

Analysis of Some Natural and Artificial Interspecific Hybrids in *Helianthus*¹

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The importance of natural hybridization and subsequent introgression as a source of raw material for evolution has been stressed by Anderson (1949) and other workers in this particular field. Heiser (1947, 1949, 1951a, b) has demonstrated that *Helianthus annuus* L, the common sunflower, hybridizes naturally with other annual species. Long (1955a, b) and Jackson (1955) have shown that morphologically similar and dissimilar perennial species of *Helianthus* may hybridize readily.

This present study was initiated after observation of a large number of herbarium specimens indicated that *Helianthus mollis* Lam. was hybridizing naturally with several other perennial taxa. Descriptions of some of these hybrids have been reported in a previous paper (Jackson and Guard, in press). The purpose of this paper is to present an analysis of certain artificial and natural hybrids centered about *Helianthus mollis*.

Methods and Materials

Mass collections of the species and hybrid were made from various localities in Indiana. Collections of each species usually consisted of 25 individual plants from a single population. From 25 to 50 hybrid plants per population were collected, the number being dependent upon the size of the population and the variability present.

The sources of the natural hybrids and species used in this study are given in table 1.

Material for cytological study was collected from naturally occurring species and hybrids and from artificial hybrids and the parental species grown in the greenhouse. Immature heads were fixed in a mixture of two parts absolute ethyl alcohol and one part glacial acetic acid. After 48 hours, the microsporocytes were squashed directly in iron-acetocarmine. Usable slides were made permanent by the introduction of Venetian turpentine. Pollen grains were stained with 5 percent cotton blue in Aman's Lactophenol. Only those pollen grains with the cytoplasm stained in a uniform deep blue after 48 hours were considered viable.

Artificial crossing was accomplished by rubbing the heads of the plants together during anthesis of the disc flowers. Plants were bagged before and after crossing in order to insure against pollen contamination from other plants.

¹A portion of the field work for this study was made possible by a grant from the Indiana Academy of Science.

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TABLE 1
Sources of the Species and Hybrids Used in This Study¹

Species or Hybrid	Number	Collector	Locality
<i>H. mollis</i>	p72	C. B. Heiser	N. St. Louis, Mo.
<i>H. mollis</i>	p171	H. Iltis	Rootsfork, Ark.
<i>H. mollis</i>	716	R. C. Jackson	Tippecanoe Co., Ind.
<i>H. grosseserratus</i>	p54	M. Ownbey	Ft. Smelling, Minn.
<i>H. grosseserratus</i>	717	R. C. Jackson	Pulaski Co., Ind.
<i>H. giganteus</i>	p3250	C. B. Heiser	Camp Douglas, Wis.
<i>H. giganteus</i>	726	R. C. Jackson	Starke Co., Ind.
<i>H. divaricatus</i>	727	R. C. Jackson	Starke Co., Ind.
<i>H. atrorubens</i>	p44	Baldwin	Virginia
<i>H. mollis</i> X			0.8 mi. N. of Chalmers,
<i>H. grosseserratus</i>	700	R. C. Jackson	White Co., Ind.
<i>H. mollis</i> X			0.4 mi. N. Bass Station,
<i>H. giganteus</i>	706	R. C. Jackson	Starke Co., Ind.
<i>H. mollis</i> X			1 mi. S. of San Pierre,
<i>H. giganteus</i>	710	R. C. Jackson	Starke Co., Ind.
<i>H. mollis</i> X			Jasper-Pulaski State
<i>H. divaricatus</i>	714	R. C. Jackson	Game Preserve, Pulaski Co., Ind.
<i>H. mollis</i> X			1 mi. S. of San Pierre,
<i>H. divaricatus</i>	715	R. C. Jackson	Starke Co., Ind.

¹ All plant numbers preceded by p represent collections kindly furnished to the writers by Dr. C. B. Heiser, Jr., Indiana University.

