

## POPULATION DIFFERENTIATION IN AN ANNUAL LEGUME: LOCAL ADAPTATION

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**Abstract.**—Studies of many plants species have demonstrated adaptive genetic differentiation to local environmental conditions. Typically these studies are conducted to evaluate adaptation to contrasting environments. As a consequence, although local adaptation has been frequently demonstrated, we have little information as to the spatial scale of adaptive evolution. We evaluated adaptive differentiation between populations of the annual legume *Chamaecrista fasciculata* using a replicated common-garden design. Study sites were established in three field locations that are home to native populations of *C. fasciculata*. Each location was planted for two years with seed from the population native to the study site (home population) and populations located six distances (0.1–2000 km) from each site (transplanted populations). Seeds were planted into the study sites with minimum disturbance to determine the scale of local adaptation, as measured by a home-site fitness advantage, for five fitness components: germination, survival, vegetative biomass, fruit production, and the number of fruit produced per seed planted (an estimate of cumulative fitness). For all characters there was little evidence for local adaptation, except at the furthest spatial scales. Patterns of adaptive differentiation were fairly consistent in two of the three sites, but varied between years. Little genetic variation was expressed at the third site. These results, combined with previous estimates of limited gene flow, suggest that metapopulation processes and temporal environmental variation act together to reduce local adaptation, except over long distances.

**Key words.**—Local adaptation, population differentiation, spatial variation, temporal variation.

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Because plants are sessile and typically have limited gene dispersal through seeds and pollen, they experience generations of selection by local environmental conditions. This selection may result in adaptive genetic differentiation if different genetically controlled character states are selected for in different populations. Such genetic differentiation is expected to enhance performance in response to local environmental conditions. Local adaptation has been documented in response to both small-scale and broad-scale environmental variation (e.g., Clausen et al. 1948; Antonovics and Bradshaw 1970; Schemske 1984; Galen et al. 1991; Jordan 1992; Sork et al. 1993; Bennington and McGraw 1995; Kindell et al. 1996). The scale of local adaptation is expected to reflect the scale of the underlying environmental heterogeneity.

The degree of local adaptation depends on a balance between local selective pressures and regional dispersal processes. Gene flow can constrain adaptation to a spatially heterogeneous environment by preventing local differentiation (Slatkin 1987). Therefore, all else being equal, a negative association is expected between dispersal and local adaptation. Only very strong selection can maintain local adaptation in the face of substantial gene movement (e.g., Antonovics and Bradshaw 1970). Gene flow may take the form of migration of seeds or pollen between environments or the extinction and subsequent recolonization of a population. Although the relationship between migration and local adaptation has been investigated (reviewed in Linhart and Grant 1996), much less is known about the contribution of metapopulation processes to local adaptation (Barton and Whitlock 1997).

As the distance separating populations increases, on average both the degree of environmental differentiation and

of genetic isolation are expected to increase. Therefore, populations are likely to be less well adapted to sites increasingly distant from their home. Despite this expectation, few studies have evaluated how patterns of local adaptation vary across a broad spatial scale. Studies typically address adaptive differentiation to ecologically distinct habitats (e.g., Clausen et al. 1948, Jordan 1992; Bennington and McGraw 1995; Nagy and Rice 1997; but see Schmitt and Gamble 1990). A survey of the patterns of local adaptation over a range of distances would provide information on the spatial scale of adaptive evolution. In turn, the spatial scale of adaptive evolution could shed light on the processes underlying intraspecific genetic differentiation. For example, similar levels of local adaptation at both small and large spatial scales would suggest that environmental heterogeneity experienced at the local scale is comparable in magnitude to that found by sampling environments over a larger area. Studies have found that patterns of local adaptation may differ among populations from different sites (e.g., Schemske 1984; Rice and Mack 1991). This lack of consistency likely reflects variation in the scale of environmental heterogeneity among sites. Alternatively, local adaptation among sites may not be expected where the temporal environmental variation within a site is greater than the spatial variation among sites.

Here we investigate the spatial scale of local adaptation in *Chamaecrista fasciculata*, an outcrossing annual with limited gene flow (Fenster 1991a,b; Fenster and Dudash 1994). The large number of populations required to determine the spatial scale of local adaptation precluded the use of a reciprocal transplant experimental design, commonly employed to evaluate local adaptation. Instead we tested for a home-site advantage in a common garden, located in the home population,

into which populations were transplanted over six distances. A superior performance of the home population relative to the transplants would suggest that observed genetic differentiation is due to adaptation to the local environment. Although other factors (e.g., drift and level of inbreeding) may also contribute to differentiation between populations, it is unlikely that these would consistently result in enhanced performance of the home-site population relative to the transplants. We used this approach to address the following questions. Is there evidence for local adaptation as measured by a home-site advantage for *C. fasciculata*? If so, what is the spatial scale of adaptive differentiation? How repeatable are patterns of adaptive differentiation in both time and space? The experiment was conducted in two years and replicated at three widely separated locations to evaluate the repeatability of results over time and space.

