Patterns of population differentiation

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Abstract

McNeilly, T.: Patterns of population differentiation. — Bocconea 7: 89-93. 1997. — ISSN 1120-4060.

Patterns of population differentiation in response to high selection pressures in adjacent environments are examined. In such situations distinct genetically based adapted populations can occur only metres apart. Population structure in small scale spatially fluctuating, and temporally heterogeneous environments are also considered. Evidence suggests that in such environments adaptation is largely due to phenotypic plasticity, rather than to fixed genotyopic differentiation.

It is widely accepted that there is a consistent general response of plants to environmental heterogeneity that results in adaptive, and hence genetically based, differences between populations. This was first shown in the classic papers of Turesson describing ecotypic differentiation in a number of widespread European perennial species. A further group of classic papers followed in the 1940s from Clausen, Keck, and Hiesey, based upon their studies of *Achillea lanulosa* and *A. borealis* in California. These species also showed very clearly the relationship between plant form and habitat type along transects varying in altitude and moisture – tall growing types from lowland habitats contrasting with dwarf types from high mountain habitats. Subsequent work by a number of authors have extended the use of transects to assess the spatial structuring of population differentiation in the wild, and in most cases they have revealed adaptive differentiation between populations growing only a few metres apart. Thus height differences greater than x3 have been shown between *Plantago lanceolata* populations separated by as little as 3 metres (McNeilly unpublished data).

On the north west coast of Ynys Môn, North Wales, Aston & Bradshaw (1966), described a very remarkable example of correlation between stolon lengths of adjacent *Agrostis stolonifera* populations on a very exposed headland, and the degree of exposure that they were subjected to from the prevailing on-shore winds. One transect sampled populations from the cliff face bottom to top and into a pasture immediately behind the cliff face. The second sampled populations along a gradual sloping changed from sea-level to the same pasture. From a common garden experiment it was found that where the environment changed suddenly over a distance of 1.5 to 3 m, mean stolon length of *A. stolonifera* plants changed from 17 cm to 47 cm over that same small distance. By contrast, where the environment changed gradually, stolon length also showed a gradual clinal change. Similar quite remarkable differences between populations sampled over a small distance have been shown in the case of *Anthoxanthum odoratum* in the Park Grass plots set up at Rothamsted where adjacent plots have, or have not, been limed since 1903. There the populations differ completely in plant height over a distance of only 10cm, (Snaydon & Davies 1976).

It is thus clear that distinct populations can exist adjacent to eachother under the influence of natural selection. Furthermore they do so despite the probability of considerable gene flow(via pollen) over the short distances between them. This, in the cases of *A. stolonifera,* and *Anthoxanthum odoratum*, would tend to blur the boundaries between populations, or prevent population divergence as in the situation in *Cynosurus cristatus* described by Ennos (1985), where sub-populations separated by 100 m showed only weak genetic divergence because of the impact of pollen flow between them. The patterns and scales of population differentiation described thus far are in response to strong selection pressures, where the integrity of populations is maintained against the opposing forces of gene flow by such strong selection. A final example is seen in the case of the zinc tolerant populations of *Agrostis capillaris* which occur on the zinc contaminated soils covering areas of less than 100 m^2 beneath electricity pylons in North Wales (Al-Hiyaly & al. 1992). These small isolated populations occur in upland *Agrostis*/*Festuca* grasslands, completely surrounded by vast non-tolerant populations, and, despite very high levels of gene flow, they maintain their zinc tolerant integrity as a consequent of the very high selection pressures favouring zinc tolerance that act upon them.

The patterns and scales of population differentiation that have been considered thus far suggest that population differentiation due to natural selection (i.e. genetically based differentiation) is the expected response to environmental heterogeneity. It would therefore follow that where environmental boundaries are sharp, population boundaries are also sharp. By contrast, where they are gradual, boundaries are gradual. We may pause however, and ask whether population differentiation i.e. micro-evolution, is always the product of environmental heterogeneity.

