Evolutionary Ecology Research, 2004, **6**: 103–114

Local adaptation within a population of *Hydrocotyle bonariensis*

Tiffany M. Knight* and Thomas E. Miller

Department of Biological Science, Florida State University, Tallahassee,
FL 32306-1100, USA

ABSTRACT

Local adaptation may occur when selection for heritable traits differs from environment to environment and gene flow among environments is restricted. In this study, we used reciprocal transplants to explore both the existence and possible causes of local adaptation in the clonal plant *Hydrocotyle bonariensis* at high and low elevations of sand dunes on St. George Island, Florida. Individuals found in high dune areas had substantially longer and more internodes and produced larger leaves than those from low dune areas. Reciprocal transplants used 10 genets from high dunes and 10 from low dunes. Greenhouse-grown, replicate plants from each genet were transplanted to high and low dune sites in the field, with and without the natural vegetation removed. The resulting plant growth was consistent with patterns of local adaptation: plants from high sites grew better in high sites than did plants from low sites and vice versa. A significant source × site interaction was found for final below-ground, but not above-ground, biomass. In plots with surrounding vegetation removed, plants from high and low dunes performed similarly in both environments, suggesting that local adaptation was related to interactions with other plants at each dune height. Small-scale local adaptation may be more likely in clonal plants undergoing little gene flow in spatially heterogeneous environments.

Keywords: clonal reproduction, *Hydrocotyle bonariensis*, local adaptation, reciprocal transplant, within-population genetic differentiation.

INTRODUCTION

The genotypes found in any particular environment represent a dynamic balance between forces that increase genetic diversity, primarily gene flow and mutation, and those that reduce it, including directional selection and drift. Where selection is intense relative to gene flow, local adaptation can occur such that genotypes have a relatively high fitness in the environment of origin but lower fitness in other environments as a result of trade-offs for particular environmental conditions (see, for example, Silander, 1985; Platenkamp, 1990;

---

* Address all correspondence to Tiffany Knight, Department of Biology, Washington University, Box 1137, St. Louis, MO 63130, USA. e-mail: tknight@biology2.wustl.edu

Miller and Fowler, 1994; Kindell *et al.*, 1996). Minimum requirements for local adaptation therefore include selection for heritable traits and sufficient environmental separation that gene flow does not overwhelm selection (Antonovics *et al.*, 1984; Bradshaw, 1984; Venable, 1984).

Local adaptation can be demonstrated using reciprocal transplant experiments, with appropriate caution about 'carry-over' effects of the maternal or original environment (e.g. Stratton, 1989). Such experiments have frequently been used to demonstrate local adaptation for species grown in widely separated populations (see review by Bradshaw, 1984). In such cases, the populations may experience very different environmental conditions with negligible gene flow between populations. On smaller scales, however, where gene flow may be significant, local adaptation may result only if the strength of selection overwhelms such gene flow (see review by Linhart and Grant, 1996). Very few studies have adequately tested for local adaptation at the within-population scale. A few studies have demonstrated local adaptation within a population to different levels of herbivory (Schemske, 1984; Sork *et al.*, 1993) and to the identity of neighbouring vegetation (Turkington and Harper 1979). Other studies have found that local adaptation has not occurred, possibly due to significant gene flow within the population (Stanton and Galen, 1997) or low intensity of selection (Cheplick and White, 2002).

Despite our expectations about gene flow and selection in different types of species and habitats, we do not know whether general patterns exist in small-scale local adaptation because too few studies have been conducted (Linhart and Grant, 1996). For example, we might predict that clonal plants have a higher propensity for small-scale local adaptation because (1) vegetative reproduction should restrict gene flow and (2) vegetative growth may allow the preferential placement of ramets in locally adaptive sites (i.e. by decreasing internode distance between ramets and/or by increasing the branching of internodes; Sutherland and Stillman, 1988). Alternatively, clonal plants may be less likely to exhibit local adaptation to recent environmental conditions because the long-lived genets are adapted to past environmental conditions (Callaghan *et al.*, 1996). Knowledge of gene flow and selection at different spatial scales should provide us with a greater understanding of morphological variation and genetic diversity within populations.