## MATERIALS AND METHODS

### *Study System*

*Chamaecrista fasciculata* Michx. is a self-compatible, predominantly outcrossing, annual legume of eastern North America (Irwin and Barneby 1982; Fenster 1991a, 1995). It grows in disturbed areas ranging from sites of gopher activity and recent burns in prairie habitats to roadsides and margins of agricultural fields. Dispersal through pollen and seeds is limited (Fenster 1991a), as are seed-bank life spans (Baskin and Baskin 1988; Fenster 1991b). In our study sites in Maryland, Kansas, and northern Illinois, seedlings emerge over a several-week period from mid-April through mid-May. Flowering begins in mid-July and continues through the first frost. As a consequence of variation in these dates among the study sites, Maryland plants have the longest growing season (germinating earlier and dying later) followed closely by Kansas. In Illinois the growing season is appreciably shorter, with both later germination and earlier frost (pers. obs.).

### *Study Design*

Population differentiation and local adaptation was evaluated over six spatial scales replicated in three locations. Three focal, or target, populations were chosen spanning the longitudinal distribution of *C. fasciculata* in North America. Target populations in Kansas and Illinois were located in tall-grass prairie habitats whereas the Maryland population, growing at the margin of an agricultural field, reflects typical eastern habitats. Four natural populations were selected at increasing distances from the target population in each location to use as seed sources. Target populations were reciprocally transplanted to form two longer transplant distances. In total, seven source populations were used in experiments in each site (0, 0.1, 1, 10, 100, 1000, 2000 km from the target; see Appendix). Due to its central location, Illinois had a second 1000-km transplant in lieu of a 2000-km population. Transplant performance was compared to the target (home-site) population over all distances. Population selection was based only on distance. Environmental variables (e.g., edaphic conditions, moisture regime) were not taken into consideration, but in some cases differed dramati-

cally from the target population. Seeds were collected separately by maternal family in each population.

Populations were grown for two generations under controlled conditions before planting in the field to reduce maternal effects due to variable field environments. A single individual from each of 10–15 maternal families from each population was grown in the greenhouse. Single donor crosses were made between randomly chosen pairs of individuals within each population. Pairs were reassigned each day pollinations were conducted. The same procedure was followed for a second generation with the same set of families, resulting in experimental seed that had experienced two generations of similar environmental conditions and mating patterns. Pollinations were conducted using single donors to minimize loss of genetic variation due to pollen competition.

For two years experimental seeds were planted into natural vegetation in field plots located within the target population in each state. Experimental seeds for each population were hand-scarified and planted 5 cm apart several weeks before the natural germination period in each location. Seeds were planted during a three-week period from late March to mid-April; first in Maryland, then Kansas, and last in Illinois. Native *C. fasciculata* had been removed before seed production for two years prior to planting. Because there is a limited seed bank in this species, removal of adults ensures a reduction of nonexperimental seed. Confusion between experimental and native seedlings was further reduced by planting experimental seeds adjacent to markers and by the slight scarring of the cotyledons associated with scarification. The Kansas site was burned prior to planting in 1995 and 1996, and the Illinois site was burned in 1996. Burns are a natural disturbance for these prairies and facilitate establishment and growth of *C. fasciculata* (pers. obs.). Germination of the experimental seeds coincided with *C. fasciculata*'s natural germination time at each of the three sites (pers. obs.).

The details of the planting design differed between years. In the first year, seeds were planted into 12 blocks at each site with seeds from each population grouped and groups randomly located within a block. Because germination rates were relatively high and seeds could be individually tracked with ease, the number of blocks was increased to 36 and seeds of a population were randomized within each block in the following year. In 1995, 30 seeds of each population were planted in each block, whereas 10 seeds per target population and seven per nontarget population were planted per block in the following year. In total, 2520 seeds were planted in each of the target sites in 1995 and 1872 seeds in the following year.

Fitness components were monitored on each individual over its life span. Seeds were scored for germination (appearance above ground) approximately one month after planting. Because the seeds were scarified prior to planting, there was no possibility of dormancy, and therefore germination measures early survivorship. Occasionally mortality was noticed (no seedling but evidence of germination, i.e., withered seedling, seed coat) and individuals were scored as germinated. Survivorship was determined at the onset of flowering in mid-July (1995) and just prior to fruit maturation in mid-September (both years). Results are presented for survivorship of germinated individuals through fruit maturation be-

cause survivorship over each time interval was not sufficiently variable. Although plots were fenced with poultry wire to reduce mammalian herbivory, in 1995 in Illinois there was near total herbivory by small mammals just prior to harvest, which left only stumps and stem pieces; therefore survivorship, but not harvest data, were collected. Prairie vole damage was minimized in 1996 in Illinois by burying roof flashing material around the experimental plots to a depth of 10 cm, with 15 cm extending above the soil. All surviving plants were harvested just prior to fruit maturation. Flowers were rarely observed at the harvest and fruit initiated this late in the season typically does not mature (pers. obs.). Harvested plants were dried, and aboveground vegetative biomass and total fruit number (pods plus persistent peduncles of dehisced fruit) quantified. In total, four fitness components were measured for each population in each block: percent germination, percent survivorship, and mean biomass and fruit production of surviving individuals. In addition, cumulative (lifetime) fitness, incorporating both survivorship and reproduction, was measured as the number of fruit produced per seed planted. Individuals that either did not germinate or died prior to reproduction were assigned a fitness of zero.

