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# An Experimental Study of Population Differences in Leaf Morphology of *Aquilegia canadensis* L. (Ranunculaceae)

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**ABSTRACT:** Eleven basal leaf characteristics were studied in four western Massachusetts populations of *Aquilegia canadensis* L. All characteristics were significantly different ( $P < 0.05$ ) among populations. Plants in the open, most xeric site (Deerfield) produced the smallest leaves. Petiole and blade lengths were independently controlled or responded separately to an environmental factor(s).

Sexually produced offspring from each population were transplanted to each site and in a greenhouse. The results show all 11 characteristics have a high degree of plasticity and the environment at each site played the dominant role in producing significant differences among the original populations for eight characteristics. Nevertheless, this experiment gives evidence of genetic differences among populations for 10 characteristics. The offspring from one site (Hawley) showed reduced plasticity for seven characteristics. The environments at the two most extreme of the four sites (Deerfield and Hawley) suppressed the expression of genetic differences. These results show it is possible to determine the relative effects that environment and heredity have on leaf characteristics utilizing sexually produced plants instead of the usual cloned material.

## INTRODUCTION

The genus *Aquilegia* (Ranunculaceae) consists of 67 species of perennial herbs, widely distributed in the temperate zone of North America and Eurasia (Munz, 1946). Of the 23 native North American species, only one, the red columbine (*A. canadensis* L.), occurs E of the Rocky Mountains. This species is found in a variety of habitats, from dry woods to rocky cliffs, ledges and peat bogs ranging from Nova Scotia to Saskatchewan and S to Florida and Texas (Gleason and Cronquist, 1963). Munz (1946) has divided the species into five varieties, each having a fairly well-defined geographic range, but he concedes there is considerable variation and it is difficult to assign many specimens to a particular variety. The two varieties occupying the southern portion of the range are often triternate while the three northern varieties are mostly biternate. The southern varieties tend to have smaller leaflets but the range of leaflet length of all varieties overlaps.

Since the publication of Munz's monograph (1946), it has become increasingly well-known that plant species inhabiting diverse sites or those that are wide-ranging are usually composed of genetic races (Heslop-Harrison, 1964). In addition, it is well-known that the environment can influence phenetic expression of vegetative parts at all development stages beginning with seed germination. More recently it has been shown that a progeny's phenotype may also be modified by environmental factors during seed development (Stearns, 1960; Rowe, 1964; Nelson *et al.*, 1970). Leaf morphology is especially susceptible to environmental modification as is evident from the extensive literature on the subject, *e.g.*, on size (Fisher, 1954), shape (Cook and Johnson, 1968), lobing (Talbert and Holch, 1957) and dissection (Lewis, 1972). Therefore, the study reported here was undertaken: (1) to determine if significant morphological differences occur in populations of *Aquilegia canadensis* occupying diverse habitats within a small geographic area; (2) to investigate the relative role that environment and heredity have on these differences, and (3) to determine if meaningful genecological studies could be performed with sexually reproduced offspring rather than the usual cloned individuals.

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To my knowledge, no studies of this type using compound leaf plants have been done.

#### METHODS

*Site description.*—Within a 37-km (23-mile) radius of Amherst, Massachusetts, the four most diverse habitats, which supported at least 25 columbine plants, were selected as study sites.

One site is located on the S slope of the Holyoke Range at elevations of 137-213 m. The slope has a 25-30° grade and is covered with a relatively open second-growth oak-hickory forest. A second site is a vertical cliff near the northwesterly base of Mount Toby at an elevation of 117 m. The face of the cliff has an average height of 5 m. Some areas of the cliff are virtually waterfalls during wet periods, and extremely dry at other times. The third site, a recently abandoned pasture, was located in East Deerfield. The pasture is a gentle 5-10° E-facing slope, at an elevation of 45 m, with very thin soils and often exposed bedrock. The fourth site was in Hawley State Forest, at an elevation of 582 m. A large population of columbines is located on a rock ridge, which averages ca. 3 m above the general level of the land, and is ca. 5 m wide. The main environmental factors present at the four sites are compared in Table 1.

*Leaf characteristics.*—Eleven characteristics of basal leaves were selected for study (Fig. 1). The choice was based partly on characteristics used to differentiate varieties of *Aquilegia canadensis* (leaflet length and whether leaves are bi- or triterminate (Munz, 1946)) and partly on the author's preliminary studies.