We tested for local adaptation within a dune population of *Hydrocotyle bonariensis* Lam. (Apiaceae) on a barrier island in northern Florida. Although individuals may produce flowers and outcross, most reproduction appears to occur though vegetative growth of stolons, a very local process. The sand dunes create a habitat with tremendous heterogeneity at small spatial scales (< 5 m). The highest locations on the dunes are characterized by dry, open conditions that support little vegetation. The often-flooded low dune locations support a different species composition as well as a denser vegetative cover (see details below) (Johnson and Barbour, 1990; Seliskar, 1990).

We first asked whether *H. bonariensis* individuals that naturally occur on high and low dunes differ phenotypically. Differences in morphology between these two sites could be the result of phenotypic plasticity or local adaptation. A reciprocal transplant experiment was then used to address the following questions: (1) Are the patterns of growth of individuals reciprocally transplanted between high and low dune sites consistent with local adaptation? (2) Is the presence of competing neighbours a possible causal mechanism for local adaptation? (3) What morphological changes are correlated with location of origin or with transplant location?

METHODS

Hydrocotyle bonariensis is a clonal plant common in many disturbed environments in the southeastern United States (Evans, 1992). It has a simple modular growth form: plants consist of long stolons (runners), from which roots, leaves and inflorescences are produced at nodes. Usually a single leaf is produced at each node, and nodes are separated by 10–30 cm of tough stolon buried at a depth of 2–5 cm. Internode length is measured as the distance between nodes, although the nodes may or may not have leaves or flowers at any particular time. Nodes can act as physiologically independent units and can be considered ramets (Evans and Whitney, 1992). A genet of *H. bonariensis* generates new ramets vegetatively through growth and branching of stolon meristems at nodes. This species is gynodioecious and an inflorescence can be produced opposite the leaf of a node during new ramet development. Numerous flowers are produced on the compound inflorescence structure, and each flower potentially produces a single schizocarp containing two seeds (Evans, 1992). Virtually all the plants in the study area were hermaphrodites: only areas closer to the shore contain a higher frequency of male-sterile plants (personal observation; J. Evans, personal communication).

Several studies have investigated plasticity and growth patterns in *H. bonariensis* (Evans, 1988, 1991). Evans (1992) demonstrated that individuals maintain taller petioles and larger leaves when shaded by surrounding vegetation. Resource sharing among interconnected ramets allows plants to grow through unfavourable, highly saline conditions (Evans and Whitney, 1992). Clones also have the potential to place ramets selectively in good patches of a heterogeneous environment by branching when favourable locations are encountered (Evans and Cain, 1995). All previous studies on *H. bonariensis* involved manipulation of ramets of single genets: differences in growth among different genets have not been investigated.

The field research was conducted on the sand dunes in St. George State Park on St. George Island (29°46′N, 84°42′W), a barrier island in the Gulf of Mexico (Franklin County, Florida). The habitat consists of a series of dunes approximately 1.0–1.5 m high, separated by low areas or slacks. The distance between dunes is approximately 6–10 m. Vegetation high on the dune tops and sides is sparse (generally < 20% cover) and dominated by drought-resistant species such as *Uniola paniculata* (Poaceae), *Ipomoea imperati* (Convolvulaceae), *Heterotheca subaxillaris* (Asteraceae), *Physalis viscose* (Solanaceae) and *Ipomopsis rubra* (Polemoniaceae). Vegetation low on the dunes is much taller and denser (> 70% cover) and includes patches of *U. paniculata*, *Schizachyrium maritimum* (Poaceae), *Juncus roemerianus* (Juncaceae) and *Sabatia stellaris* (Gentianaceae) (Johnson and Barbour, 1990).

To document morphological variation in *H. bonariensis* with dune height, we collected one haphazardly chosen genet from each of 10 high dune sites and from each of 10 low dune sites. Genets were separated by at least 5 m. For each genet, mean leaf width, petiole length, internode length and the total number of nodes were determined. We used *t*-tests to compare morphologies of genets from high and low dune sources.