#### Statistical Analysis

To quantify the scale of local adaptation and genetic differentiation, fitness components of the target population were compared to those of the transplanted populations. All analyses were conducted on block means. For percent germination, biomass, fruit production, and cumulative fitness, populations were compared using analysis of variance (ANOVA) with planting location (MD, KS, IL), year (1995, 1996), transplant distance (0, 0.1, 1, 10, 100, 1000, 2000 km), and block (nested within year and planting location) as main effects (analyses not shown). For all characters there were significant two- and three-way interactions with planting location, therefore separate ANOVAs were conducted for each planting location with year, transplant distance, and block as main effects. If the effect of transplant distance on a character varied across years, that is, a significant year-by-distance interaction, separate analyses were also conducted for each year. The home population (distance = 0) was compared to each transplanted population using a Dunnett's test in each location and, if appropriate, year. Block was treated as a random effect in all analyses, all others were fixed. Vegetative biomass, flower production, and cumulative fitness were square-root transformed prior to analysis.

Survivorship from germination through harvest was not sufficiently variable to meet the assumptions of ANOVA in all sites. Therefore, survivorship of seedlings to fruit production was redefined as a dichotomous variable for each block for analysis. For example, populations planted in Maryland with survivorship  $\geq 80\%$  in a block were scored as a 1, indicating high survivorship, and those with  $< 80\%$  survivorship as a 0, or low survivorship. The value of 80% was chosen so that the ratio of high:low survivorship within each year was close to 50:50, providing sufficient variation for analysis. In Kansas the threshold was set at 93%, and it was 55% in Illinois. Differences in the threshold values reflect

variation in survivorship at the three planting locations. This categorical translation of survivorship was analyzed using log-linear categorical analysis with maximum likelihood to estimate parameters (PROC CATMOD, SAS Institute 1990). Analyses were conducted separately for each planting location and groups of three adjacent blocks were combined to increase sample size within each block, resulting in four blocks in 1995 and 12 in 1996. The initial model included distance, year, distance  $\times$  year, and block (nested within year). Following examination of results of the initial model, nonsignificant interactions were sequentially dropped to find the simplest model without significant residual variation (Knoke and Burke 1980). Model selection did not affect significance values for any terms. Multiple comparison tests are not available for categorical analysis, so transplants were compared separately to the home population using linear contrasts and an overall  $\alpha = 0.05$  was maintained by using a Bonferroni adjustment.

#### RESULTS

*Percent germination.*—In all sites, transplanted populations varied in percent germination (Fig. 1). Percent germination of the two longest-distance transplants in Kansas and the two shortest-distance transplants in Illinois was less than the home population. In Maryland the influence of transplant distance on germination percentage differed between years (distance  $\times$  year  $F_{6,276} = 3.33$ ,  $P < 0.004$ ). Whereas there were significant differences in percent germination among the transplanted populations in 1995, none differed significantly from the home population (Fig. 1). However, in 1996 germination of the home population was poor and all transplanted populations exceeded the home population mean (Fig. 1).

*Survivorship.*—There were significant differences in high survivorship among populations in Maryland and Kansas, but not Illinois (Fig. 2). In Maryland, the two populations transplanted the furthest distance showed substantially reduced high survivorship compared to the home population. A similar pattern was seen for the longest-distance transplant in Kansas with a 27% decrease in high survivorship.

*Vegetative biomass.*—There was significant variation in vegetative biomass among populations transplanted different distances in all planting locations (Fig. 3), and the effect of transplant distance in Maryland differed between years ( $F_{6,260} = 7.13$ ,  $P < 0.001$ ). Intermediate-distance transplants had the greatest biomass in Maryland and Kansas. For Maryland and Kansas, the two longest-distance transplants had the lowest vegetative biomass, whereas Kansas individuals planted in Illinois were significantly larger than the native plants (Fig. 3).

*Fruit production.*—Fruit production did not differ among populations in Illinois (Fig. 4). For both Maryland and Kansas, fruit production differences between populations were environmentally dependent and varied between years (distance  $\times$  year MD:  $F_{6,260} = 10.46$ ,  $P < 0.001$ ; KS:  $F_{6,265} = 6.11$ ,  $P < 0.001$ ). In Maryland in 1995, none of the transplanted populations differed from the home-site population, although there was variation among populations (Fig. 4). In Kansas in 1995, the 1000-km transplant outperformed the

