

VARIATION IN *HELIOPSIS HELIANTHOIDES* (L.) SWEET (COMPOSITAE)¹

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INTRODUCTION

Heliopsis helianthoides is composed of three subspecies. The distribution of ssp. *helianthoides* is centered in the eastern United States, namely the Appalachian Mountain region where it occurs in wooded, or partially shaded, moist areas. The distribution of ssp. *occidentalis* is centered in the northern Great Plains growing in the dry, open prairie. The third subspecies, ssp. *scabra*, is centered in the Ozark Mountain area and the lower Great Plains region where it grows on dry glades, wooded slopes and valleys. Morphologically these three subspecies are distinct in their own centers of distribution (fig. 1). Subspecies *helianthoides* is charac-

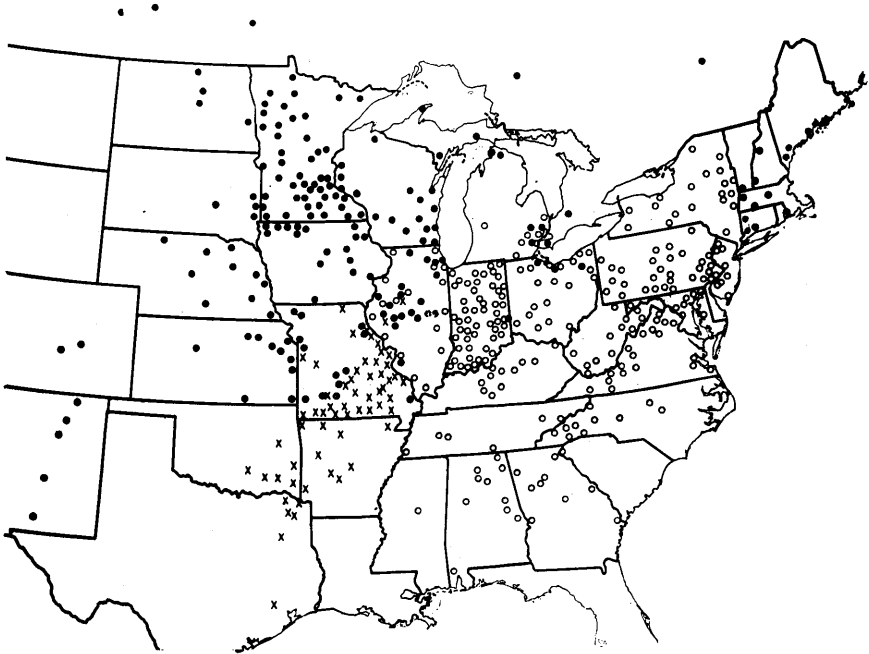


FIGURE 1. Distribution of *Heliopsis helianthoides* in United States and Canada (ssp. *helianthoides*, open circles; ssp. *occidentalis*, solid circles; ssp. *scabra*, X).

terized by glabrous stems and leaves, short peduncles, small heads, and broad ovate-lanceolate leaves with long petioles, whereas ssp. *occidentalis* is characterized by scabrous leaves and upper stems, long peduncles, large heads, and deltoid leaves with short petioles. Subspecies *scabra* is characterized by scabrous leaves and upper stems, long peduncles, heads nearly as large as those of ssp. *occidentalis*, and rather narrow ovate-lanceolate leaves with long petioles.

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In a preliminary study of the variation of *Heliopsis helianthoides* (Fisher, 1952), it was shown from a transect study of herbarium material which had been collected within a hundred miles of a line arbitrarily drawn from North Dakota to Virginia, that the species exhibited a very gradual change in its morphological characters from one extreme of the geographical range to the other. Since the preliminary study, a statistical approach to the study of variation of this taxon has been pursued more extensively.

METHODS

Although both living and herbarium material were used in this study, most of the data assembled are from herbarium material borrowed from the major herbaria of the United States. After the range of distribution for *Heliopsis helianthoides* was determined, a map of the area was divided into quadrats of approximately 125 square miles each. Herbarium material was then assembled according to quadrat and measured for leaf blade-petiole angle, petiole length, peduncle length, head width, and pubescence (table 1).

The leaf to be used for measurement was selected from the fourth node below a mature head, since the shape of the leaf was observed to change during the

TABLE 1

Measurements of four characters of Heliopsis helianthoides from herbarium material assembled into equal-area quadrats. (Means, standard deviation and coefficients of variation; angles in degrees, length and width in centimeters.)