To investigate patterns of local adaptation using reciprocal transplants, we removed 10 genets, each including at least 16 nodes, from high dunes and 10 from low dunes on 29 July 1995. All collected plants were separated by more than 5 m, and no more than two plants were taken from any dune location: we assumed that each plant represented a unique genotype. Each genet was cut into 16 ramets of a single node each, and each ramet was planted in a 15-cm pot containing a 1 : 1 mixture of Metro-mix and island sand. These plants were maintained in a greenhouse in Tallahassee, Florida, for 5 weeks to minimize possible carry-over effects from growth in habitats of different quality. Plants were not fertilized but were watered as needed. Ramets of one low genotype failed to grow in the greenhouse: this genotype was eliminated from the field experiment.

Non-genetic carry-over effects create a problem for all transplant experiments because they may persist for long periods (Stratton, 1989; but see Billington *et al.*, 1990) and are therefore difficult to separate from genetic differences among families. By the time the plants were transplanted to the field, each plant consisted mostly of new ramets produced in the greenhouse. All plants started with 0–1 leaves and grew an average of 4–5 leaves during the 5-week greenhouse period. This growth period in the greenhouse resulted in plants of similar appearance.

Four haphazardly located replicates, each containing two high plots and two low plots (each 1 m^2), were set up on St. George Island 2 months before planting. Vegetation was manually removed from a randomly chosen high and low plot at each location. Vegetation removals were maintained during the tenure of the field experiment. The native vegetation in the remaining plots was disturbed as little as possible. On 2 September, the clones from the greenhouse were transplanted into the field plots. In each plot, one representative of each genotype was planted at a randomly selected point in a 4 × 5 array.

Leaf width and length of all ramets were determined in the field on 11 November. All plants were harvested from the field on 2 December. Although *H. bonariensis* appears to produce new growth throughout the year, a significant amount of growth occurs after late summer and early autumn rains (personal observation). At harvest, several traits were quantified for each plant: survival and, for survivors, number of nodes, mean internode length, number of leaves and petiole length. Plants were divided into above- and below-ground parts, dried at 60°C for 48 h and then weighed.

Survival data were first analysed by logistic regression with main effects of source (originating from high or low dune), site (transplanted back to high or low dune), vegetation treatment (control or removed) and all possible interactions. Significance of effects was determined by likelihood ratio tests. There was a significant site × vegetation interaction; therefore, we applied logistic regressions separately to each vegetation treatment (control, vegetation removed) and examined the effects of site, source and site × source on survival.

Total, above-ground and below-ground biomasses of plants were analysed with a mixed-model analysis of variance with effects of source, clone (i.e. genet) nested within source (10 clones per source), site, source × site, and genotype nested within source × site. Separate analyses were conducted for plots with natural vegetation and plots from which natural vegetation was removed. Only clones with survivors in both low and high plots were included. Results showing transplants grew better in the habitat of origin than transplants from the other site, together with a significant source × site interaction, would provide evidence for local adaptation.

Evidence of local adaptation in these plants would permit comparison to the same analyses conducted on plants grown without competing vegetation. If interaction with surrounding neighbours was a contributing factor to any pattern of local adaptation, then removal of neighbours should eliminate or reduce patterns of local adaptation (Kindell *et al.*, 1996).

To determine the contribution of genotype, source, site, vegetation and their interactions in determining plant characters (internode distance, number of nodes and leaves, leaf width, petiole height), we analysed each character with a mixed-model analysis of variance similar to that used to test for local adaptation, except that the vegetation treatment was included as a main effect and with appropriate interactions. Biomass data and number of leaves were log transformed before any statistical analysis.

RESULTS

The growth form of naturally occurring plants from high on the dune was very different from that of plants growing low on the dune (Table 1). Plants high on the dune were much longer, primarily because they contained many more nodes, although internode distances were also longer. It is unknown whether these differences are due to height-specific growth rates, because the rate at which internodes rot, separating ramets within genets, is not known. Rotted tips at the ends of runners were much more common on plants from low areas. High dune plants also had significantly wider leaves and longer petioles than did low dune plants (Table 1).

Approximately 65% of the plants in the reciprocal transplant experiment survived in the vegetated plots (Table 2), and none flowered. Vegetation treatment and site showed a significant interaction; survival was much higher in the unvegetated plots than in the vegetated plots at the high site. Separate analyses of data from vegetated and unvegetated treatments revealed that survival was significantly greater at high than at low dune sites (vegetation intact, $\chi^2 = 5.94$, $P = 0.015$; vegetation removed, $\chi^2 = 6.84$, $P = 0.009$). Source and the source × site interaction produced no significant effect in either case.