Cytological Observations

The species studied here all have the reported haploid chromosome number of seventeen. These counts were verified during this study. Meiotic stages beginning with diakinesis and continuing through anaphase II were studied in the species and hybrids. Observations on pairing were made exclusively at diakinesis since this was the only stage where the chromosome pairs could be spread out sufficiently for detailed study.

As a measure of pairing in the earlier stages, the mean minimum chiasma frequency at diakinesis was used. Closed bivalents were considered as being held together by a single chiasma at either end while open bivalents were treated as being held together by a single chiasma. Most of the closed bivalents were circular in shape and the open bivalents were held together at one end. No univalents were observed in any of the hybrids or species reported here. The chiasma frequency and pollen fertility of the species and hybrids are given in table 2. Standard error was calculated for chiasma frequency.

TABLE 2

Mean Minimum Chiasma (Xa.) Frequency Per Cell and Pollen Fertility of the Species and Artificial Hybrids¹

Species and Hybrids	No. of cells studied	Xa. frequency			% Stain- able Pollen
		range	x	s	
<i>H. mollis</i> (p72)	50	20-29	28.7+1.8		97.0
<i>H. mollis</i> (p171)	50	29-26	22.5+1.5		98.9
<i>H. grosseserratus</i> (p54)	50	21-28	23.8+2.0		99.7
<i>H. divaricatus</i> (727)	50	20-26	22.6+1.2		100.0
<i>H. giganteus</i> (p3250)	50	20-30	22.0+1.8		99.4
<i>H. giganteus</i> (726)	50	20-28	23.5+1.7		99.7
<i>H. atrorubens</i> (p44)	50	29-32	31.0+1.0		92.4
<i>H. grosseserratus</i> (p54)					
X <i>H. mollis</i> (p72)	50	20-27	22.4+2.0		94.4
<i>H. mollis</i> X					
<i>H. divaricatus</i> (727)	50	19-24	20.8+1.5		49.4
<i>H. giganteus</i> (p3250)					
X <i>H. mollis</i> (p72)	50	20-26	22.9+1.6		59.7
<i>H. mollis</i> (p171) X					
<i>H. atrorubens</i> (p44)	72	17-22	18.9+1.5		34.0

¹Cytological data for the hybrid between *H. mollis* and *H. divaricatus* are from a natural hybrid. The artificial hybrid has not yet been produced.

Cytology of the parental species: Meiosis was normal in *H. mollis*, *H. divaricatus* L., and *H. grosseserratus* Martens. In material from two of five plants of *H. giganteus* L. from a natural population a single chromatin bridge was observed in 5 of 25 cells at first telophase, but in plant p3250 used in the artificial crosses meiosis was normal. In *H. atrorubens* L. (p44) atypical meiotic behavior was noted. At early diakinesis chains of four chromosomes were seen in some cells. Fragments were observed at late diakinesis, metaphase I and anaphase I. A single chromatin bridge sometimes accompanied by a fragment was noted in 5 of 54 cells studied at first anaphase.

Cytology of the hybrids: Several natural hybrids between *H. mollis* and *H. divaricatus* were studied since the artificial hybrid has not yet been produced. In one plant a chain of four chromosomes was observed at diakinesis. No other aberrations were noted. In the artificial hybrid between *H. mollis* (p72) and *H. grosseserratus* (p54) all phases of meiosis were normal. The aberrations observed in *H. giganteus* (p3250) X *H. mollis* (p72) have been reported previously (Jackson, 1956). Briefly, fragments were found at early diakinesis and at first metaphase. A few single chromatin bridges were noted, and in one cell a double bridge was observed. Generally bridges were infrequent; apparently they break in early anaphase because the remnants of what appeared to be broken bridges were seen in a number of cells. The hybrid *H. mollis* (p171) X *H. atrorubens* (p44) exhibited fragments at metaphase

I, and a single chromatin bridge was observed at anaphases I and II. In several cells the bridge at first anaphase was accompanied by a fragment.