QUA- DRAT	LEAF BASE ANGLE			PETIOLE LENGTH			PEDUNCLE LENGTH			HEAD WIDTH		
	\bar{X}	s	v	\bar{X}	s	v	\bar{X}	s	v	\bar{X}	s	v
B-14	97.0	12.1	12.4	.52	.24	4.61	20.18	5.90	2.92	1.82	.3	1.6
C-11	104.2	8.4	8.0	.6	.3	5.7	22.7	3.1	1.3	1.6	.3	1.7
C-12	100.0	9.5	9.5	.4	.3	6.8	19.6	5.4	2.7	1.8	.1	.7
C-13	105.1	7.2	6.8	.7	.3	4.8	18.6	5.4	2.9	1.7	.3	2.2
D-2	109.8	8.3	7.5	1.0	.3	3.2	17.2	5.3	3.0	1.5	.1	1.1
D-7	105.0	2.6	2.4	.7	.4	6.7	17.0	7.3	4.2	1.7	.4	2.8
D-8	107.0	16.5	15.4	1.1	.2	2.5	18.0	8.6	4.7	1.5	.5	3.4
D-11	102.0	8.6	8.4	.8	.2	2.5	17.0	5.8	3.4	1.7	.3	1.7
D-12	103.0	9.2	8.9	.5	.3	6.0	18.5	3.7	2.0	1.7	.5	2.9
E-1	112.0	18.2	16.2	1.6	.7	4.6	16.0	8.4	5.2	1.4	.2	1.4
E-2	111.0	9.0	8.1	2.6	.4	1.6	14.0	3.7	2.6	1.4	.4	3.2
E-3	112.0	13.5	12.0	2.6	1.1	4.2	12.2	4.7	3.8	1.7	.2	1.4
E-9	100.0	7.1	7.1	.8	.5	6.8	16.0	5.1	3.1	1.6	.3	2.0
E-10	111.0	8.1	7.2	1.5	.3	2.0	15.4	5.6	3.6	1.5	.2	1.4
E-11	101.2	3.4	3.3	.8	.4	5.7	17.8	3.7	2.0	1.8	.1	.5
E-12	102.1	8.1	7.9	.6	.2	3.9	16.9	4.2	2.4	1.7	.4	2.5
E-13	95.2	9.2	9.6	.6	.3	5.4	15.5	5.6	3.6	1.4	.3	2.5
F-1	113.0	4.6	4.0	1.7	.5	3.0	15.2	7.9	5.1	1.4	.2	2.0
F-2	118.0	5.8	4.9	2.2	.5	2.5	14.4	5.6	3.8	1.4	.2	1.7
F-3	116.4	13.0	11.1	2.2	.8	3.7	12.5	4.8	3.8	1.2	.4	4.0
F-4	115.0	6.4	5.5	2.0	.8	4.1	14.1	2.6	1.8	1.6	.4	2.5
F-5	115.2	20.6	1.7	2.7	.6	2.4	8.8	1.2	1.4	1.3	.4	3.3
F-6	115.0	9.0	7.8	1.7	.6	3.8	12.8	3.4	2.6	1.3	.2	1.5
F-8	104.7	6.7	6.3	1.1	.6	5.8	17.4	5.1	2.9	1.7	.2	1.4
F-9	107.8	4.3	3.9	1.1	.4	4.1	17.6	3.1	1.7	1.5	.9	5.8
F-10	105.0	9.6	9.1	1.2	.2	2.3	14.5	6.7	4.6	1.4	.1	.7
F-11	106.3	14.6	13.7	.7	.3	4.8	18.5	6.5	3.5	1.9	.2	1.1
F-12	112.2	11.7	10.4	.4	.2	6.2	14.5	7.2	3.8	1.6	.1	.8
F-13	98.7	6.6	6.6	1.1	.1	.8	11.2	3.4	3.0	1.3	.8	6.2
F-14	99.6	6.7	6.7	1.4	.1	.9	7.6	1.7	2.2	1.4	.1	.9
F-15	96.5	2.6	2.6	1.1	.1	.9	14.7	3.0	2.0	1.3	.2	1.8

TABLE 1—(Continued)