Table 1. Morphological measures of *Hydrocotyle bonariensis* clones collected from low and high dune locations on St. George Island (mean ± standard error)

	Low	High
Mean number of nodes	11.33 ± 3.52	164.33 ± 31.1
Mean internode distance (cm)	4.28 ± 0.62	7.41 ± 0.51
Mean leaf width (cm)	2.83 ± 0.32	4.60 ± 0.32
Mean petiole length (cm)	4.67 ± 0.77	6.88 ± 0.30

Note: Features from low and high sources are significantly different in all cases ($P < 0.001$).

Table 2. Mean survival of *Hydrocotyle bonariensis* reciprocal transplants from low and high dunes grown with and without surrounding vegetation on St. George Island

	Low site		High site	
Source	Vegetation	No vegetation	Vegetation	No vegetation
Low dune	0.528	0.611	0.750	0.917
High dune	0.625	0.625	0.775	0.625

In the reciprocal transplant experiment with intact vegetation, clones differed significantly in total biomass, as did plants grown at different dune heights (Table 3). Plants grown at high dune sites were, on average, 50% larger in total biomass than those at low dune sites (Fig. 1). Although plants from the low site demonstrated fairly similar growth when transplanted to high and low sites, plants from high sites grew twice as large when transplanted to their site of origin than to the low site. While there was no significant source effect, the source × site interaction was marginally significant: plants from each source grew better at their sites of origin than did plants from the other habitat (Fig. 1), consistent with local adaptation.

When the vegetation was removed, site effects on total biomass were still significant: plants grown high on the dunes had significantly greater total biomass than those grown on the low dunes (Table 3, Fig. 1). Effects of both clone and the source × site interaction were no longer significant, however, suggesting that the presence of vegetation contributes to local adaptation.

Above- and below-ground biomass of transplants at vegetated sites showed different patterns of growth. The largest proportion of the total biomass was below ground in all treatments (Fig. 1). Source had no significant effect on above- or below-ground biomass, but clone-within-source effects were significant for both (Table 3). Site effects were significant for below-ground biomass: plants grown high on the dune had up to three times

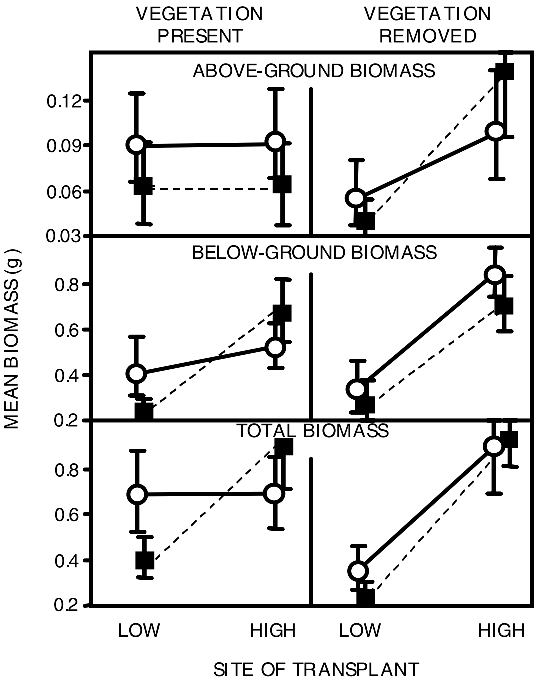

Fig. 1. Total, above-ground and below-ground biomass of *Hydrocotyle bonariensis* grown at high and low sites and from high and low source populations, with and without surrounding vegetation (mean ± standard error). Open circles represent plants of low dune source; closed squares represent plants of high dune source. Biomasses represent back-transformations of means from log-transformed data. Note difference in scale for above-ground biomass.