Length of petiole, first petiolule, second petiolule (if present) and central leaflet were measured to the nearest millimeter on pressed specimens. Data were key-punched and programs written that added length of first and second petiolule and central leaflet to give blade length; this was added to petiole length to give total leaf length. Width of the leaf was measured, and the computer calculated total length/width ratio for each leaf and petiole length/blade length ratio. Number of lobes on the terminal central leaflet and number of separate leaflets were counted. The 11 leaf characteristics were obtained from one basal leaf per plant, collected when the plants were in fruit, in mid-June to mid-July 1966.

*Reciprocal transplant experiment.*—For the reciprocal transplant experiment seeds were collected from open pollinated plants at the four study sites and planted in a greenhouse where a second generation of seeds was produced under uniform conditions. Variation in phenotype due to environmental factors was thereby eliminated (Stearns, 1960; Rowe, 1964; Nelson *et al.*, 1970). These second-generation seeds were used to establish seedlings in a greenhouse and subsequently 200 were

TABLE 1.—A comparison of the main environmental factors present at the four study sites

Sites	Substrate	Light conditions	Temperature	Moisture stress
Deerfield	thin soil	open	hot with greatest extremes	wilting widespread
Toby	shelves, pockets, and cracks in cliff	direct sunlight afternoons	moderately warm	none observed
Hawley	thin to moderately deep soil	deep shade	cool with least extremes	none observed
Holyoke	thallus outcrops	moderate shade	warm to hot	wilting plants common

used in the experiment, *i.e.*, 50 seedlings from parental stock representing each of the four original sites. Each of the four seedling lots was separated into five sets of 10 each. One set of 10 seedlings from each origin was selected at random and planted in mid-October 1966 at each of the four original study sites; a fifth set was grown in a greenhouse. Forty established columbine plants were removed from each site and replaced with transplant seedlings at random.

Because it was impossible to locate all plants in the spring of 1967 (animals or snow and ice had dislodged some labels), the actual number of plants from which data were obtained is given in Table 3.