QUA- DRAT	LEAF BASE ANGLE			PETIOLE LENGTH			PEDUNCLE LENGTH			HEAD WIDTH		
	\bar{X}	s	v	\bar{X}	s	v	\bar{X}	s	v	\bar{X}	s	v
G-2	118.0	10.0	8.4	1.8	.6	3.3	11.8	4.6	3.9	1.3	.3	2.7
G-3	115.0	9.5	8.2	1.7	.4	2.6	11.3	4.6	4.0	1.3	.2	1.6
G-4	116.1	10.6	9.1	2.2	.2	1.1	13.5	6.4	4.7	1.4	.3	2.1
G-5	122.0	14.7	12.0	2.1	.4	2.0	10.3	4.1	3.9	1.2	.2	1.8
G-6	125.3	6.9	5.5	1.8	.7	4.0	9.9	2.2	2.2	1.2	.1	.8
G-8	114.2	11.1	9.7	1.6	.5	3.5	13.9	8.0	5.7	1.5	.2	1.6
G-9	118.0	10.9	9.2	1.2	.6	5.2	16.7	4.4	2.6	1.6	.4	2.5
G-10	119.3	14.5	12.1	1.3	.3	2.5	14.0	3.3	2.3	1.4	.2	1.6
G-11	108.7	9.3	8.5	.6	.3	5.3	18.0	1.4	.6	1.6	.7	4.2
G-12	103.2	10.6	10.2	.8	.3	4.4	15.6	5.7	3.6	1.6	.5	3.3
G-13	99.0	5.0	5.0	1.2	.5	4.4	10.0	2.0	2.0	1.7	.1	.5
H-2	119.6	12.0	10.0	2.4	.5	2.4	11.2	6.1	5.4	1.2	.2	2.1
H-3	122.5	14.5	11.8	1.9	.5	2.5	13.0	4.2	3.2	1.2	.5	4.1
H-4	116.0	10.0	8.2	2.2	.5	2.5	13.0	3.3	2.5	1.4	.4	2.9
H-6	124.8	13.0	10.4	2.1	.4	2.2	10.9	2.8	2.5	1.2	.3	2.7
H-7	114.6	13.9	12.1	1.9	.5	3.0	9.4	4.1	4.3	1.3	.3	2.6
H-8				1.8	.6	3.8	11.4	3.4	2.9	1.4	.1	1.0
H-9	113.7	16.4	14.4	1.2	.4	3.5	16.1	5.0	3.1	1.6	.2	1.7
H-10	116.8	9.2	7.8	1.7	.5	2.9	11.1	5.9	5.3	1.3	.2	1.5
H-11	112.3	11.2	9.9	.6	.3	5.5	13.5	3.4	2.5	1.6	.5	3.6
H-12	101.1	9.5	9.3	1.1	.5	4.8	15.7	5.0	3.1	1.7	.4	2.4
H-13	107.2	8.9	8.3	1.0	.6	6.3	15.8	7.8	4.9	1.2	.6	5.5
H-14	104.0	9.4	9.0	.9	.4	4.4	14.5	6.9	4.7	1.7	.5	3.1
I-2	127.7	16.1	12.6	2.0	.5	2.7	10.2	4.6	4.5	.9	.1	1.8
I-4	118.3	12.4	10.4	2.4	.7	3.0	12.4	3.8	3.0	1.2	.3	3.1
I-5	123.6	6.7	5.4	3.1	.9	3.0	10.6	2.0	1.8	.9	.1	1.7
I-6	125.0	9.4	7.5	2.3	.7	3.3	9.5	5.0	5.2	1.1	.3	2.8
I-7	117.5	4.4	3.7	2.2	.6	3.0	7.6	2.4	3.1	1.0	.3	3.8
I-8	125.4	13.0	10.3	1.6	.2	1.6	9.8	3.0	3.0	.9	.3	3.0
I-9	122.0	17.5	14.3	1.5	.6	4.2	12.9	4.8	3.7	1.4	.5	4.1
I-10	128.0	9.1	7.1	1.5	.6	4.4	10.0	3.4	3.4	1.2	.2	1.8
I-12	117.5	14.8	12.5	1.5	.7	4.6	13.7	6.3	4.5	1.5	.4	3.0
I-13	119.2	9.4	7.8	1.1	.4	3.6	12.1	6.8	5.6	1.9	.4	2.1
I-17	98.3	8.0	8.1	.6	.2	3.9	22.1	7.6	3.4	1.8	.4	2.6
J-3	128.4	7.6	5.9	2.2	.4	2.0	9.0	4.8	5.3	1.1	.3	2.8
J-4	122.0	5.5	4.5	2.2	.3	1.6	10.8	3.4	3.1	1.1	.3	3.2
J-5	110.5	2.4	2.1	2.9	.8	2.8	10.8	4.1	3.7	1.2	.5	4.4
J-7	122.6	6.6	5.3	2.3	.8	3.8	9.0	3.0	3.3	1.0	.4	4.8
J-9	128.0	10.0	7.8	1.3	.5	3.8	13.5	4.3	3.1	1.2	.4	3.8
J-10	119.8	3.6	3.0	1.4	.5	3.5	15.7	4.2	2.6	1.2	.2	1.8
J-11	120.8	7.6	6.2	1.5	.1	1.1	17.2	5.5	3.1	1.4	.2	1.3
J-12	124.0	5.3	4.2	1.6	.2	1.6	9.6	2.2	2.2	1.6	.4	2.8
J-17	95.0			1.2			25.0			1.6		
K-5	115.5	3.3	2.8	2.6	.9	3.6	12.3	6.2	5.0	1.3	.4	3.0
K-7	126.6	9.7	7.6	2.1	.6	3.0	8.6	3.3	3.8	.9	.1	1.5
K-9	128.0	6.6	5.1	2.2	.6	3.1	8.8	2.6	2.9	.9	.2	2.5
K-11	119.2	9.7	8.1	1.4	.2	1.5	13.3	2.2	1.6	1.2	.4	3.4
K-12	105.0			1.3			8.0			1.2		
K-17	104.8	4.3	4.1	.6	.5	.8	23.5	6.0	2.5	1.8	.5	3.2
L-11	128.6	10.4	8.0	1.0	.4	3.7	15.0	3.8	2.5	1.0	.2	2.0
L-12	127.8	4.3	3.3	1.2	.9	6.7	17.7	4.8	2.7	1.1	.3	3.2
L-13	123.0			1.3			13.0			1.4		
L-17	105.8	6.6	6.2	.8	.1	2.0	20.7	3.2	1.5	1.7	.2	1.1
M-12	118.6	6.6	5.5	1.5	.2	1.7	17.1	6.3	2.3	1.2	.3	3.0
M-18	106.5	7.4	6.9	.7	.5	6.4	20.5	6.3	3.0	1.6	.3	2.3