Table 3. Results of analysis of variance of above-ground and below-ground biomass of *Hydrocotyle bonariensis* grown in a reciprocal transplant design from high and low dune sources and at high and low dune sites

	MS	d.f.	*F*	*P*
Plots with intact vegetation				
Total biomass				
Source	0.0012	1	0.0030	0.948
Clone within source	0.4372	16	3.5387	0.008
Site	0.6394	1	4.5665	0.042
Source × site	0.5693	1	4.0655	0.054
Site × clone within source	0.1235	16	0.4768	0.943
Error		63		
Above-ground biomass				
Source	0.0021	1	0.0043	0.948
Clone within source	0.5097	16	3.0812	0.015
Site	0.0228	1	0.1198	0.732
Source × site	0.0119	1	0.0624	0.805
Site × clone within source	0.1654	16	0.4519	0.955
Error		63		
Below-ground biomass				
Source	0.0043	1	0.0041	0.950
Clone within source	1.1146	16	3.9448	0.005
Site	3.4736	1	10.8914	0.003
Source × site	1.7127	1	5.3701	0.029
Site × clone within source	0.2825	16	0.4855	0.938
Error		63		
Plots with vegetation removed				
Total biomass				
Source	0.1575	1	0.6194	0.440
Clone within source	0.2543	15	1.0816	0.441
Site	3.3159	1	13.8972	0.001
Source × site	0.0985	1	0.4129	0.527
Site × clone within source	0.2351	15	0.9242	0.547
Error		60		
Above-ground biomass				
Source	0.3141	1	0.1842	0.672
Clone within source	1.7714	15	1.1977	0.366
Site	6.6034	1	4.5064	0.046
Source × site	2.2000	1	1.5011	0.234
Site × clone within source	1.4790	15	1.0536	0.423
Error		60		
Below-ground biomass				
Source	1.3200	1	1.6145	0.218
Clone within source	0.8275	15	0.8507	0.621
Site	9.3379	1	9.9709	0.005
Source × site	0.0194	1	0.0207	0.887
Site × clone within source	0.9727	15	1.2583	0.277
Error		60		

Note: Separate analyses were conducted for plots with and without vegetation. Data were log-transformed before analyses.

greater biomass than those grown low on the dune. Interestingly, the source × site interaction was significant for the below-ground, but not above-ground, biomass. The above-ground biomasses of transplanted individuals from high and low sources were not significantly affected by different sites (Fig. 1, vegetation intact), but the below-ground biomasses demonstrated a pattern consistent with local adaptation: plants from each source were larger when grown at their sites of origin.

When the vegetation was removed, a very different pattern emerged (Fig. 1, no vegetation). Both above- and below-ground biomass were significantly affected by site differences – much more below-ground biomass was found at high sites – but no significant effects of clone or site × source were noted (Table 3). Removing vegetation appeared to increase the growth of plants high on the dune, suggesting some sort of competitive release.

Plant morphology was particularly affected by the dune height at which plants were grown: plants transplanted to high sites produced longer internodes and petioles and larger leaves but not more leaves (Table 4, Fig. 2). There was a marginally significant effect of vegetation on petiole length: generally, taller petioles were produced when surrounding vegetation was present (Fig. 2). The significant three-way interaction for internode length among site, source and vegetation appears to be due to a strong effect of vegetation on transplants from the high dune source when they were planted back into the high site (Fig. 2). Plants from high sites showed a greater difference in morphology than did those at low sites (Table 4): internode length and leaf width were much more variable for plants from high sites (Fig. 2).

DISCUSSION

On St. George Island, the morphology of *Hydrocotyle bonariensis* varied dramatically with dune height. Plants from low dune areas had many fewer nodes, shorter internode distances, smaller leaves and shorter petioles than those from high dune areas (Table 1). The reciprocal

Table 4. *F*-values from mixed-model analyses of variance on morphological features of *Hydrocotyle bonariensis* in reciprocal transplants

Effect	d.f.	Number of leaves	Internode length	Petiole length	Leaf width
Source	1	0.06	0.03	1.99	0.26
Clone (source)	17	4.51	1.15	0.72	0.69
Site	1	0.95	19.45***	25.00***	10.75**
Vegetation	1	1.86	0.99	3.55$^+$	1.51
Site × vegetation	1	0.56	0.67	1.28	1.49
Source × site	1	0.03	3.43$^+$	1.65	4.00*
Source × vegetation	1	0.15	0.28	1.54	0.30
Site × clone (source)	17	0.54	1.32	0.98	1.36
Vegetation × clone (source)	17	0.71	0.65	1.75	0.83
Site × source × vegetation	1	0.07	3.96*	0.03	0.88
Site × vegetation × clone (source)	17	1.21	0.74	0.68	0.96
Error	142				

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; $^+P < 0.07$.