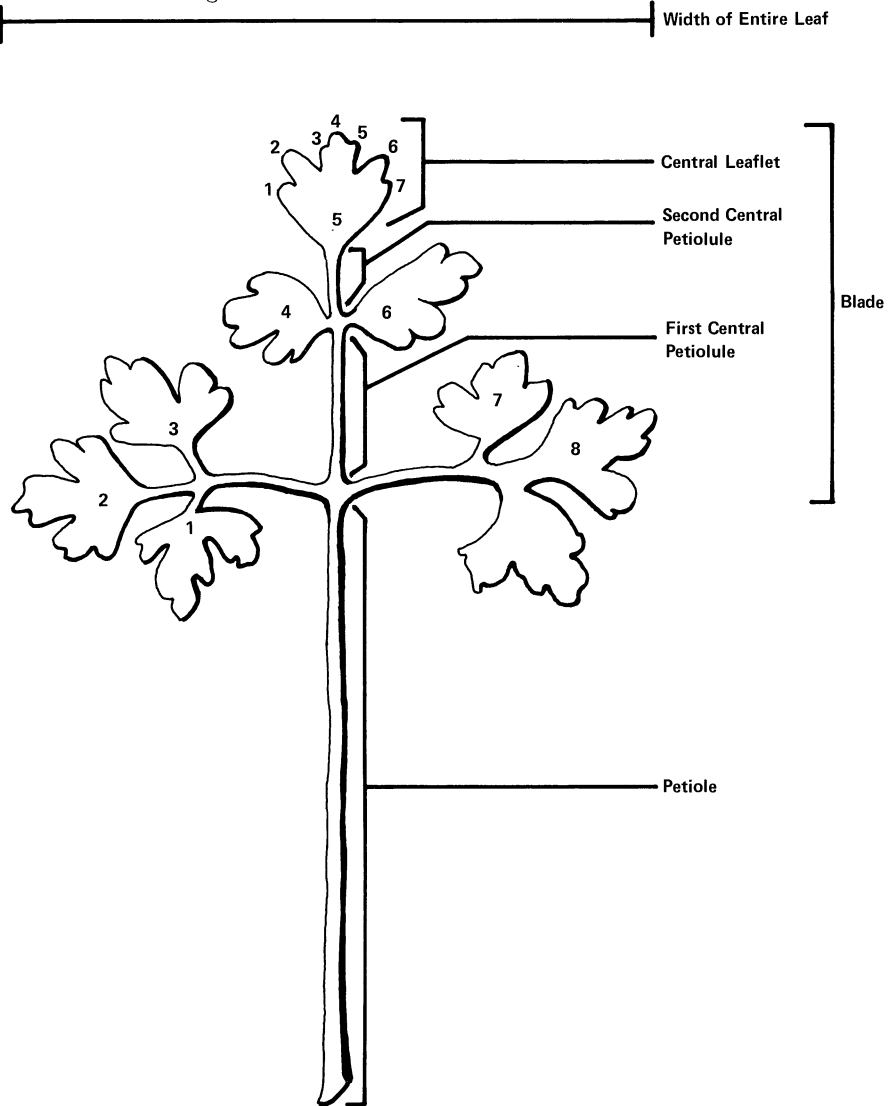


Fig. 1.—A basal leaf of *Aquilegia canadensis* L. with seven lobes on the central terminal leaflet, eight separate leaflets, width of entire leaf and the linear characteristics, petiole, first and second petiolule, central leaflet and blade lengths

## RESULTS AND DISCUSSION

*Four original populations.*—One-way analyses of variance showed the F ratio of each characteristic was significant ( $P < 0.05$ ). Therefore, even when growing within a small geographical area, columbine populations can have variable leaf morphology. These analyses give no indication of which populations were different from each other; hence, Duncan's new multiple range test (Steel and Torrie, 1960) was performed on each of the 11 leaf characteristics (Table 2). Columbines in Deerfield pasture produced smaller leaves, with few, many-lobed, small leaflets in comparison to columbines at other sites. Clearly, Deerfield plants followed what Lewis (1972) calls the universal xeromorphic rule, that plants grown in xeric sites have small, narrow, many-lobed leaves. However, Holyoke plants had a significantly greater number of leaflets than Deerfield plants, which is counter to the xeromorphic trend. A physiological explanation is provided by Gates *et al.* (1968). They showed that the temperature of a leaf measuring 1 x 1 cm or less remains close to air temperature even in semiarid regions. The Deerfield plants with a mean central leaflet length of 1.77 cm approach this size. Therefore, Deerfield plants have no physiological need for further dissection.

An examination of the linear components making up the total length of the leaves shows that Holyoke plants have longer leaves because they have longer petioles than Toby, Hawley and Deerfield plants (Table 2). The Deerfield plant's total leaf and petiole lengths were similar to the Toby and Hawley populations but had shorter blade lengths. The shorter blades of Deerfield plants were due to shorter first petiolules and central leaflets and only a third as many plants with second petiolules as Toby and Hawley plants (Table 2). The petiole/blade ratio shows that Deerfield plants had longer petioles with respect to the blades than the other populations. These results suggest that petiole and blade lengths were independently controlled or responded separately to an environmental factor(s). A similar conclusion was reached by Cook and Johnson (1968) for the leaves of *Ranunculus flammula* L.

*Reciprocal transplant studies.*—The next step was to determine the relative role environment and heredity have in controlling the observed differences in the original populations. The classical method of doing this is to grow plants from diverse sites in a common garden (Turesson, 1922). While a common garden is adequate

TABLE 2.—The population means for the characteristics having significant differences among the four sites in Western Massachusetts

Characteristics	Origins			
	Deerfield <sup>b</sup>	Mt. Toby <sup>c</sup>	Hawley St. For. <sup>b</sup>	Holyoke Range <sup>b</sup>
No. lobes in middle leaflet	16.0A	12.9AB	13.6AB	11.7B
No. separate leaflets	5.8B	6.2AB	5.8B	7.2A
Petiole length <sup>a</sup>	94.4B	105.9B	102.4B	128.0A
First central petiolule length	19.5B	28.6A	28.8A	32.0A
Second central petiolule length	0.2B	1.2AB	1.2AB	1.7A
% plants with second petiolule	12.5	38.9	37.5	50.0
Central leaflet length	17.7C	21.3B	25.1A	24.5AB
Blade length	37.3B	51.1A	55.0A	58.3A
Petiole/blade ratio	2.6A	2.1B	1.9B	2.2AB
Total leaf length	131.7B	157.1B	157.5B	186.3A
Leaf width	54.5B	69.2A	80.8A	81.3A
Length/width ratio	2.5A	2.3AB	2.1B	2.4AB