growing period of the plant. When the leaf was poorly preserved, it either was not measured or was first removed and boiled in water until it could be sufficiently flattened for measurement. The leaf was then dried again and replaced on the herbarium sheet. Only sheets with abundant material were used in this manner. Type or other authentic specimens were not used for the statistical study.

The leaves of ssp. *helianthoides* tend to be broadest near the middle of the leaf and taper to the petiole, whereas ssp. *occidentalis* tend to be broader below the middle and contract sharply into the petiole. The leaves of ssp. *scabra* are also ovate but more lanceolate in shape, otherwise appearing at the base about the same as ssp. *helianthoides*. Since these extreme leaf shapes exist in this taxon it was felt that a method was desirable by which the angle formed by the base of the leaf blade and the petiole could be measured.

The leaf blade-petiole angle was measured by locating a line AB merely by following the midrib and petiole of the leaf (fig. 2). The widest point of the leaf was then determined and chords CD and EF were drawn parallel to AB, or the

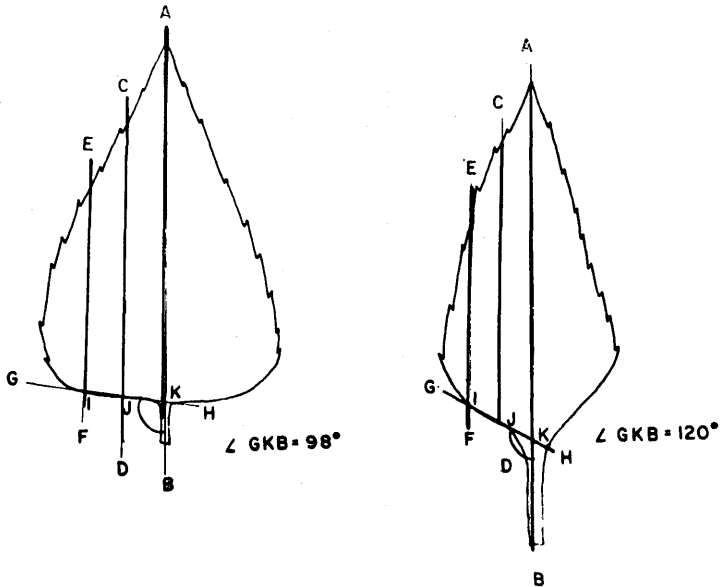


FIGURE 2. Method for measuring leaf base-petiole angle. See text.

midrib-petiole, through points one-third and two-thirds of the distance between the midrib and the widest point on the leaf, respectively. Points I and J are located where chords CD and EF transect the base of the leaf margin. A straight-edge when placed along points I and J locates the point at which the petiole joins the blade. A protractor when placed along the straight-edge offers ready measurement of angle GKB or the leaf base-petiole angle. In figure 2 it can readily be seen that angle GKB would measure nearly 90° in a truncate leaf, and much greater than 90° in an ovate type with a cuneate base. With the exception of the leaf base-petiole angle, this can most easily be accomplished by transposing a transparent millimeter grid on the leaf and reading to the nearest millimeter. This is a modification of the method used by Woodson (1947) for determining the leaf shape in *Asclepias tuberosa*.

The statistical treatments have been limited to calculation of mean, standard deviation, standard error, and the coefficient of variation. The statistical values

are not projected onto the data maps. Instead it seems more desirable to illustrate the variation pattern in these species of *Heliopsis* by a more graphic method (fig. 3 and 4). The single vertical bar in figure 3 represents the mean value for petiole length. The angle subtending the vertical bar represents the mean value for leaf blade-petiole angle. Pubescence was scored on a 0 to 4 scale, the 0 end of the scale representing glabrous plants and the 4 end of the scale representing scabrous plants. The two remaining characters studied, namely head width and peduncle length, are represented in figure 4. Head width values are represented by a solid circle while mean peduncle values are represented by a subtending vertical bar.