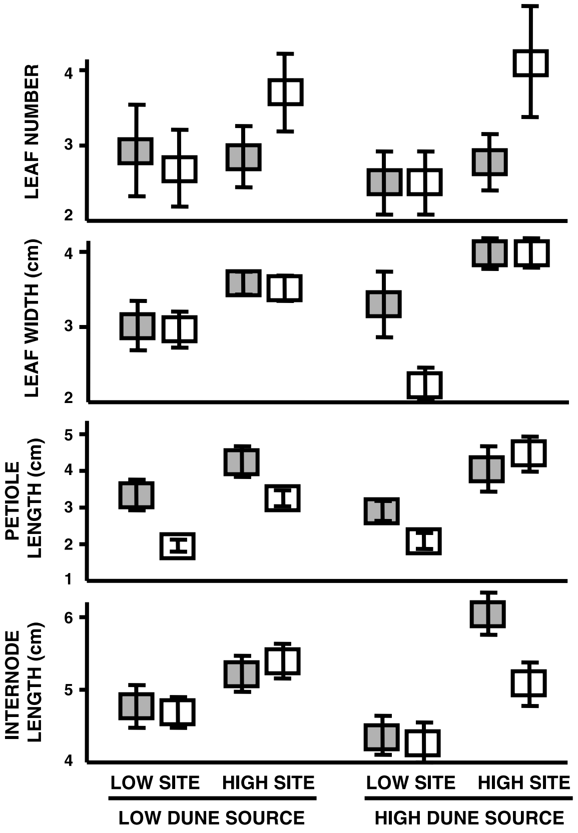

Fig. 2. Mean leaf number, leaf width, petiole length and internode length (with standard errors) of *Hydrocotyle bonariensis* grown at high and low sites and from high and low source populations, with and without surrounding vegetation. Shaded boxes represent values from plants grown with surrounding vegetation; open boxes represent values from plants grown without surrounding vegetation. Values for leaf number represent back-transformations of means from log-transformed data.

transplant experiment demonstrated that this morphology reflects both environmental and genetic differences between plants from high and low dune sites. Source × site interactions were consistent with local adaptation: when grown at high dune sites, plants originating from high dune sites outperformed plants from low dune sites and vice versa (Table 3). Such patterns could have arisen either from selective mortality at each site or from 'foraging' movement of these clonal plants. There were also significant differences among clones from the same site.

The greater biomass at site of origin appears to be related to interactions with neighbouring plants: no such effect was observed when vegetation was removed (Fig. 1). Thus, source × site interactions may have been due to competition for light or soil resources. However, it is surprising that more of a response to vegetation removal was observed on the high dunes (with < 20% vegetation cover) than on low dunes (> 70% cover). Both of these light and soil resources vary with dune height: light levels at the soil surface decrease with increasing vegetation density from high to low dune areas, whereas soil moisture remains low at high sites throughout the year but are seasonally high at low sites (T.E. Miller, in prep.).

Although consistent with adaptation to small-scale differences in environments, increased fitness at the site of origin could also be due to residual effects of the maternal environment (Stratton, 1989) or other types of carry-over effects, such as interactions with local microorganisms (Turkington and Mehrhoff, 1990). Differences in environmental carry-over effects between plants from 'high-quality' and 'low-quality' environments should, however, cause the plants from one source to do consistently best in both environments. Instead, we found that plants from the apparently harsher low environment had higher fitness when transplanted back to the low environment than did the plants from the more benign high environment. We argue that such a pattern is more consistent with local adaptation than with carry-over effects, although such effects cannot be entirely ruled out.

