

EVOLUTIONARY RESPONSE

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Evolutionary response of plant populations depends on 1) the presence of genetic variation in traits relevant to climate change and 2) the magnitude and direction of natural selection in future environments. This chapter reviews recent studies on the genetics and evolution of plant populations and outlines the variety of methods that can be used to assess possible evolutionary responses of arctic plants to climate change.

There is considerable evidence that arctic plant populations harbor high levels of genetic variation relevant to climate change (review in McGraw and Fetcher 1992). Ecotypic variation has been observed in a surprising number of arctic plant species, and genotypic variation in metric traits (morphology, phenology, life history, etc) is generally characteristic of plant species that rely heavily on clonal reproduction. In contrast, several recent studies of metric variation in sexual plant populations suggest that the heritability of many traits may often be near the threshold of experimental detectability (Mitchell-Olds 1986, Schwaegerle and Levin 1991, Stratton 1992, Platenkamp and Shaw 1992). These studies suggest that plant populations may often harbor little or no variation at genetic loci influencing morphological and life-history traits. This is particularly true for fitness traits (Platenkamp and Shaw 1992) such as those relevant to climate change. The apparent disparity in levels of heritable variation between plants with predominantly sexual reproduction and plants with significant clonal reproduction may reflect several problems. First, there are good theoretical reasons to expect higher levels of genetic variation in late successional, long-lived species than in early successional species (Odum 1969, Loveless and Hamrick 1984). Second, genetic analysis of quantitative traits has been performed almost exclusively on annual plant species; little is known about narrow-sense heritability of metric traits in clonal species. And third, little is known about the persistence of environmental effects in clonal plant material (Hume and Cavers 1981, Foster et al. 1984, Schwaegerle 1996) that would upwardly bias estimates of genotypic variation in populations of clonal species.

1. Genetic variation within and among populations

Perhaps the best method for determining the capacity of arctic plants to adapt to future environments is to examine the types of evolutionary changes that have occurred in the past. Conditions vary widely in the range of most arctic plant species so that plants experience a broad range of selective regimes. The extent to which these populations have adapted to local conditions may be our best indicator of their capacity for future evolutionary change. Recipro-

cal transplant and common garden experiments can be used to measure divergence among populations from contrasting environments (e.g. Shaver et al. 1986, Matyas 1994, Schmidting 1994, Stettler et al. 1994). These studies can focus on growth (see Sultan 1992, Sultan and Bazzaz 1993) and/or physiological response (e.g. Chapin and Oechel 1983, Blais and Lechowicz 1989, but also see Chapin and Shaver 1996). Reciprocal transplant experiments uniquely can provide a measure of how critical these evolutionary differences are to the persistence of a population at a site (see McGraw and Antonovics 1983).

Evolutionary response to selection is a direct function of genetic variation within populations. In long-lived plant species immediate evolutionary response to environmental change may depend upon genetically based differences among extant genotypes. Individual plants in the field may vary in phenological, physiological, and morphological traits that differentially influence their success in alternate environments. Common garden experiments using clonal propagation of individual genotypes can be used to assess genetic differences in traits relevant to environmental change. These methods are described by Platenkamp and Shaw (1992), Sultan and Bazzaz (1994), and Schwaegerle (1996). In contrast, long term response to selection depends upon sexual recombination among extant clones and hence the narrow-sense heritability of traits. Estimation of narrow-sense heritabilities is more involved than assessing genotypic variation. Falconer (1989; Chapter 6-11) provides an introduction to these methods (also see Mitchell-Olds and Rutledge 1986).

Although evolution of arctic plant populations depends on genetic variation in quantitative, polygenic traits (morphology, phenology, physiology, etc), a variety of molecular techniques may also shed light on the capacity of these populations to adapt to future environments. Phylogenies constructed from DNA sequence data or restriction fragment length polymorphisms can reveal biogeographic affinities and the evolutionary history of a species. Alternatively, allozyme electrophoresis can provide information on breeding systems and/or gene flow within and among populations. In contrast with the transplant and common garden experiments described above, these methods often involve considerable time and expense and only indirectly address the problem of evolutionary response to climate change.