Populations of *Dactylis glomerata* and *Bromus erectus* from two contrasting habitats, (a *Quercus pubescens* wood, and a grass sward, respectively the product of natural colonisation of vineyards abandoned 120 and 20 years prior to sampling), were compared for their responses to shade/light, and soil moisture (Roy 1985). Despite the considerable differences in light intensity and soil moisture between the wood and the sward habitats, no significant differences were found in dry matter production by the populations of either species when grown in controlled light environments. The *B. erectus* populations did not differ in the ratio spike biomass/leaf biomass in response to changing soil moisture. In addition, despite the onset of water stress conditions 6 weeks earlier in the sward than in the wood, differences in flowering time between populations, particularly in *B. erectus*, differed by less than four days. In this case there is no evidence of adaptive evolution of the kind described above in either *D. glomerata* or *B. erectus.*

Further examples of situations where there is no evidence of population differentiation in response to environmental heterogeneity have been recorded in *Pseudotsuga menziesii* in N. America (Chen & al. 1986). Variation in needle and twig anatomy was examined in ten individuals from each of 46 populations of *P. menziesii* in south-western British Columbia. It was found that individuals accounted for most of the variation in the data, from which the authors concluded that the production of intra-population variants is a more significant evolutionary event than inter-population differentiation in these populations of *P. menziesii*. The question does arise however as to the extent of the adaptive significance of the characters measured. Nonetheless, a number of other studies have also indicated a high degree of intra-population variation in conifers compared with inter-population variation, for example in *Abies procera* (Maze & Parker 1983); *Picea sitchensis* (Yeh & El-Kassaby 1980). A similar situation was reported (Robson & al. 1988) for the herbaceous taprooted perennial *Balsamorhiza sagittata*, where variation in five leaf characters and thirteen shoot characters was predominantly at the level of individual plants within populations, and such intra-population variation was greater than that between populations. In this case the numbers of individuals sampled was somewhat small, the two 'population' samples being of (only) seven and ten individuals, sampled in western north America (Canada, USA).

A final example which records the absence of clear adaptive response to environmental variables in plant populations is illustrated by a study of *Phlox paniculata* populations in central Texas (Schwaegerle & Bazzaz 1987). Attempts were made to uncover correlations between population responses to experimentally induced gradients in soil moisture and nutrient status, competition, and light, all being features which varied in the sites from which the populations were collected. Although there were significant differences in the laboratory determined responses of populations to environmental gradients, and the field sites differed significantly from each other, the differences recorded between populations in experimental conditions could not be interpreted as being of an adaptive nature. The apparent lack of adaptive differentiation between these populations was attributed to the complexity of the environmental variables which characterised the different sites from which the populations were sampled, and the absence therefore of any single overriding environmental factor which might cause micro-evolutionary differentiation between the populations. It could also be the case here, and in the case of the populations of *Dactylis* and *Bromus* described earlier, that selection pressures are insufficient to cause such changes, since changes in phenotype in response to environment — phenotypic plasticity — may allow sufficient adaptive adjustments rather than selection driven changes in genotype. However, in such situations, selection may promote the survival of phenotypically plastic individuals, this plasticity itself being genetically based. Indeed in *Dactylis glomerata* where plants were grown in full incident light and 24% of incident light, anthesis occurred up to twelve days later than in full light conditions (Roy 1985), a very convincing example of the adaptive significance of phenotypic plasticity.

A further situation in which phenotypic plasticity would appear to account for adaptation has been described in *Plantago major* subsp. *pleiosperma* by Blom & Lotz (1985). Populations were sampled from sites in which there were relatively extreme variations in environment, such as in grazing and flooding intensity, humidity, soil chemical and physical conditions, all of which varied over very short distances. As a consequence individuals in a particular environment would be likely to be subject to high levels of gene flow, a situation in which selection would favour phenotypically plastic responses to environmental heterogeneity, unless the selection pressures were extremely high, such as those due to heavymetal toxicity. This is borne out by data from a transplant experiment, where variance in vegetative development was mainly affected by site variables, i.e. a phenotypically plastic response was induced. Other plant characters, such as date of first flowering and reproductive effort showed at least some degree of genetic control, but also showed a phenotypic plasticity component.

Finally the adaptive significance of phenotypic plasticity was also shown in *P. maritima* by Gregor (1956) for a dwarf population growing in an exposed area of Iceland consisting of a mosaic of hummocks and hollows. A corresponding mosaic of dwarf and taller plants was found in the wild, the taller plants occurring in hollows. When transplanted to an experimental garden, these differences disappeared in five out of the six samples assessed, indicating that adaptation and survival was based upon phenotypic adjustment (plasticity).

We can thus see that response of plants to environmental heterogeneity can be of two basic types. Firstly we may see – in some cases to a remarkable degree — the evolution of distinct populations even over very short distances, the components remaining distinct because of the high selection pressures involved which overcome any effects of gene flow. Secondly, we may, by contrast, see that a diverse range of genotypes may adopt, as a consequence of plasticity, a much smaller range of phenotypes in response to environmental factors, thus enhancing the fitness of those individuals. In the context of the conservation of plant materials, differences or similarities that may be seen in the wild may not always reflect genetically based variation. Interpretation of such differences can only be made from controlled experiments with the materials in question.

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