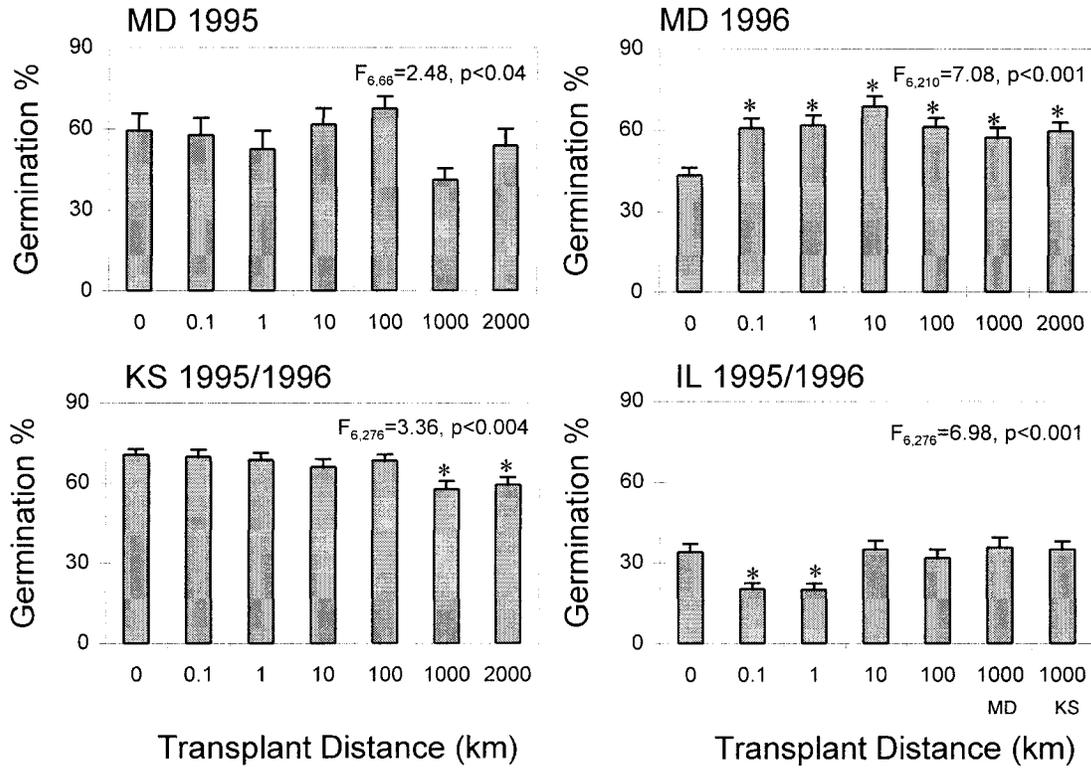


FIG. 1. Percent germination for local and transplanted *Chamaecrista fasciculata* populations to test for local adaptation. The experiment was replicated in Maryland (MD), Kansas (KS), and Illinois (IL) over two years. Populations that differ at  $P < 0.05$  from the home population are indicated by an asterisk.

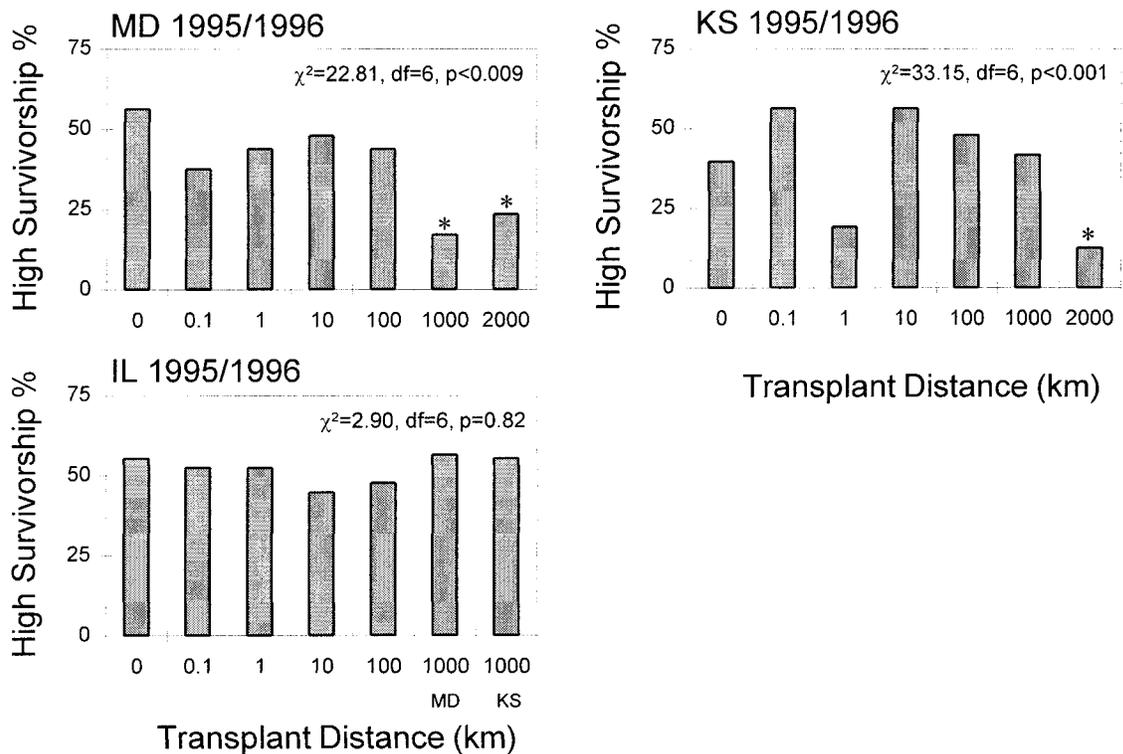


FIG. 2. Percent high survivorship (blocks with survivorship above a threshold value) for local and transplanted *Chamaecrista fasciculata* populations to test for local adaptation. The calculation of high survivorship differs among sites (see text); therefore, it is only meaningful to compare populations within each location. See Figure 1 for details.