2. Change in the selective regime

The evolution of arctic plant populations depends on the direction and magnitude of natural selection in future environments. The extent to which experimental warming results in a shift in the selective regime and the similarity

of this selective regime among ITEX sites can be assessed using methods developed by Lande and Arnold (1983) and others (Wade and Kalisz 1990, Rausher 1992, and references therein). These methods can reveal morphological and life-history traits (or combinations of traits) that are favored by natural selection. Field manipulations such as ITEX chambers can provide estimates of the force of natural selection on arctic plant populations in future environments. Most importantly, these analyses can be conducted with only the plant response data prescribed by Molau and Edlund in the ITEX Manual.

References

- Blais, P. A. and M. J. Lechowicz. 1989. Variation among populations of *Xanthium strumarium* (Compositae) from natural and ruderal habitats. *Am. J. Bot.* 76:901-908.
- Chapin, F. S., III, and W. C. Oechel. 1983. Photosynthesis, respiration, and phosphate absorption by *Carex aquatilis* ecotypes along latitudinal and local gradients. *Ecology* 64:743-751.
- Chapin, F. S., III, and G. R. Shaver. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77:822-840.
- Falconer, D. S. 1989. Introduction to quantitative genetics, third edition. Longman, New York.
- Foster, G. S., R. K. Campbell, and W. T. Adams. 1984. Heritability, gain, and C effects in rooting of western hemlock cuttings. *Can. J. For. Res.* 14:628-638.
- Hume, L. and P. B. Cavers. 1981. A methodological problem in geneecology. Seeds versus clones as source material for uniform gardens. *Can. J. Bot.* 59:763-768.
- Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- Loveless, M. D. and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* 15:65-95.
- Matyas, C. 1994. Modeling climate change effects with provenance test data. *Tree Physiol.* 14:797-804.
- McGraw, J. B. and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life-cycle stages of selection. *J. Ecol.* 71:879-897.
- McGraw, J. B. and N. Fetcher. 1992. Response of tundra plant populations to climatic change. pp 359-376. *In Arctic ecosystems in a changing climate: an ecophysiological perspective.* Academic Press, San Diego.
- Mitchell-Olds, T. 1986. Quantitative genetics of survival and growth in *Impatiens capensis*. *Evolution* 40:107-116.
- Mitchell-Olds, T. and J. J. Rutledge. 1986. Quantitative genetics of survival and growth in natural plant populations: A review of the theory. *Amer. Natur.* 127:379-402.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Platenkamp, G. A. J. and R. G. Shaw. 1992. Environmental and genetic constraints on adaptive population differentiation in *Anthoxanthum odoratum*. *Evolution* 46:341-352.
- Rausher, M. D. 1992. The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution* 46:616-626.
- Schmidtling, R. C. 1994. Use of provenance tests to predict response to climatic change: loblolly pine and Norway spruce. *Tree Physiol.* 14:805-817.
- Schwaegerle, K. E. 1996. Method for assessing genotypic variation in plant traits relevant to environmental change. *In Book of Abstract, 7th ITEX Workshop.* Danish Polar Center, Copenhagen.
- Schwaegerle, K. E. and D. A. Levin. 1991. Quantitative genetics of fitness traits in a wild population of phlox. *Evolution* 45:169-177.
- Shaver, G. R., N. Fetcher, and F. S. Chapin, III. 1986. Growth and flowering in *Eriophorum vaginatum*: annual and latitudinal variation. *Ecology* 67:1524-1535.
- Stettler, R. F. and H. D. Bradshaw, Jr. 1994. The choice of genetic material for mechanistic studies of adaptation in forest trees. *Tree Physiol.* 14:781-796.
- Stratton, D. A. 1992. Life-cycle components of selection in *Erigeron annuus*: II. Genetic variation. *Evolution* 46:107-120.
- Sultan, S. E. 1992. What has survived of Darwin's theory? *Evol. Trends Plants* 6:61-71.
- Sultan, S. E. and F. A. Bazzaz. 1993. Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. *Evolution* 47:1050-1071.
- Wade, M. J. and S. Kalisz. 1990. The causes of natural selection. *Evolution* 44:1947-1955.