Analysis of Populations

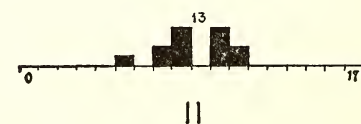
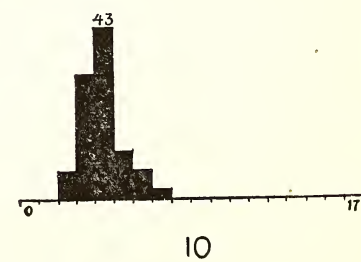
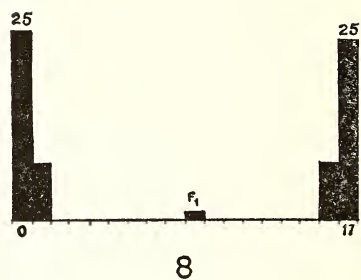
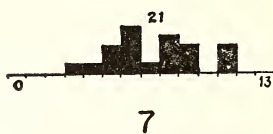
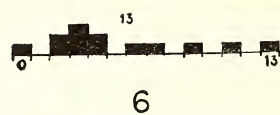
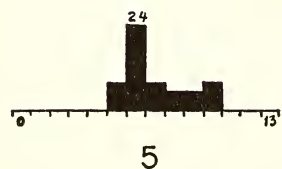
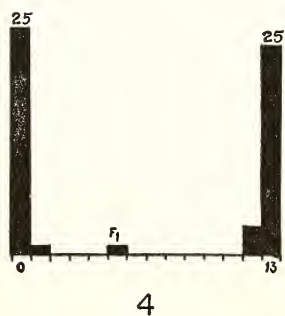
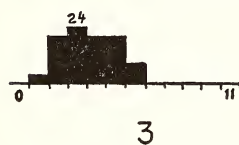
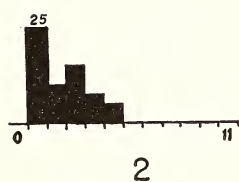
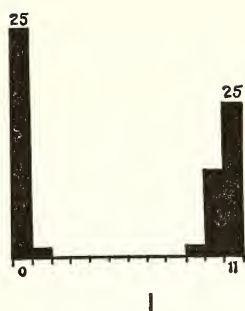
Species and natural hybrids from which population analysis were made were collected in Indiana during the summer and fall of 1953 and 1954. Analysis of artificial hybrids and backcrosses were made from plants grown in the greenhouses at Purdue University. Measurements of all plants were taken after they were pressed and dried.

The variation of morphological characters of the species and hybrids have been shown in histogram form using the Hybrid Index Method devised by Anderson (1936). It is a convenient way of graphically showing the differences within and between populations which are not easily grasped otherwise. The shortcomings of this method have been dealt with by Baker (1947), who criticized its use without adequate genetic data, by Heiser (1949) and by Anderson himself (1949). The method has been used extensively for studies of natural hybridization. In many of these studies artificial hybrids were not produced and the weighting of index values was arbitrary.

In this study all but one of the F_1 hybrids were produced, and a number of backcross progeny were grown and studied. By examination of the histograms in figure 8 it can be seen that F_1 hybrid between *H. mollis* and *H. occidentalis* reported elsewhere (Jackson and Guard, in press). *Helianthus giganteus* X *H. mollis* was an exception. This hybrid (fig. 4) resembled the pistillate parent more than the pollen parent. Thus, in examining histograms of natural hybrid populations, one should always refer to the position of the F_1 hybrid scored by the same index. Variation to the right or left of the F_1 may be taken as an indication that introgression has occurred in a particular direction.

Parental species populations: Several populations of each species were sampled, but only one for each species has been used for the histograms presented in this section. Variation between populations in which hybridization had occurred was generally slight, and could most easily be attributed to edaphic or physiographic factors.

