

## Adaptation, variation and selection in marginal areas

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### Summary

The word adaptation and its derivatives are reviewed as well as the characteristics of environmental marginality. Plant traits are discussed in the light of their adaptive significance, specially pointing at their phenotypic expression under stress. Variation in marginal plant populations is discussed on the basis of accumulated knowledge on quantitative traits and isozymes. The common opinion that marginal populations are genetically depauperated is questioned on the basis of observations that show high degrees of environmental heterogeneity. This in turn would cause a disruptive mode of natural selection close to the species margin. Species' modes of adaptation and mating systems are briefly discussed and finally natural selection for stability is suggested to be of significance in marginal areas, a fact that should be duly recognized in modern plant breeding programmes aiming at maximum stability (sustainability) but not necessarily maximum yield.

### Introduction

It can be taken as an axiom, that breeding under marginal conditions must be at the mercy of natural selection. Plant breeding away from the margin, in central areas of the species, may sacrifice adaptation to higher yields by manipulating important yield components of the plant, here crop physiology plays an important role for improving yields. Such tinkering with adaptation may only be done in marginal areas when dealing with annuals that only have to survive one growing season. Generally at the species margin, adaptation is of first order importance, yield comes second.

To find a proper starting point for this general presentation, the ambiguities that are inherent in the word 'adaptation' and its derivatives have been revisited, mainly on the basis of the work of Theodosius Dobzhansky, summarized in 'On Some Fundamental Concepts of Darwinian Biology' (1968).

#### *Adaptation*

Dobzhansky writes: 'When words are borrowed from everyday language to serve as technical terms, misunderstanding is liable to result. Adaptation is plagued with ambiguity, for it is used also in contexts which are

biologically irrelevant. Pieces of furniture, or implements are said to be 'adapted' for certain purposes. Biological adaptation is concerned with survival and/or reproduction; it is found only in living bodies - -'. Jepsen et al. (1949) have defined adaptation as 'Correlation in a way useful to the organism, between structure, function and environment'. I interpret this as a special trait useful to the organism. The same authors continue by adding 'Also the progressive changes bringing about increase in such relationships in organisms'. Simpson (1953) adds to this 'An adaptation is a characteristic of an organism advantageous to it or to the conspecific group in which it lives', thus pointing at a population genetic interpretation. I interpret this as an evolutionary process dependent on conspecific groups and on the environment.

#### *Adaptedness*

Dobzhansky writes: 'Adaptedness first arose with the origin of life, since this life did not become extinct; the origin of life was, however, not an adaptation. - - - Man is not adapted to feed on pasturage, while horses and cows are so adapted; palms and bananas have no adaptedness to live in Canadian forests, while larches and spruces do have such an adaptedness; certain microorganisms grow in laboratory media and others do not.

- - - In general, adaptedness can be achieved either by individual adaptability or by genetic adaptability'. My interpretation of the word adaptedness would be the degree or level of adaptation. How this should be measured is debatable. Dobzhansky has treated 'The problem of Quantification of Adaptedness' in the fundamental article mentioned earlier, he writes: 'For individual adaptedness, the probability of survival, of reaching the reproductive stage of the life cycle, and in the case of man, the degree of the sense of well being (which is also hard to measure), are thinkable criteria. For populations, a statistic has been proposed named variously the Malthusian parameter, intrinsic rate of natural increase, or innate capacity for increase'. This then becomes a population biological concept, related to the Lotka-Volterra equation of logistic growth and indeed developed further by population biologists.

#### *Adaptability*

The words of Dobzhansky: 'If a species could inhabit a single and perfectly constant environment, evolution could conceivably arrive at a genotype optimally adapted to that environment. Evolution would then come to a halt. In reality, not only every species but probably every individual has confrontations with many environments, because environments vary in space and in time. Adaptedness in a narrow range of environments is overspecialization; an overspecialized organism may be highly successful for a time, but it risks death or extinction if the environment changes. Hence the importance of adaptability.