RESULTS

Variation in Petiole Length and Leaf Blade-Petiole Angle

Upon examination of figure 3 it is evident that there are no well defined limits between the subspecies in respect to petiole length and leaf blade-petiole angle. Instead, there is an even gradient or cline extending not only from the eastern to the western portions of the species range, but also extending north and south.

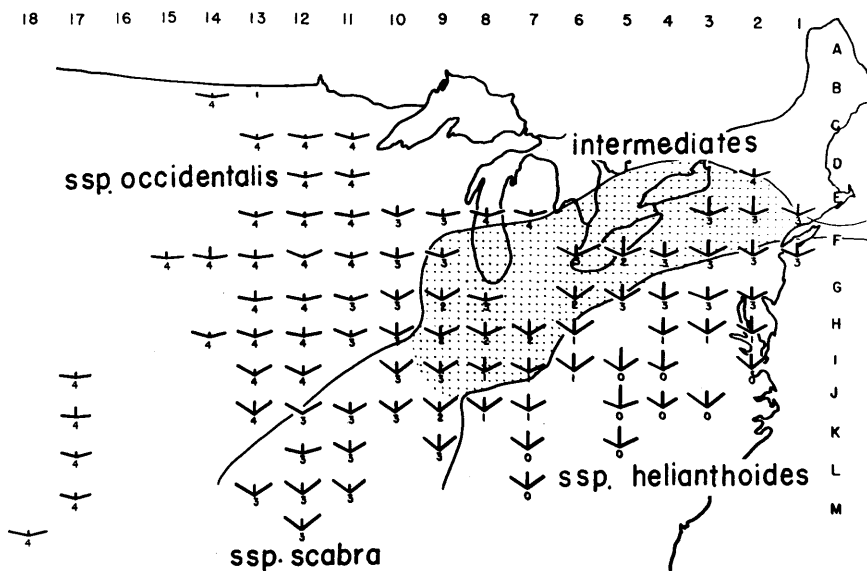


FIGURE 3. Graphic representation of quadrat means for petiole length (vertical bar), leaf blade-petiole angle (subtending angle), and index values for pubescence. Stippled area indicates zone of intermediates between subspecies.

In respect to petiole length, the range of "pure" *ssp. helianthoides* is represented by the 2.0 to 3.1 cm. zone in the eastern area, while the range of "pure" *ssp. occidentalis* is represented by the 0.4 to 0.9 cm. zone in the northwestern portion of the species range. The 1.0 to 1.9 cm. zone (stippled area) represents intermediates between these taxa. *Heliopsis helianthoides ssp. scabra*, which is centered in the Ozark Mountain area, exhibits the same range of measurements as the intermediates separating *ssp. helianthoides* and *ssp. occidentalis*. There is a rather sharp disjunction of measurements in regard to petiole length separating *ssp. occidentalis* and *ssp. scabra*. There is no disjunction of this character between *ssp. scabra* and the intermediate zone of plants.

Variation in leaf base-petiole angle (fig. 3) again indicates a very gradual variation pattern oriented east and west as well as north and south. The range for "pure" *ssp. helianthoides* was determined to be between 120° and 128° , while *ssp. occidentalis* was found to possess leaf blade-petiole angles ranging from 95° to 109° . The distributional range limits of *ssp. scabra* of the Ozark region are ill-defined in regard to this character. The statistical values of this subspecies are within the range of measurements of the plants of the intermediate zone between *ssp. occidentalis* and *ssp. helianthoides*.

There is, on the average, a 10 degree differential in measurements for the leaf blade-petiole angles separating *ssp. occidentalis* and *ssp. scabra*. This indicates a rather definite limit of distribution for these two subspecies in regard to this character. On the other hand, *ssp. scabra* cannot be separated from *ssp. helianthoides* on this basis.