Although most of the species discussed here are found in northern Indiana, they do not always grow in the same habitat. Ecological or physiological barriers serve to keep them separated. *Helianthus mollis* is generally a prairie species and occurs in greatest abundance in this habitat. In regions of extensive cultivation it is limited to fence rows and railroad right-of-ways. Smith (1952) has discussed the ecology of *H. divaricatus* in some detail. Generally this species has been observed growing in open sites, usually along wooded areas. Where the species grows in the open, it is usually more vigorous and has more flowers than plants growing in partial shade. *Helianthus giganteus* is usually found in wetter habitats than the other species. In northern Indiana it has been collected in bogs, along lake edges, along streams, and in low wet pastures. The habitat requirements of *H. grosseserratus* are much the same as *H. mollis*, and the two are frequently found in extensive stands along railroad tracks in the Lake Area. *Helianthus atrorubens*



occurs mostly in dry open habitats along roadsides, in open pine woods, and low wet areas in the Atlantic coast region from New Jersey southward.

The flowering periods of the species considered here may overlap one another at times. The earliest species to flower is *H. divaricatus*. Anthesis has been known to occur as early as the first week in July in Indiana. One population of this species growing in an open disturbed area was observed to flower through the 27th of August, and in this same area the species hybridized with *H. mollis*. *Helianthus mollis* has been collected in full flower in the last week of July. In some areas flowering may extend through the middle of August, and frequently into September when the plants have been mowed. The flowering period of *H. giganteus* is about the same as *H. mollis*. In *H. grosseserratus* anthesis generally occurs from the last of August through September.

Where the histograms of the parental species are shown *H. mollis* is always the histogram farthest to the right. The total number of plants scored is indicated above each histogram. Histograms of the parental species are shown in figures 1, 4, and 8.

Natural hybrid populations: The characters used for scoring the plants are given separately for each hybrid combination. The same population of *H. mollis* has been used for comparison with the other species throughout. In each case it has been necessary to revalue the index scores according to the new index that was erected. This was necessary because characters clearly separating *H. mollis* from one species may be overlapping with another.

According to Anderson (1949), it is usually advisable to assign different score values to certain characters, either because they can be more accurately measured and so deserve more consideration as criteria, or because they are known to rest upon a wider genetic background. Some of the characters used here have been given higher index values because they are apparently controlled by multiple factors as indicated by backcross segregation. Other characters have been found to vary widely in hybrid populations while being restricted in species populations. Probably these variations in hybrid populations are

Legends

General: Histograms of the species, artificial and natural hybrids, and the backcross progeny.

Fig. 1. *H. mollis* (716) to the right, *H. divaricatus* (727) to the left.

Fig. 2. *H. mollis* X *H. divaricatus* (715).

Fig. 3. *H. mollis* X *H. divaricatus* (714).

Fig. 4. *H. giganteus* (726) to the left, *H. mollis* (716) to the right, and the F_1 hybrid between the two species.

Fig. 5. *H. (mollis* x *giganteus)* X *H. mollis*.

Fig. 6. *H. mollis* X *H. giganteus* (706).

Fig. 7. *H. mollis* X *H. giganteus* (710).

Fig. 8. *H. grosseserratus* (717) to the left, *H. mollis* (716) to the right, and the F_1 hybrid between the two species.

Fig. 9. *H. mollis* X *H. grosseserratus* (700).

Fig. 10. *H. (grosseserratus* x *mollis)* X *H. grosseserratus*.

Fig. 11. *H. (grosseserratus* x *mollis)* X *H. mollis*.

also due to multiple gene inheritance, and they have accordingly been given higher index values.

In the measurements, leaf base angle or a combination of leaf base and apex angles were used. The leaf base angle is the angle between the line of the midrib of the leaf, and a line from the point of attachment of the leaf to the stem, to the widest point on the leaf blade. The leaf apex angle is obtained in much the same manner, beginning at the leaf apex. The leaf index is the leaf length divided into the leaf width.