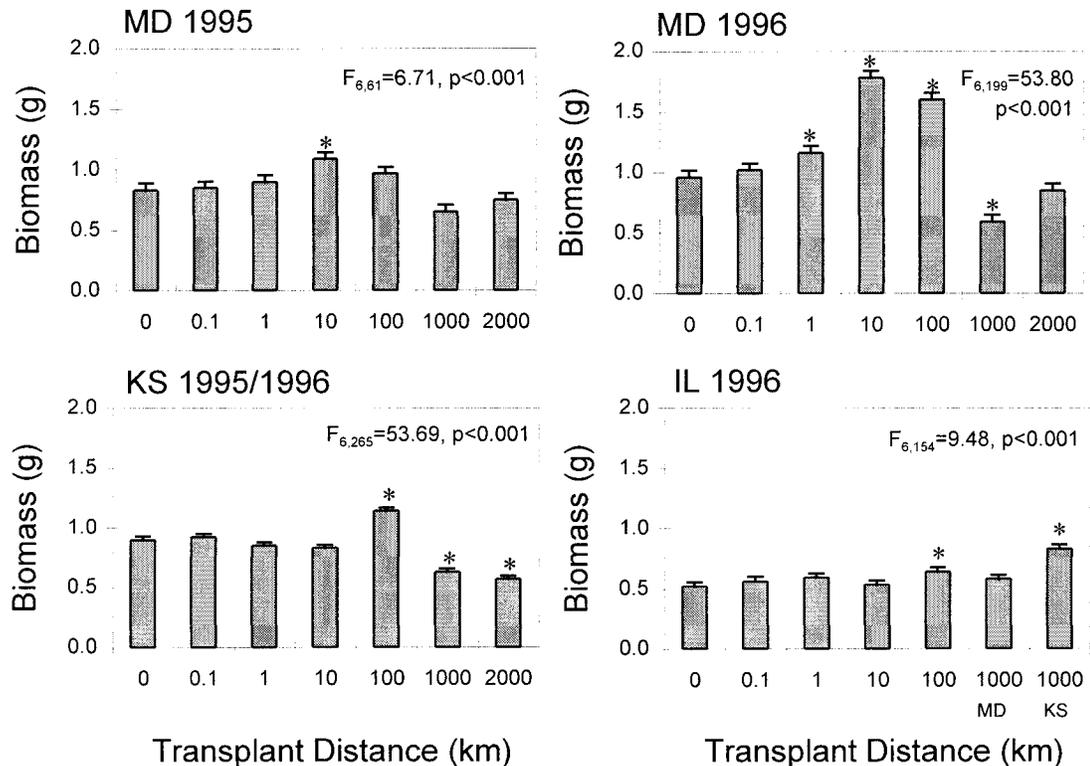


FIG. 3. Vegetative biomass for local and transplanted *Chamaecrista fasciculata* populations to test for local adaptation. All Illinois plants were eaten before harvest in 1995. Biomass is square-root transformed. See Figure 1 for details.

home population. However, in 1996 in both states, intermediate populations outperformed the home population and the longest distance transplants produced fewer fruits (Fig. 4).

#### Cumulative Fitness

In both Maryland and Kansas, fitness differences among populations depended on the year (distance  $\times$  year KS:  $F_{6,276} = 6.10$ ,  $P < 0.001$ ; MD:  $F_{6,271} = 8.25$ ,  $P < 0.001$ ). Although fitness of transplanted populations varied significantly in Kansas in 1995 and Illinois in 1996, none differed significantly from the home population (Fig. 5). For both years in Maryland and Kansas in 1996, fitness of intermediate-distance transplants exceeded the home population (not significant in Maryland 1995), whereas fitness of longer-distance transplants and two shorter-distance transplants was less than the home population (Fig. 5).

#### DISCUSSION

There was little evidence for a home-site advantage, except in comparisons to populations transplanted the furthest distances. In Maryland and Kansas, the longest-distance transplants tended to have lower germination rates (Kansas only), survivorship, vegetative biomass, fruit production, and cumulative fitness. However, this pattern was not consistent for both of the longest-distance transplants or for both years. For transplant distances of less than 1000 km, home-site advantage was limited to reduced germination in two populations in Illinois, and reduced fitness in one population in Maryland

in 1995 and one in Kansas in 1996 (all 0.1- or 1-km transplants). The two populations in which fitness was less than the home site also tended to have lower survivorship and fruit production (significant for Kansas). Patterns of genetic differentiation and local adaptation were fairly consistent across fitness components, as found in other studies (e.g., Jordan 1992; Nagy and Rice 1997; but see Van Tienderen and Van der Toorn 1991). Although there is limited local adaptation at less than 1000 km, intermediate-distance transplants sometimes outperformed the home population (biomass, fruit production, and fitness in Maryland and Kansas in 1996). In total, there is limited genetic differentiation among populations for transplant distances of less than 1000 km, and when found, it is not typically associated with reduced performance in a novel environment.