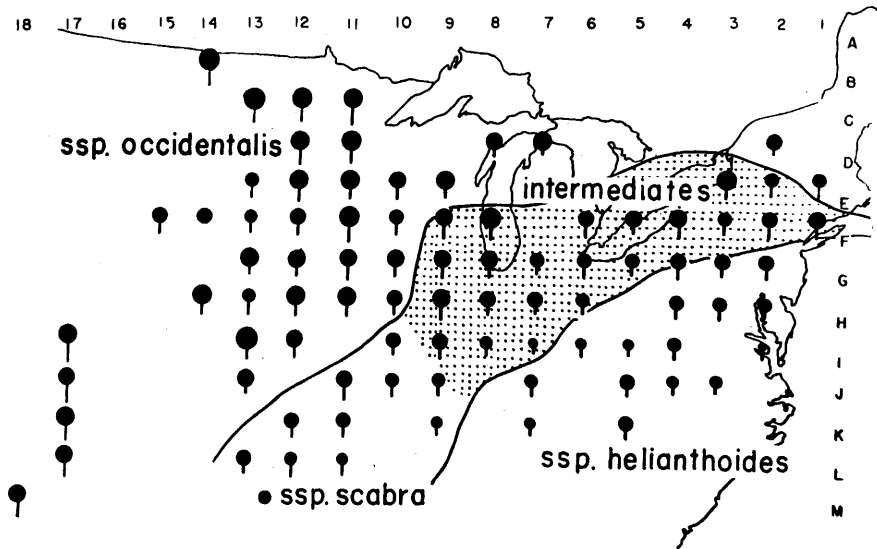


FIGURE 4. Graphic representation of quadrat means for head width (solid circles) and peduncle length (subtending vertical bar). Stippled area indicates zone of intermediates between subspecies.

Variation in Peduncle Length and Head Width

Peduncle length and head width values are represented in figure 4. These two characters have essentially the same pattern of variation as was found in the leaf blade-petiole angle and petiole length. Subspecies *helianthoides* was found to possess peduncle length values ranging from 7.0 to 12.0 cm., while *ssp. occidentalis* varies from 14.7 to 23.7 cm. Between these two taxa (stippled zone) there is a zone of plants with intermediate values which nearly parallels the intermediate zone of the other characters analyzed.

In respect to peduncle length values, *ssp. scabra* is again intermediate between *ssp. occidentalis* and *ssp. helianthoides*. In general there is no discontinuity of measurements for peduncle length separating *ssp. scabra* and *ssp. helianthoides*. On the other hand, there is discontinuity of measurements for peduncle length separating *ssp. occidentalis* and *ssp. helianthoides* along the northwestern limits of the intermediate zone.

The overall statistics for peduncle length show definite clines or gradients oriented between ssp. *helianthoides* and ssp. *occidentalis*, and between ssp. *occidentalis* and ssp. *scabra*, but not between ssp. *helianthoides* and ssp. *scabra*.

The projection of data for head width indicates the same type of character gradient as for the previous characters analyzed. The range of head width values for "pure" ssp. *helianthoides* is 0.9 to 1.2 cm., while the 1.6 to 1.9 cm. zone represents "pure" ssp. *occidentalis* (fig. 4). There is no discontinuity of measurements for head width values separating ssp. *occidentalis* and ssp. *scabra*. There is a gradual cline from the Ozark Mountain area to the northern plains area. There is also a very gradual cline from the northern plains area into the intermediate zone of the midwest. There exists a zone of head width measurements projecting sharply southward along the Appalachian Mountains. It is difficult to account for this projection of head width values. Although environmental influence is not entirely discounted, it is difficult to see how it is a valid reason since the other characters analyzed did not show a similar pattern. It is not implied that the same environmental influence would necessarily have the same influence on all characters.

In general there is no discontinuity in measurements for head width values separating the taxa of of *Heliopsis helianthoides*.

Variation of Pubescence

Prior to this study the taxa of *Heliopsis* found in the United States were separated on the basis of pubescence. Pubescence values exhibit a very gradual gradient from completely glabrous plants of the southeastern portion of the species range to scabrous plants of the upper Great Plains. Plants with a pubescence value of 4 have a range closely corresponding to the range of "pure" ssp. *occidentalis*, while plants with a pubescence value of 0 to 2 have a range closely corresponding to the range of "pure" ssp. *helianthoides*. Between the ranges of these two taxa is found a zone of quadrats with intermediate pubescence values of 2 and 3 (fig. 3).

Subspecies *scabra* is characterized by a pubescent value of 3, nearly agreeing with ssp. *occidentalis* in this regard. The intermediate zone between ssp. *occidentalis* and ssp. *helianthoides*, on the other hand, is characterized by pubescence values ranging from 1 to 3. There is discontinuity in pubescence values separating ssp. *helianthoides* and ssp. *scabra*.

DISCUSSION AND CONCLUSIONS

Although these subspecies are morphologically and ecologically distinct within their respective centers of distribution, they are highly interfertile (Fisher, 1957). The artificial F₁ hybrids exhibit only a slight decrease in fertility. From an examination of present data it is evident that typical ssp. *helianthoides* and ssp. *occidentalis* are connected by a broad band of intermediates, covering an area of several hundred miles. The transition between these areas is very gradual for most characters analyzed. There is no disjunction either in distribution or in characters, except in northeastern United States. Here very little, if any, intergradation can be detected. In Michigan where the two taxa overlap, it is difficult to assign a subspecific epithet to any given plant. When a plant from Virginia is crossed with a plant from Minnesota, the hybrid resembles a plant from Indiana or Illinois. The intermediate zone between these two subspecies extends from northwestern Illinois and southwestern Wisconsin into Central Ohio.