<sup>a</sup> All linear measurements expressed in millimeters. Means followed by unlike letters were significantly different at the 5% level

<sup>b</sup> Based on 24 plants

<sup>c</sup> Based on 18 plants

TABLE 3.—Population means of leaf characteristics at site grown by origin of grandparents<sup>1</sup>

Characteristic	Origin	Deer- field	Mt. Toby	Hawley St. For.	Holyoke range	Green- house
Number of lobes of middle leaflet	Deerfield	9.7B	9.5BC	8.7B	10.9BC	12.5B
	Toby	12.6B	9.5BC	10.3B	11.1BC	19.3A
	Hawley	12.7BC	10.2C	12.4BC	16.9B	17.7AB
	Holyoke	11.3BC	14.5BC	8.5BC	8.0C	12.2BC
	Mean	11.6AB	10.4AB	10.3B	12.5AB	15.3A
Number of separate leaflets in entire leaf	Deerfield	5.9AB	4.0ABC	5.3ABC	5.7AB	6.7AB
	Toby	4.7BC	3.2C	3.9C	6.7B	5.3BC
	Hawley	5.6AB	3.8C	3.9BC	5.9AB	7.8A
	Holyoke	5.3BC	5.0BC	3.0C	6.7AB	7.6AB
	Mean	5.5AB	3.7C	4.1BC	6.1A	6.9A
Petiole length	Deerfield	47.1CD	106.5BC	91.2BC	106.6BC	125.6B
	Toby	45.2CD	73.5C	98.8BC	124.8B	164.6A
	Hawley	64.1CD	66.8C	91.4C	73.4C	139.1A
	Holyoke	29.8D	109.0BC	66.0CD	74.3CD	133.2A
	Mean	47.2C	80.4BC	89.4B	98.7AB	139.5A
First central petiolule length	Deerfield	8.8D	16.0BCD	17.4CD	27.0C	39.6A
	Toby	8.0D	13.5CD	15.3CD	26.8C	43.2A
	Hawley	15.2CD	14.6C	18.7CD	18.3C	46.6A
	Holyoke	6.0D	36.5AB	11.8D	12.6CD	45.0A
	Mean	9.6C	17.3BC	15.9BC	22.8B	43.6A
Second central petiolule length	Deerfield	0.5B	0.0B	0.4B	4.5AB	5.4A
	Toby	0.0B	0.0B	0.0B	1.6B	1.8B
	Hawley	0.4B	0.0B	0.0B	0.1B	5.2A
	Holyoke	0.3B	0.0B	0.0B	0.3B	6.4A
	Mean	0.2B	0.0B	0.1B	1.8AB	4.8A
Percent of plants with a second petiolule	Deerfield	28.6	0.0	28.6	33.3	50.0
	Toby	0.0	0.0	0.0	62.5	50.0
	Hawley	14.3	0.0	0.0	11.1	50.0
	Holyoke	33.3	0.0	0.0	33.3	66.7
	Mean	14.8	0.0	6.9	34.5	48.7
Central leaflet length	Deerfield	11.4D	19.0CD	20.8C	24.2C	34.3B
	Toby	11.1D	17.5CD	19.2CD	24.2C	48.0A
	Hawley	14.0C	14.0C	20.4C	17.8C	34.8B
	Holyoke	9.0D	25.5BCE	17.2CD	15.3CD	38.3B
	Mean	11.1C	17.6BC	19.4BC	21.4B	37.5A
Blade length	Deerfield	20.9DE	35.0D	38.7D	56.1CD	79.3A
	Toby	19.1E	31.0DE	34.6D	52.7C	93.0A
	Hawley	29.7CDE	28.6CD	37.0D	36.3CD	86.6A
	Holyoke	15.3E	62.0B	29.2CD	28.3CD	89.8A
	Mean	21.5C	34.9B	36.3B	46.0B	86.8A
Petiole length by blade length ratio	Deerfield	2.4AB	3.1A	2.4AB	2.0AB	1.7BC
	Toby	2.3AB	2.5AB	3.3A	2.5AB	1.8BC
	Hawley	2.2B	2.6AB	2.4AB	2.4B	1.6BC
	Holyoke	2.1BC	1.8BC	2.2ABC	2.8B	1.5C
	Mean	2.3A	2.5A	2.7A	2.4AB	1.6B
Total leaf length	Deerfield	68.0C	141.5AC	130.0BC	162.8AB	204.9A
	Toby	64.4C	104.5BC	133.4BC	177.5AB	206.1A
	Hawley	93.9BC	95.4BC	130.7BC	109.8BC	225.7A
	Holyoke	45.1C	171.0AB	90.8BC	102.7BC	223.0A
	Mean	68.7C	115.3BC	118.9BC	144.7B	226.3A
Leaf width	Deerfield	30.8CD	50.0BC	51.5C	78.2BC	134.8A
	Toby	29.4CD	47.0C	54.6CD	85.6B	160.1A
	Hawley	41.1CD	45.2BC	57.4BC	57.8BC	135.9A
	Holyoke	21.8D	79.5C	40.8CD	41.6CD	146.1A
	Mean	31.2C	51.1BC	59.5BC	66.0B	143.3A
Length/width ratio of leaf	Deerfield	2.2AB	3.1A	2.6A	2.3AB	1.6BC
	Toby	2.2AB	2.4A	2.8A	2.2AB	1.3C
	Hawley	2.3AB	2.3AB	2.3AB	2.2AB	2.1B
	Holyoke	2.2AB	2.1AB	1.6B	2.7A	1.4BC
	Mean	2.2AB	2.4AB	2.5A	2.3AB	1.7B