Helianthus mollis X. *H. divaricatus*: Three populations of hybrids were found, and two were sampled. The characters used for scoring the parental species and hybrids, and their index scores are as follows:

<i>H. divaricatus</i>		Intermediates	<i>H. mollis</i>
Head dia. in mm.			
9-12	(0)	13-14.9 (1)	15-20 (2)
Ray number 8-13	(0)	14-16 (1)	17-22 (2)
Leaf index .26-.36	(0)	.37-.42 (1)	.43-.68 (2)
Leaf apex angle			
9.14°	(0)	15-17.9° (1)	18-26° (2)
Stem pubescence			
0	(0)	1(1), 2(2)	3(3)

Population 715 was growing on sandy soil deposited from the excavation of a drainage ditch where the ditch passed a small wooded area. *Helianthus divaricatus* grew along the edge of the woods in its typical habitat, and *H. mollis* occurred in the open along a railroad track that paralleled the ditch. The hybrid population was rather small and showed a decided variation toward *H. divaricatus* (fig. 2). Some of the plants could be separated from *H. divaricatus* only by the pubescence of the stem. In population 714 the variation toward *H. divaricatus* was again quite pronounced, but not as much as in 715. Individuals of 714 were growing along a fireroad on the Jasper-Pulaski State Game Preserve. The habitat was similar to population 715. A sample collection from 714 is shown as a histogram in figure 3.

Helianthus mollis X *H. giganteus*: The characters used for scoring the parental species and hybrids, and their index values are as follows:

<i>H. giganteus</i>		Intermediates	<i>H. mollis</i>
Head dia. in mm.			
8-12	(0)	13-14.9 (1)	15-20 (2)
Leaf index			
.14-.20	(0)	.21-.23(1), .24-30(2), .31-.42 (3)	.43-.68 (4)
Leaf base angle			
10-19°	(0)	20-24° (1), 25-29° (2) 30-33° (3)	34-50° (4)
Stem pubescence			
(1)	(0)	2(1), 3(2)	4 (3)

Two hybrid populations were sampled. Three more were found but these consisted of very few clones. Population 706 was growing along a small highway drainage ditch. All the plants in the population were collected for study. Two of the plants were the parental species and the hybrids showed a range of variation between the two parental species (fig. 6). Population 710 was growing on sandy soil from a recently dug ditch. Both parental species were growing in the same vicinity, but *H. giganteus* was represented by fewer individuals. Variation in this population was stronger in the direction of *H. mollis* (fig. 7).

The two parental species here are invariably ecologically separated. *H. giganteus* occurs in decidedly wet habitats while *H. mollis* is found in drier sites. All hybrids found in this study appear to result from the invasion by *H. mollis* into wetter areas along the levees of drainage ditches. Wherever it comes into close proximity with *H. giganteus* hybridization occurs. Natural hybrid derivatives from such crosses have in the past been designated under the epithet *H. doronicoides* Lam., and the species name was undoubtedly applied to such a natural hybrid (Jackson, 1956).

The F_1 hybrid between *H. giganteus* and *H. mollis* was backcrossed to *H. mollis*. The progeny are represented by the histogram in figure 5. As may be expected, there was a definite trend in variation toward the recurrent parent.

Helianthus mollis X *H. grosseserratus*: The characters used for scoring the parental species and hybrids and their index values are as follows:

<i>H. grosseserratus</i>	Intermediates	<i>H. mollis</i>
Head dia. in mm.		
9-13 (0)	13.1-14.9 (1)	15-20 (2)
Ray number		
10-14 (0)	14-15 (1)	17-20 (2)
Leaf index		
.10-.16 (0)	.17-.26(1), .27-.33(2), .34-.42(3)	.43-.68 (4)
Length to lateral veins in cm.		
4.3-7.5 (0)	1.4-4.2 (1)	.5-1.3 (2)
Leaf base angle		
7-13° (0)	14-24°(1), 25-33°(2)	34-50°(3)
Stem pubescence		
0 (0)	1(1), 2(2), 3(3)	4 (4)

Population 700 (fig. 9) was scored on a scale of 0 to 17 using all the characters listed above. Most of the individuals of this population were varying toward *H. mollis* or were like an F_1 hybrid in index value.

The F_1 hybrid between *H. mollis* and *H. grosseserratus* was backcrossed to each of the parents. In the backcross to *H. grosseserratus*

60 plants were obtained. Two plants died in the seedling stage and some did not flower. The histogram based on this backcross is shown in figure 10. In the backcross to *H. mollis* 25 plants were obtained. Of these, three had not grown beyond the rosette stage at the time the others flowered, and six of them were under 26 cm. in height, showing no evidence of flowering. The histogram representing the remainder of the progeny is shown in figure 11.