Subspecies *occidentalis* intergrades to a much lesser extent with ssp. *scabra*, but hybridization is apparent in northeastern Kansas, northwest and northeast Missouri where the ranges of the two taxa overlap. The artificial cross between these taxa is easily made and the hybrids are similar to many herbarium specimens collected by Rev. B. F. Bush who collected extensively in Missouri. Many of his

specimens were collected in the same locality and distributed to the various herbaria of this country. If these specimens can be considered a population sample, and essentially they are, even though they were collected on different occasions, a typical hybrid swarm can be reconstructed. Typical specimens of both parents as well as many intermediates can easily be detected. From herbarium specimens and living material observed and collected by the author, it appears that back crossing and subsequent introgression of characters occurs at about the same rate in either direction. The factor most responsible for keeping these two taxa apart is probably ecological, since the habitat preference of the two taxa is quite different. Subspecies *scabra* is found most commonly on the relatively dry ridges and slopes in the Ozark mountain region while ssp. *occidentalis* occurs chiefly in the prairie regions of the Great Plains. Partly discontinuous character clines would be expected with more or less distinct habitats. Subspecies *scabra* apparently does not intergrade with ssp. *helianthoides*. This suggests that a barrier, other than a reproductive one, must be present which keeps these two taxa apart.

In an attempt to explain the pattern of variation in *Heliopsis helianthoides* it is necessary to consider three hypotheses. First, mutation, recombination, and natural selection within the taxa must be considered as a possible explanation of the character gradients or clines. Second, extensive hybridization with repeated backcrossing where the ranges of the taxa overlap seems probable. Third, a combination of these two hypotheses seems likely.

Character clines are probably very common among plant species, but the usual methods of taxonomy, which deal with combinations of characters and aim at detecting discontinuities, are likely to permit them to go undetected. Among the best examples of clines is the one reported by Fassett (1942) in *Diervilla lonicera*. He found that a cline of pubescence ranged from 80 percent frequency at Espanola, Ontario, to 0 percent frequency at Callander, slightly more than 100 miles east.

Gregor (1939) recognized two types of clines in *Plantago maritima*, the topocline and the ecocline. The topocline is similar to the geographic cline which expresses quantitative characters such as the length and width index values of bracts and sepals. Ecoclines are clines related to ecological gradients within a restricted area.

Woodson (1947), in his study of variation in *Asclepias tuberosa*, has shown three definite centers of distribution, namely the Ozark, Appalachian and Orange Island regions. He concludes that reciprocal introgression has occurred from initial hybridization through backcrossing, producing a more or less perfect gradation of the genotype from the Appalachian region in the eastern portion of the species range to the Ozark region in the midwest.

Clausen (1951) has found that character clines do not actually exist in *Layia platyglossa* from studies conducted on races grown in a uniform research garden where the influence of differences in the environment in producing modifications was reduced to a minimum. He states that clines are not commensurable with natural entities, and are oversimplified abstractions dealing with the variation of individual characters. *Layia platyglossa* then, according to Clausen, shows characteristic trends in variability and these trends indicate evolutionary discontinuities.

Assuming that *Heliopsis helianthoides* occupied at one time the eastern part of the United States, namely the Appalachian region where the climatic and associated environmental factors are relatively constant, and migrated toward the Great Plains where the transition in such environmental influences is gradual, then clinal or ecotypic variation might be prevalent. This could be due to gene mutation, gene recombination, and natural selection occurring as the species migrated from one ecological area to another.

If natural selection and not hybridization is the primary cause of variation in *Heliopsis helianthoides*, and it is not implied that natural selection is divorced from

gene mutation and recombination, but rather are complimentary forces, then the gene complexes are a reflection of the environmental complexes. Mutant genes might drift through the populations and might acquire selective value, when the species migrated into new or slightly different environments. As Stebbins (1950) has pointed out, the direction of evolution is determined largely by selection acting on the gene fund already present in the population, the component genes of which represent mutations that have occurred many years before.

Natural selection is an important factor in perpetuating an accumulation of small genetic changes. Populations are, after all, mixtures of several biotypes which differ in fitness for different environments. Thus, when seeds of a plant are scattered to a slightly new or different environment, the species, if its genotype is already modified through gene mutation and recombination, may persist and migrate from one ecological area to another.

The second explanation of these clines is hybridization of individuals of either subspecies where their ranges of distribution overlap. It is not enough merely to account for this phenomenon by hybridization alone without including introgression, *i.e.*, gene flow between interfertile taxa through their hybrids. This has been termed introgressive hybridization by Anderson and Hubricht (1938) and is commonly referred to as introgression. The theory is based on the assumption that partial geographic isolation and morphological diversification precedes reproductive diversification.