On average, genetic isolation and environmental differentiation are expected to increase as distance between populations increases. In response to these evolutionary forces, among-population differentiation and local adaptation is found in many plant species over the spatial scales studied here and smaller scales (reviewed in Linhart and Grant 1996; also Antonovics and Bradshaw 1970; Galen et al. 1991; Jordan 1992; Sork et al. 1993; Bennington and McGraw 1995); although local adaptation is not ubiquitous (e.g., Antonovics and Primack 1982; Schemske 1984; Cheplick 1988; Rapson and Wilson 1988; Rice and Mack 1991; Helenurm 1998). In *C. fasciculata* gene flow through seed and pollen is limited (Fenster 1991a), and limited gene dispersal is expected to enhance local-scale genetic differentiation. Therefore, it is surprising that there was little evidence for an association

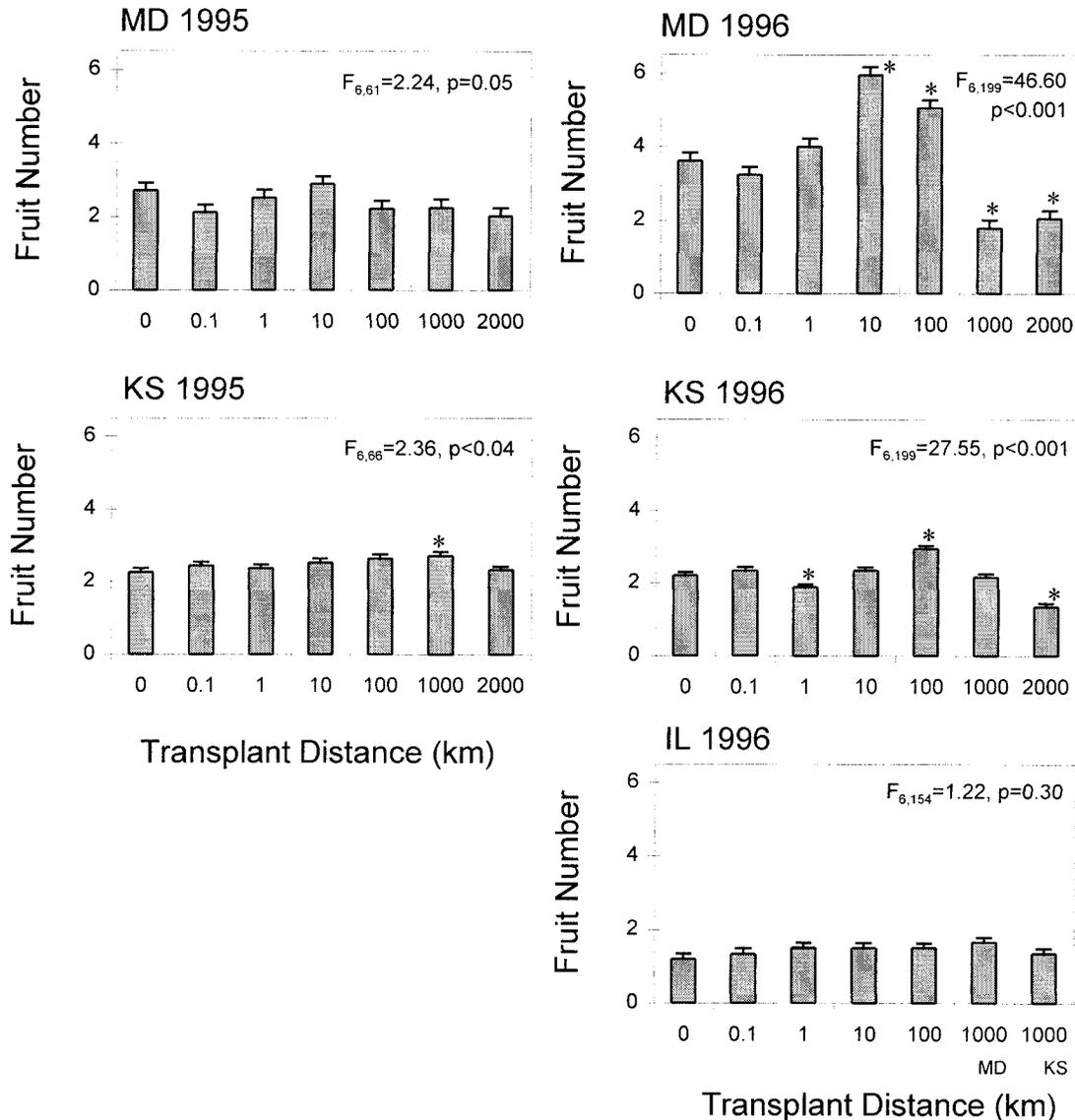


FIG. 4. Fruit production for local and transplanted *Chamaecrista fasciculata* populations to test for local adaptation. Number of fruit per plant is square-root transformed. See Figures 1 and 3 for details.

between distance of transplant and performance relative to the home-site population for transplants less than 1000 km. It is possible that smaller-scale local adaptation was not found because the spatial scale evaluated here was too large and local adaptation, like gene flow, is occurring at the within-population level. However, it seems unlikely that local adaptation would be found at spatial scales of less than 100 m, while distances above that but less than 1000 km were adaptively equivalent. Alternatively, smaller-scale local adaptation may not have been found because rare long-distance pollen dispersal, which may have been missed when gene flow was evaluated, effectively homogenizes populations up to 10 km apart.