Physiological and genetic adaptabilities must be distinguished. Every genotype has a 'norm of reaction', which is the array of phenotypes it can produce over the range of existing and possible environments'. I think adaptability can be defined as follows: To maintain itself in harmony with a changing environment, the organism must not only be adapted, but also adaptable.

#### *Adaptive value*

In conjunction with Darwinian fitness Dobzhansky writes: 'Natural selection is the process which tends to maintain or improve the genetic adaptedness in old environments, and contrive adaptedness to new environments'. Referring directly to the work of Darwin, I interpret adaptive value as fitness ( $w$ ), given as  $1-s$ ,  $s$  being the selection coefficient. This, then can be taken further from the locus to the genotype and to the fitness of the population ( $\bar{w}$ ).

#### *Some related concepts*

A whole range of important expressions originate from the above definitions, such as homeostasis, plasticity and flexibility. Also the confusing philosophy of acclimatization, including the interesting field of physiological preconditioning and general studies of acquired characters must be mentioned. The rest of this paper could be spent on the last mentioned alone. At this time I would like to emphasize just two, namely acclimatization and phenotypic plasticity. Acclimatization is the physiological adjustment to the environment, and is of outstanding importance in marginal plant cultivation. Phenotypic plasticity is the ability to change phenotype in different environments. Both have been of great importance in making use of  $G \times E$  interactions in cultivated plants.

#### **The marginal environment**

Physiochemical factors, such as temperature, humidity, soil chemistry, wind, ice and snow may one at a time or by interaction set the limit for a plant natural distribution at the margins of species. Studies on cumulative mortality of perennial plants close to their margin have shown that, due to large variations in the environment in time, plant stand mortality may accumulate in bursts, finally reaching over 90% and often causing complete eradication (Eiche & Gustafsson, 1970). This heterogeneity in time may be from day-to-day, week-to-week, month-to-month and between some seasons from year-to-year. Environments are weakly autocorrelated in time, to use the terminology of MacArthur & Levins (1967) or Levins (1968). Such conditions may frequently cause complete harvest failures and cultivated crops, perennials and trees must show highest possible tolerance to endure critical 'bottleneck' years.

Marginal environments appear to be very highly heterogeneous in space. Farmers or foresters, working in the Sahelian zone or in the subarctic, know the crucial importance of microsite selection when cultivating plants. Land inclination and profiles, water and nutrients may affect plant growth and survival in an almost threshold manner, the environment is highly mosaic in space, often much more so than under more central conditions.

The marginal environment may, due to 'bottle-necks', force plant populations towards a common durable modification. We can see that e.g. on the snow-

pressure affected spruce trees or the wind stressed coastal tree populations. What we can not see directly, except after freezing mortality, is the influence of a critical temperature on hardiness or on the timing of flowering and seed set. This may restrict late flowering, late maturing individuals from reproduction, thus having fitness values of zero. It is particularly common in the north to have a complete failure of the generative cycle, due to distorted meiosis. Plants then turn to clonal growth and regeneration, an alternative mode of reproduction.

Observation of different quantitative traits under such conditions may cause us to classify them as having more or less adaptive significance. Traits of high adaptive value are forced to uniformity, while less adaptive ones may show much more variability within a population. This in fact may also be reflected in the genetic structure of populations, on the additive genetic variation of quantitative traits (Stern & Roche, 1974). As we shall see, this does not however eliminate genetic variation at the single locus level.

### Plant genetic variation along the margin

A recent very large summary of allozyme diversity in plant species by Hamrick & Godt (1990), including 653 studies on 449 species representing 165 genera, indicates some interesting facts about genetic variation in plant species. I have extracted information on what is known about marginal plant species based on this large survey plus some special studies that are available on marginal populations (Tigerstedt, 1973, 1979; Alden & Loopstra, 1987; Tremblay & Simon, 1989).