Variation in plant morphology may be the key to understanding the mechanism behind local adaptation in *H. bonariensis*. Below-ground biomass showed a source × site interaction, whereas above-ground biomass demonstrated no such pattern (Table 3). Both above-ground traits (leaf characters) and below-ground traits (internode distances) were affected by source × site interactions, but only internode distance exhibited a significant source × site × vegetation effect. This result suggests that plants originating from high and low dune areas differ in some aspect of the allocation of biomass to below-ground parts that allows plants to perform best at their sites of origin. This allocation difference in the stolons may be related to storage functions or to vegetative growth differences, including resource foraging (Evans, 1992; Evans and Cain, 1995).

Clonal plant growth in a coastal dune system may represent an ideal situation for the evolution of small-scale local adaptation. The environmental cline between high and low environments is extreme, especially for water. Although *H. bonariensis* frequently flowered at sites closer to the shore, plants at our sites flowered only occasionally, and their flowers rarely produced seeds (personal observation). Nothing is known about degree of outcrossing in hermaphrodites of this species. This combination of possibly strong selection with low local gene flow could favour the evolution of locally adapted genotypes within a continuous population. Evidence of local adaptation has also been demonstrated within a population of another clonal species, *Trifolium repens* (Turkington and Harper, 1979). Studies that found evidence of local adaptation within a population in non-clonal species have generally considered subpopulations that are separated by relatively large distances (e.g. Sork *et al.*, 1993: *Quercus rubra* subpopulations separated by > 100 m), or have other types of barriers that prevent gene flow (e.g. Schemske, 1984: *Impatiens pallida* reproduction was almost strictly through cleistogamy).

Our understanding of local adaptation assumes that there are trade-offs in plant performance in different environments. Traits related to higher fitness in one environment necessarily lower fitness in other environments; otherwise, a 'super morphology' could dominate all environments (see Chapin *et al.*, 1986). Our results suggest an interesting pattern in such trade-offs. Plants from the high sites grown in high and low vegetated sites differed twofold in biomass, whereas plants from low sites had relatively similar biomass when grown in the two environments (Fig. 1). This difference – more variable performance in plants from high than plants from low dune areas – is associated with the stability of the native environments for each type. The low environment is highly variable, experiencing strong seasonal cycles in both light and water availability. The high dune environment is relatively stable; light levels are generally high and water levels usually low except immediately after rains (T.E. Miller, in prep.). ‘Low’ genotypes may have adapted to be buffered from such changes in the environment and are thus less affected by transplanting between high and low sites. On the other hand, ‘high’ genotypes that evolved in relatively constant environments may be relatively sensitive to environmental change.

Our results have important implications for the processes that may maintain genetic diversity within populations of clonal plants. Because clonal reproduction does not involve recombination, clonal plants may be expected to have lower genetic diversity than sexual plant populations (Eckert, 2002). However, broad comparisons of genetic diversity from published studies show that populations of clonal plants are not less diverse than predominantly sexual plants (Hamrick and Godt, 1990). One mechanism that may explain this pattern is greater within-population local adaptation in clonal plants. Within-population local adaptation has seldom been investigated, yet may be quite common in clonal plants, where there may be strong small-scale differences in selective environments coupled with low gene flow.

ACKNOWLEDGEMENTS

The authors thank the St. George State Park staff for access to sites and advice; Cindy Hays, John Geiger and the Advanced Field Biology class, fall 1995, for help in the field; Alice Winn for ideas and discussion; and Joseph Travis for statistical advice. Cindy Hays, Jamie Kneitel and Gretchen LeBuhn provided helpful comments on the manuscript.

REFERENCES

Antonovics, J., Jacquard, P. and Heim, G. 1984. *Genetic Differentiation and Dispersal in Plants*. Berlin: Springer-Verlag.

Billington, H.L., Mortimer, A.M. and McNeilly, T. 1990. Survival and reproduction in adjacent grass populations: effects of clone, time, and environment. *J. Ecol.*, **78**: 1–14.

Bradshaw, A.D. 1984. Ecological significance of genetic variation between populations. In *Perspectives in Plant Population Ecology* (R. Dirzo and J. Sarukhan, eds), pp. 213–228. Sunderland, MA: Sinauer Associates.

Callaghan, T.V., Carlsson, Å. and Svensson, B.M. 1996. Some apparently paradoxical aspects of the life cycles, demography and population dynamics of plants from the subarctic Abisko area. *Ecol. Bull.,* **45**: 133–143.