for showing that discontinuous variation occurs in wide-ranging species as a consequence of adaptation to habitat (Heslop-Harrison, 1964), a closer correlation of the role of environment in the segregation of ecotypes was provided by the Carnegie group at Stanford (Clausen *et al.*, 1940, 1948) by using a series of transplant gardens. Because gardens provide plants with an advantage by eliminating competition, Porter (1966) reciprocally transplanted clones of switchgrass from one site to the other with minimum disturbance of the natural vegetation. This latter method was used in this study but since columbines are not readily cloned, sexually produced plants were utilized.

One-way analyses of variance were performed on data from the same leaf characteristics studied in the four original populations. These analyses, in which F ratios compared variability among sites grown/within sites grown, gave significant F values ( $P < 0.005$ ) for all 11 characteristics. This indicates greater variability than found in the four original populations. However, results of a multiple range test on means, by origin of each grandparent—when grown at each field site and greenhouse—showed greenhouse-grown plants had leaf characteristics most of whose means were larger than the means of plants grown at the four native sites (Table 3). These results show the environment limited expression of genetic potential for leaf size at all four origins and that greenhouse-grown plants obviously accounted for a large part of the variability. Therefore, these data were reanalyzed keeping the field and greenhouse data separate.

*Field-grown plants.*—Because the objective of this experiment was to try to separate environmentally controlled from genetically controlled leaf characteristics two-way analyses of variance were used. In one part of the analysis data are grouped by origins and where the plants were grown is disregarded, while in the other part of the analysis data are grouped by where the plants were grown regardless of their origin.

The F ratios comparing leaf characteristics by origin—disregarding where they were grown—were never significant ( $P > 0.10$ ). This indicates that none of the characteristics studied were under strong genetic control.

However, the F ratios comparing means by site where grown, disregarding origin, were highly significant ( $P < 0.005$ ) for all linear characteristics except the second petiole and the number of separate leaflets ( $P < 0.10$ ), while the number of lobes was not significant ( $P > 0.10$ ). This indicates that characteristics with significant F ratios are under strong environmental control and have a high degree of plasticity, as defined by Bradshaw (1965), *i.e.*, the amount by which a given genotype can be modified by the environment. These analyses also show the four sites had sufficiently different environments to modify leaves significantly. These comparisons further indicate that all linear characteristics except the second petiole had smaller means than the original populations at the site at which they were grown (Table 2 vs. mean rows of Table 3). These differences may be due to the experimental plants being only a year old. In spite of this, field transplants showed the same general trend as the four original populations. That is, at Holyoke, transplants had the largest means while at Deerfield they had the smallest means, for

TABLE 3.—(continued)

Number of plants grown at each site	Deerfield	7	2	7	9	10
	Toby	7	6	9	9	10
	Hawley	7	5	9	9	10
	Holyoke	6	2	5	3	10

<sup>1</sup> All linear measurements expressed in millimeters. The rows marked Mean are the means of leaf characteristics by where grown disregarding origin. Means followed by different letters when read either horizontally or vertically by characteristic (except for rows marked Mean) were significantly different at the 5% level

all linear characteristics except second petiolule (mean rows, Table 3). Analyses of the number of lobes and number of leaflets again showed no discernible pattern.