- Plant species, on average, maintain higher levels of allozyme variation within populations than invertebrates or vertebrates. The reason for this must be the sedentary characteristic of plants; animal habitat selection is compensated for by higher genetic variation within the population and a much larger offspring number.
- Isozyme studies in marginal populations indicate, that just or nearly as much variation is retained in them as in more central populations.
- Perennial, outcrossing, windpollinated species of the later stages of succession have higher levels of allozyme variation within populations and less among populations than species with other modes of adaptation. Also they often conform on an allozyme level to a Hardy & Weinberg equilibrium. Thus an annual inbreeder would have more

of its genetic variation tied to populations in particular sites. In tree populations along the treeline, this generalization is not quite true, isolated pockets of trees may exhibit large differences in gene frequencies, although they are generally highly heterozygotic.

- Predominantly clonal plant species may maintain as much genetic diversity within populations as sexually reproducing species. This may indicate a heterozygous advantage of well adapted clones.
- Linkage disequilibrium is common in predominantly inbreeding species, specialized genotypes may be represented in certain marginal areas. In predominantly outbreeding species such chromosomal structures are very rare.
- Patterns of allozyme variation are not correlated with the variation of morphometric traits of a quantitative nature. Thus morphometric uniformity that may be caused by a marginal environment is not reflected at the allozyme level.
- In some cases environmental heterogeneity and genetic variation can be shown to be interdependent, in other cases the patchy genetic structure may be the result of limited pollen and seed dispersal.

### Selection in marginal areas revisited

Natural selection is believed to have 3 fundamental modes; normalizing within populations centrally located, disruptive (diversifying) between populations in a heterogenous environment and directional in populations at species margins. This was the general model used by Carson (1955) for characterizing *Drosophila* populations and it was also generally accepted by e.g. Dobzhansky. Levins, in a series of papers (1962, 1963, 1964) and summarized in 1968 set the stage for a different model of natural selection, looking at mendelian species as adaptive systems. Here the species mode of adaptation was modelled on the basis of a fitness set and an adaptive function. Basically the important components in this model building was the tolerance of an individual in relation to environmental heterogeneity in space and time. This would cause species to adopt alternative modes of adaptation.

Since the early 1970s much new information about plant population genetic structures has accrued as allozyme analyses became available. At the moment, one has a fairly clear concept about population structure based on allozymes and also on morphometric

traits. The first efforts to compare these two sources of variation show that they often do not match. At the moment one is turning once again to quantitative traits. By using molecular genetic markers one is now trying to explain the discrepancy between allozyme and morphometric variation. Results are not available as yet.

However, the high degree of genetic variation that populations exhibit at a species' margins questions the validity of simple directional selection that would cause genetic uniformity. Also, observations on environmental variation, often stochastic in nature at the margin, is much wider than earlier realized. This variation is both space and time dependent. Under such conditions natural selection on adaptively important traits may in fact have a strong diversifying component, perhaps masked by environmental pressures. In addition to this, plant populations at the margin are often sparse and isolated by distance. In the case of trees in Alaska and Finland, such population pockets may, due to drift, show high degrees of between population genetic diversity.

In large plant breeding efforts of today more emphasis than before is laid on breeding for wide adaptation, stability and tolerance. CIMMYT in Mexico, ICRISAT in the semi-arid tropics and IITA in the humid tropics have adopted a diversifying selection scheme in their breeding for wide adaptation, variously called divergent-convergent selection or shuttle breeding. This idea is also closely related to prebreeding and the efficient use of gene bank materials in breeding programmes. Breeding populations are thus 'shuttled' between several locations in the tropics/subtropics to retain high degrees of genetic variation, wide adaptation and disease resistance of a horizontal quality. The final step in such plant breeding programmes is usually done locally (nationally) by tapping breeding populations for their rich variation and higher than normal diversity.

I propose a similar approach in the effective use of gene bank materials specially adapted to the northern margins. Intercrossing populations of marginal species, that may show genetic diversity due to spatial isolation should create breeding populations with

a maximum width of adaptation. Such populations should be the nuclei for breeding in marginal areas where adaptation and adaptability count first.

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