Chapin, F.S., Vitousek, P.M. and Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *Am. Nat.*, **127**: 48–58.

Cheplick, G.P. and White, T.P. 2002. Saltwater spray as an agent of natural selection: no evidence of local adaptation within a coastal population of *Triplasis purpurea* (Poaceae). *Am. J. Bot.*, **89**: 623–631.

Eckert, C.G. 2002. The loss of sex in clonal plants. *Evol. Ecol.*, **15**: 501–520.

Evans, J.P. 1988. Nitrogen translocation in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia*, **77**: 64–68.

Evans, J.P. 1991. The effect of resource integration on fitness related traits in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia*, **86**: 268–275.

Evans, J.P. 1992. The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. *Oecologia*, **89**: 265–276.

Evans, J.P. and Cain, M.L. 1995. A spatially explicit test of foraging behavior in a clonal plant. *Ecology*, **76**: 1147–1155.

Evans, J.P. and Whitney, S. 1992. Clonal integration across a salt gradient by a nonhalophyte, *Hydrocotyle bonariensis*. *Am. J. Bot.*, **79**: 1344–1347.

Hamrick, J.L. and Godt, M.J. 1990. Allozyme diversity in plant species. In *Plant Population Genetics, Breeding, and Genetic Resources* (A.D.H. Brown, M.T. Clegg, A.L. Kahler and B.S. Weir, eds), pp. 43–63. Sunderland, MA: Sinauer Associates.

Johnson, A.F. and Barbour, M.G. 1990. Dunes and maritime forests. In *Ecosystems of Florida* (R.L. Myers and J.J. Ewel, eds), pp. 429–480. Orlando, FL: University of Central Florida Press.

Kindell, C., Winn, A.A. and Miller, T.E. 1996. The effects of surrounding vegetation and transplant age on the detection of local adaptation in the perennial grass *Aristida stricta*. *J. Ecol.*, **84**: 745–754.

Linhart, Y.B. and Grant, M.C. 1996. Evolutionary significance of local genetic differentiation in plants. *Annu. Rev. Ecol. Syst.*, **27**: 237–277.

Miller, R.E. and Fowler, N.L. 1994. Life history variation and local adaptation within two populations of *Bouteloua rigidiseta* (Texas grama). *J. Ecol.*, **82**: 855–864.

Platenkamp, G.A. 1990. Phenotypic plasticity and genetic differentiation in the demography of the grass *Anthoxanthum odoratum*. *J. Ecol.*, **78**: 772–788.

Schemske, D.W. 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution*, **38**: 817–832.

Seliskar, D.M. 1990. The role of waterlogging and sand accretion in modulating the morphology of the dune slack plant *Scirpus americanus*. *Can. J. Bot.*, **68**: 1780–1787.

Silander, J.A. 1985. The genetic basis of the ecological amplitude of *Spartina patens*: II. Variance and correlation analysis. *Evolution*, **39**: 1034–1052.

Sork, V.L., Stowe, K.A. and Hochwender, C. 1993. Evidence for local adaptation in closely adjacent subpopulations of northern red oak (*Quercus rubra* L.) expressed as resistance to leaf herbivores. *Am. Nat.*, **142**: 928–936.

Stanton, M.L. and Galen, C. 1997. Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup, *Ranunculus adoneus*. *Am. Nat.*, **150**: 143–178.

Stratton, D.A. 1989. Competition prolongs expression of maternal effects in seedlings of *Erigeron annuus* (Asteraceae). *Am. J. Bot.*, **76**: 1646–1653.

Sutherland, W.J. and Stillman, R.A. 1988. The foraging tactics of plants. *Oikos*, **52**: 239–244.

Turkington, R. and Harper, J.L. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. *J. Ecol.*, **67**: 245–254.

Turkington, R. and Mehrhoff, L. 1990. The role of competition in structuring pasture communities. In *Perspectives on Plant Competition* (J. Grace and D. Tilman, eds), pp. 309–340. San Diego, CA: Academic Press.

Venable, D.L. 1984. Using intraspecific variation to study the ecological significance and evolution of plant life histories. In *Perspectives in Plant Population Ecology* (R. Dirzo and J. Sarukhan, eds), pp. 213–228. Sunderland, MA: Sinauer Associates.