 36% are diploids and 64% polyploids.

3. Of the extraneous species reaching their northern limit in Indiana, 50% are polyploid; of those reaching their southern limits, 69% are polyploid.

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