However, it is more likely that local adaptation does not follow an isolation-by-distance model due to the genetic processes that underlie population establishment as well as population differentiation. In early successional or colonizing

plant species such as *C. fasciculata*, metapopulation processes may influence both population establishment and differentiation. High extinction and colonization rates associated with metapopulation dynamics may limit local adaptation because populations do not have sufficient time to adapt to local conditions (Barton and Whitlock 1997). In addition, small or variable population sizes may limit local adaptation because drift overwhelms selection, thus limiting genetic variation and recombination potential (Hill and Robertson 1966; Parker 1991). Limited within population genetic variation for life-history characters has been documented for *C. fasciculata* (Kelley 1993). Several other colonizing or early successional species also demonstrate limited local adaptation (e.g., Cheplick 1988; Rice and Mack 1991; Scheiner 1998).

The contribution of metapopulation processes to the evolutionary dynamics of *C. fasciculata* suggests that populations may not be adapted to particular sites but rather to a range

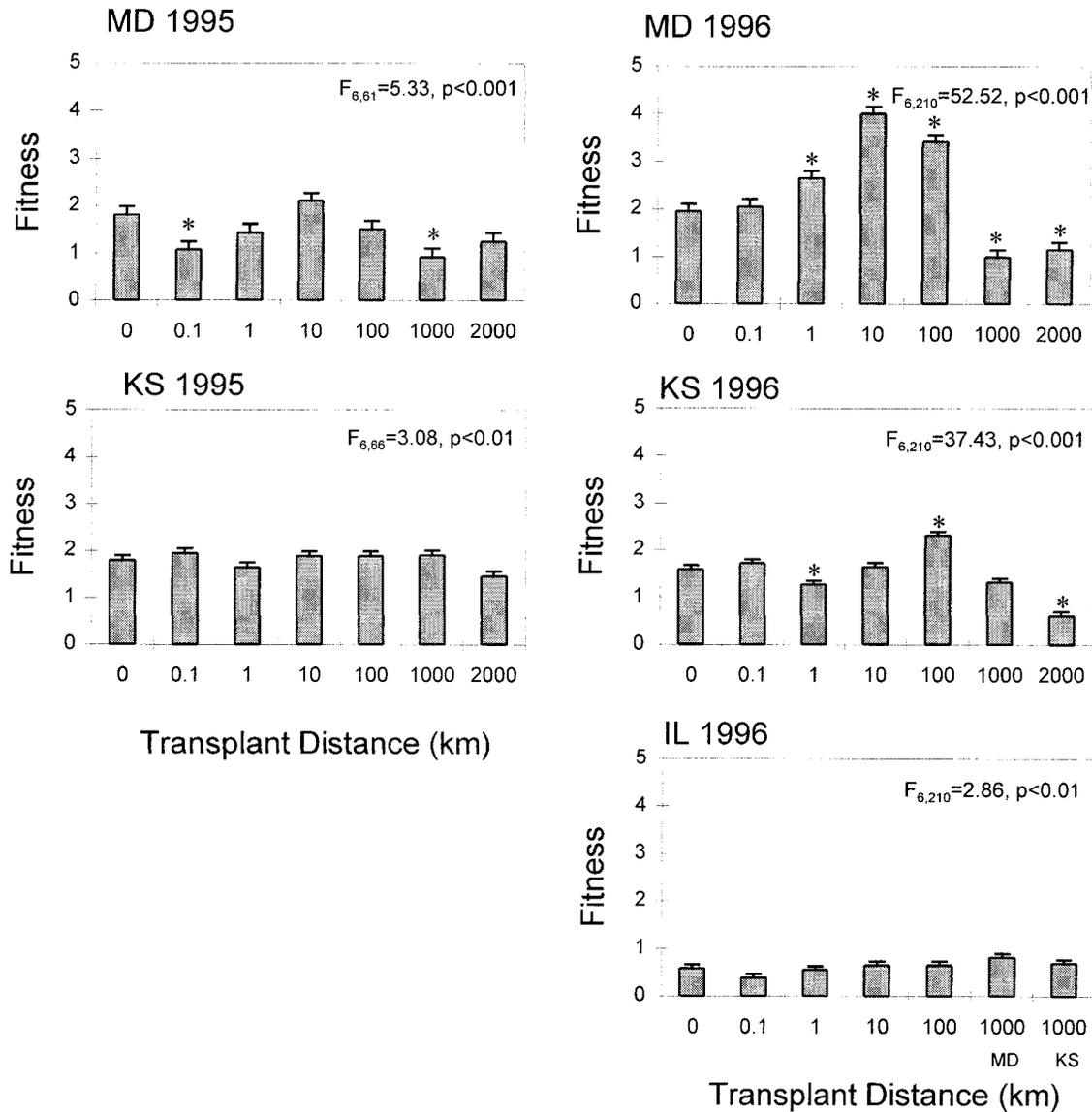


FIG. 5. Cumulative fitness (fruit produced/seed planted) for local and transplanted *Chamaecrista fasciculata* populations to test for local adaptation. Fitness is square-root transformed. See Figures 1 and 3 for details.