In both backcrosses a series of pubescence grades ranging from 0 to 3 was discernible. A gradation was also observed for leaf index and leaf base angle. Some of the backcross progeny from the cross to *H. grosseserratus* resembled that species very closely. Possibly they would have been determined as this species by casual examination in the field. Other of the backcross progeny were quite similar to *Helianthus brevifolius* E. E. Wats., and in the opinion of the writers the species named by Watson (1929) is a hybrid derivative from a cross between *H. mollis* and *H. grosseserratus*. Inasmuch as *H. brevifolius* is believed to be of hybrid origin it is herein reduced to hybrid status:

Helianthus X *brevifolius* E. E. Watson (pro sp.)

Helianthus brevifolius E. E. Wats. Pap. Michigan Acad. 9: 305-475. 1929.

Discussions and Conclusions

The species studied here are morphologically distinct taxa. However, all are interfertile and the F_1 hybrids between them are as vigorous or more vigorous than the parental species. There was a range of stainable pollen in the hybrids of 34 percent in *H. mollis* X *H. atrorubens* to 94.4 percent in *H. mollis* X *H. grosseserratus*. This was generally a much higher pollen fertility range than has been found in interspecific hybrids of annual species of *Helianthus* (Heiser, 1949, 1951a, b).

Probably the primary cause of reduction in fertility of the hybrids is a certain amount of chromosomal repatterning. This was indicated by translocation configurations in *H. mollis* X *H. divaricatus* and has also been found in *H. mollis* X *H. occidentalis* (Jackson and Guard, in press). Translocation configurations were also found in *H. atrorubens*. Evidence for an inversion difference was found in *H. mollis* X *H. atrorubens* and in *H. giganteus* X *H. mollis*. However, it will be recalled that this type of configuration was found in both *H. atrorubens* and *H. giganteus* so that it may represent an intraspecific as well as an interspecific difference. Chromosomal repatterning within and between plant species is not an uncommon phenomenon as indicated by the numerous examples cited by Stebbins (1950) and Clausen (1951). Thus far, changes in chromosome structure have not been sufficient to exclude gene flow between the perennial species of *Helianthus* in which hybridization has been found to occur. In the crosses of *H. mollis* to *H. divaricatus*, *H. grosseserratus*, and *H. giganteus* the difference in mean minimum chiasma frequency of the parental species and hybrids was not significant. This indicates a rather high chromosome homology of the species.

There appear to be several types of isolating mechanisms which tend to keep some of these species separated. For the most part they fit into the classification given by Stebbins (1950, p. 196) in that both external and internal barriers are present. *Helianthus mollis* and *H. atrorubens* are generally spatially isolated with the latter found in the southeastern part of the United States while the former is mostly a prairie species. This separation may have been for a considerable length of time, but the species are still infertile and the artificial hybrid was vigorous and formed 34 percent stainable pollen.

Helianthus grosseserratus and *H. divaricatus* are partially isolated from *H. mollis* by blooming dates, but occasionally the two overlap with *H. mollis* enough for hybridization to occur. In disturbed areas the flowering of *H. divaricatus* is prolonged by the increased vigor of the plant when it grows in the open. This allows for an overlapping with *H. mollis* and subsequent hybridization. The one natural hybrid swarm between *H. mollis* and *H. grosseserratus* was probably due to mowing of *H. mollis* with the result that new lateral branches that developed flowered at the same time as *H. grosseserratus*. *Helianthus giganteus* grows in decidedly wetter habitat than *H. mollis* but hybrids are found along drainage ditches and other such disturbed areas that provide habitats for both species to grow in close proximity.