The two-way analyses of variance also showed significant F ratios ( $P < 0.05$ ) for interaction between origin and site grown for three characteristics—petiole, first petiolule and blade length. This indicates a transplant population's response to the environment of a site is influenced by the origin of that population's grandparents, *i.e.*, its genotype, with respect to these three characteristics. It does not indicate which population(s), when grown at which site(s), is causing the significant interaction.

Therefore, multiple range tests were performed keeping data for each of the 11 characteristics separate by origin of the grandparents when grown at each of the four sites. These multiple range tests showed these three characteristics had significant differences among origins at Holyoke and Toby only. That is, at Holyoke Toby plants had longer petioles than Holyoke and Hawley plants, while at Toby Holyoke plants had significantly longer blade lengths than plants from the other three origins and longer first petiolules than plants from Toby and Hawley. These analyses show Hawley plants did not have significantly different means for these three characteristics when grown at the four origins (Table 3). However, plants from the other three origins responded similarly in that these three characteristics were always smallest when grown at Deerfield but otherwise variable with no consistent pattern (Table 3). This indicates that Deerfield, Toby and Holyoke populations have a slightly different genetic makeup than the Hawley population for the control of these three characteristics (petiole, first petiolule and blade length). The Hawley population has reduced plasticity, in comparison to the three other populations, for these three characteristics. These conclusions are in agreement with those of Bradshaw (1965) and Cook and Johnson (1968) that stability of a character can vary from one genotype to another, is genetically determined, and plasticity is a property specific to individual characteristics, not to whole organs, such as a leaf. It is also of interest to note that at Deerfield (the driest site) only the Hawley plant's mean central leaflet length is greater than 1 cm while at the other three sites and in the greenhouse the mean central leaflet length of plants from all origins is always greater than 1 cm.

Even though the two-way analyses did not show significant interactions of origin-*vs.* site-grown for the other eight characteristics, multiple range tests showed there were significant differences among origins (*i.e.*, the means of one column, Table 3) at one or more sites for five characteristics: leaflet length, width, leaf length/width ratio, petiole length/blade length ratio and number of lobes. These results also indicate genetic differences among populations.

Utilizing the results of the multiple range tests and comparing means within origins when grown at each of the four sites (*i.e.*, the means of one row, Table 3) show the only characteristic without significant differences among sites where grown was petiole length/blade length. Hawley plants had significantly different means for only two characteristics, number of lobes and number of leaflets. However, for all other characteristics, one or more populations had significantly different means among sites where grown. Therefore, the Hawley population had reduced plasticity for seven characteristics in comparison with the other populations. This indicates the Hawley population either did not have genes to allow plasticity in these seven characteristics or that, if present, they were unable to express significant differences in the environments present at the four origins. Conversely, the plants that originated from Deerfield and Toby showed the same trend; this trend coincides with the results of the native plants at each of the four origins.

*Greenhouse-grown plants.*—The multiple range analyses show there were significant differences among origins for five characteristics (Table 3): leaflet length,



second petiolule length, leaf's length/width ratio and number of leaflets. These results are further indications of genetic differences among populations. Therefore, the only characteristic for which there is no evidence of genetic differences among populations is leaf length. This is another indication that the petiole and blade are under separate control.

Deerfield plants always had the smallest means, although not always significantly so, for all linear characteristics except second petiolule (Table 3). This indicates that Deerfield plants are probably genetically smaller for these linear characteristics than plants from the other three populations.

The two sites with the most extreme of the four environments (Deerfield and Hawley) each had one significantly different mean for leaf characteristics among transplants. The other two sites (Toby and Holyoke) and greenhouse-grown plants, with less extreme environments, produced plants that had 3-6 characteristics with significant differences among means from the four origins. Therefore, the environment at the extreme sites (Deerfield and Hawley) suppressed genetic differences among offspring of the four populations. However, no consistent pattern emerged in the expression of the various characteristics, suggesting that different sets of genes were operating on different characteristics in the different environments.

These results leave no doubt that meaningful genecological studies can be performed with sexually reproduced offspring.

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