of environments determined by the scale of colonization. *Chamaecrista fasciculata* appears to be highly plastic and can adjust to the environmental variation found within a 100-km area. However, individuals are less able to adjust to the environmental extremes represented by the long-distance transplants. Appropriate plastic response to a range of environmental conditions is likely to be selectively favored in this species of disturbed habitats that experiences frequent population turnover. For example, prairie populations often explode in size following fires and then dwindle with an increasing number of years since burning (pers. obs.). In this way, metapopulation processes may select for plastic adjustment to a range of environments (Scheiner 1998). If lack of differentiation for fitness components between populations reflects phenotypic plasticity, the same phenotype expressed in different populations is likely to indicate phenotypic convergence rather than genetic identity. Crosses between pop-

ulations can be used to evaluate whether similar phenotypes are due to the same underlying genetic structure (Fenster and Galloway 2000).

Although the expression of genetic differentiation between *C. fasciculata* populations is influenced by the environment, patterns of adaptive differentiation are fairly consistent across locations. Maryland and Kansas both show reduced performance in long-distance transplants, enhanced performance of intermediate-distance transplants, and performance similar to the home population for the shortest-distance transplants. The Illinois site is the exception to this pattern. The environment in Illinois was the least favorable for *C. fasciculata*; germination, survivorship, vegetative biomass, and fruit production were all lower in Illinois than either of the other sites. There was little expression of genetic variation among populations in Illinois. Although there were significant differences between the target populations for fitness components when

planted in Maryland and Kansas, the same populations rarely differed when plants were grown in Illinois. Reduced expression of genetic effects in this site may be associated with the relatively stressful growing environment (e.g., Mazer and Schick 1991; Bennington and McGraw 1996; Merila 1997).

Adaptive differentiation for fitness components also shows temporal variation. Differentiation among populations varied among years for fruit production and fitness in Kansas and all characters except survivorship in Maryland. For characters in which population genetic variation differed between years, there tended to be greater among-population variation in 1996 than in 1995. Temporal variation in population differentiation implies that selection for local adaptation varies over time. In addition, temporal variation cautions against drawing conclusions from short-term studies. Because local adaptation is only expected when the scale of spatial variation in the environment exceeds that of temporal variation within a region, temporal variability, in combination with population turnover, may enhance the role of phenotypic plasticity as a response to local environmental variation.

In summary, evaluating local adaptation over a range of spatial scales in *C. fasciculata* has contributed to a new understanding of the processes underlying intraspecific differentiation in this species. If the study had only been conducted over spatial scales relevant to the previously measured gene dispersal, there would be no evidence for local adaptation. The finding of local adaptation predominantly at larger scales served as a basis for the development of a hypothesis about contribution of metapopulation dynamics to intraspecific variation in this system. Although additional research is needed to fully evaluate this hypothesis, it is supported by our findings of genetic differentiation between phenotypically similar populations reported in Fenster and Galloway (2000).

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APPENDIX

Locations of *Chamaecrista fasciculata* populations sampled. Populations were chosen solely based on distance from target population (distance = 0) within each state; 1000- and 2000-km distances are transplants between target populations. MD, Maryland; KS, Kansas; IL, Illinois.

State	Distance (km)	Location
MD	0	West side of fruit tree quarantine field, near Powder Mill and Spring Valley Rds., USDA Beltsville
	0.1	East side of fruit tree quarantine field, near Powder Mill and Spring Valley Rds., USDA Beltsville
	1	Roadside, Spring Valley Rd., USDA Beltsville
	10	Roadside at junction of E–W Hwy 410 and Hwy 295
	100	Margin of agricultural field, Smithsonian Edgewater site, Edgewater
KS	0	Tall-grass prairie near headquarters, Konza Prairie Research Natural Area (KPRNA), Manhattan
	0.1	Tall-grass prairie near headquarters, KPRNA
	1	Tall-grass prairie near entrance of KPRNA
	10	Tall-grass prairie 10 km from headquarters, KPRNA
	100	Tall-grass prairie on Rockefeller tract, near Lawrence
IL	0	Tall-grass prairie at Gooselake Prairie, Morris
	0.1	Tall-grass prairie at Gooselake Prairie, Morris
	1	Tall-grass prairie at Gooselake Prairie, Morris
	10	Tall-grass sand prairie at Braidwood Prairie, Braidwood
	100	Tall-grass sand prairie at Zander Woods, Zander