Internal barriers in the backcross progeny include three of the four types listed by Stebbins (1950). In backcross progeny of the hybrids *H. mollis* X *H. grosseserratus* and *H. mollis* X *H. giganteus* a few of the plants had little or no stainable pollen (Table III). Hybrid sterility in the backcross hybrid of *H. grosseserratus* X *H. mollis* was probably genic. In the backcross *H. (giganteus* x *mollis*) X *H. mollis* the cause of sterility may have been both chromosomal and genic. Weak individuals and failure of flowering occurred in some of the backcross progeny of the hybrid between *H. mollis* and *H. grosseserratus*. In all the F₁ plants hybrid sterility occurred in varying degrees, but they were quite vigorous and flowered prolifically.

Introgression in some of the natural hybrid populations reported here may not, as yet, be of great biological significance, but the foundation for further introgression is certainly present. Apparently the flow of genes between populations is still confined to rather small areas.

An important question concerning species formation in *Helianthus* is how so many species have evolved which have a sympatric distribution. The hypotheses held by Dobzhansky (1941), Mayr (1942), and Muller (1942) is that in sexually reproducing, cross-breeding organisms geographic isolation must precede the formation of other isolating barriers. This hypotheses would seem to apply to diploid perennial species of *Helianthus*, although according to Stebbins (1950) sympatric speciation in cross pollinated perennial species is theoretically possible. According to Dobzhansky and others, it can be inferred that the perennial species of *Helianthus* were at one time isolated. This has not resulted in much sexual separation of the species because they are generally rather highly interfertile. However, when one compares the morphological dif-

TABLE 3

Distribution of Percentage of Stainable Pollen Among the Progeny of Backcrosses

Backcross	Number of Plants	Percentage range of Stainable Pollen
<i>H. (mollis x giganteus)</i> X		
<i>H. mollis</i>	3	0
	2	13.7 - 20.0
	3	40.6 - 49.9
	2	52.0 - 59.6
	3	65.6 - 69.1
	2	83.8 - 87.6
	2	92.4 - 94.6
.....		
<i>H. (grosseserratus x mollis)</i>		
X <i>H. mollis</i>	6	55.5 - 77.6
	2	83.6 - 88.1
	3	91.6 - 98.1
.....		
<i>H. (grosseserratus x mollis)</i>		
X <i>H. grosseserratus</i>	2	0 - 1.2
	1	49.2
	2	72.0 - 74.3
	7	84.2 - 88.6
	16	92.3 - 99.3

ferences between interfertile species, it appears that genetic changes affecting morphological characters have been numerous. On the basis of evidence acquired through this study and from results of other workers, one can conclude that in *Helianthus* speciation has resulted in many morphologically distinct taxa which are still quite closely related genetically.

Such a situation may be of an advantage to the genus. Some of the species are sympatric in distribution but separated ecologically, and others are spatially isolated. However, man is destroying well-defined habitats and creating new ones, and he is introducing species into areas where they did not previously occur. Interspecific hybridization has been reported for many areas and doubtless occurs in others. The result of hybridization and introgression may well be the formation of new types or taxa which have slightly different habitat requirements and are thus able to exploit the new environments which have been produced.

Summary

Helianthus mollis has been found to hybridize naturally with a number of other perennial species. Natural hybrid populations have been analyzed by the Hybrid Index Method. Introgression has occurred in the examples studied, but it may not yet be of biological significance. Artificial hybrids and some backcrosses have been produced. Most of

the F_1 hybrids were intermediate between the two parents. The exception to this was *H. giganteus* X *H. mollis* which resembled *H. giganteus* more closely. Some of the backcross progeny resembled the recurrent parent and a number showed various gradations between the species for key characters. Cytological studies of the species and hybrids have shown that a limited amount of chromosomal repatterning has occurred between and within the species. This has resulted in varying amounts of sterility, particularly in interspecific crosses. Little reduction in chiasma frequency of the hybrids indicate that the chromosomes of the parental species are still rather highly homologous. Isolating mechanisms and their effect on the separation of the species have been discussed. It is suggested that ecological isolating barriers are no longer as strict as they once were, due to the influence of man on the plant environment. From the evidence at hand, it appears that speciation in *Helianthus* has resulted in numerous morphologically distinct taxa which are still closely related genetically.

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