The centers of distribution of the three subspecies of *Heliopsis helianthoides* are easily detected as the upper Great Plains, the Ozark, and the Appalachian regions. During the Cretaceous Era, North America was dissected by inland seas of water which extended up the present Mississippi valley as far as southern Illinois. This embayment separated the ancient Appalachian and Ozarkian plateaus. The withdrawal of the Cretaceous seas brought about the reunion of the Ozark and Appalachian plateaus, but by the Pleistocene, continental ice sheets extended as far south as the Missouri and Ohio River valleys with the exception of the driftless area of Wisconsin, northeast Iowa and northwest Illinois (Finch and Trewartha, 1949). Neither did the glaciated area extend farther west than southwest North Dakota and central South Dakota and east central Nebraska.

The above described disturbances could easily have brought about separation of the putative ranges of ssp. *occidentalis*, ssp. *scabra*, and ssp. *helianthoides*. Undoubtedly at the close of the Pleistocene the retreat of the ice created new habitats into which many species of plants dispersed. With colonization of these new habitats these subspecies of *Heliopsis* could have undergone wholesale hybridization and backcrossing. Following this initial phase of hybridization to the present day, introgression has produced a zone hundreds of miles wide, represented by plants intermediate in phenotypic characters between relatively uniform phenotypes at either geographic extreme of the species range.

At the onset of hybridization between two taxa, standard deviations of populations within the zone of hybridization would ordinarily be expected to show higher values than later. In *Heliopsis* this is not seen; instead, quadrats with high standard deviation values seem not to follow any set pattern. For this reason quadrats with high standard deviation values are accounted for by excessive variation of the environmental factors in the area in which the taxon grows. Furthermore, the quadrats in the intermediate zone, assuming introgression pressure is equal between the subspecies, might be expected to yield higher mean values due to heterosis (except in angle measurements). This is apparently true in *Asclepias tuberosa*, and Woodson (1947) has termed it the "crest of variability."

If the process of hybridization and extensive backcrossing has been going on over a considerable period of time to the extent that a genetic "leveling" effect has been reached, the plants of the intermediate zone would not necessarily express high standard deviation values. It has been repeatedly observed during the

course of this investigation that the variation is not between individuals of the population, but between populations.

It is not implied that during the period of putative hybridization of the two taxa, gene mutation, recombination, and the influence of the various environmental factors would not be present and operative. This does, however, suggest a third hypothesis, that is, a combination of the above two hypotheses as a possible explanation of the variation found in this species.

It is very difficult to assign definitely one or the other of the above hypotheses to the variation pattern in *Heliopsis helianthoides*. Natural selection, although admittedly very important in the evolution of any population or system of populations, cannot completely account for this type of variation from the evidence presented. There is an overall gradual intergradation of characters between ssp. *helianthoides* and ssp. *occidentalis*; but in certain portions of the range, namely Michigan, New York and Vermont, the gradient changes abruptly in respect to most characters. Also there is an abrupt change in some characters analyzed and not in others in portions of the range. Precipitous changes in character gradients when not accompanied by corresponding changes in the environment is evidence against natural selection and favors the theory of hybridization as the primary cause of the variation pattern in *Heliopsis helianthoides*. Theoretically, extensive hybridization and backcrossing between the two taxa over a considerable length of time could produce a broad zone of intermediates which exists between ssp. *helianthoides* and ssp. *occidentalis*. Furthermore, the subspecific taxa are relatively homogenous within their respective centers of distribution. The greatest amount of variation is where the subspecies ranges overlap; therefore, the more logical of the three explanations for the variation pattern is hybridization between the two subspecies.

SUMMARY

Heliopsis helianthoides (L.) Sweet of the United States and Canada has been studied over its entire range of distribution. This species of *Heliopsis* is found to consist of three morphologically distinct taxa, namely ssp. *helianthoides* of the eastern United States, ssp. *scabra* of the Ozark region, and a newly described taxon, ssp. *occidentalis* of the upper Great Plains region. Gradual intergradation of characters was found to exist between ssp. *occidentalis* and ssp. *helianthoides*, and to a lesser extent between ssp. *occidentalis* and ssp. *scabra*. Very little, if any, intergradation exists between ssp. *scabra* and ssp. *helianthoides*.

Three hypotheses have been considered in an attempt to explain the pattern of variation found to exist in this species of *Heliopsis*. First, mutation, recombination, and natural selection within the taxa must be considered as a possible explanation of the character gradients or clines. Second, extensive hybridization with repeated backcrossing where the ranges of the taxa overlap seems probable. Third, a combination of these two hypotheses also seems likely.

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