CORE AND PERIPHERAL POPULATIONS AND GLOBAL CLIMATE CHANGE

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ABSTRACT

Environmental conditions outside the periphery of a species' distribution prevent population persistence, hence peripheral populations live under conditions different from those of core populations. Peripheral areas are characterized by variable and unstable conditions, relative to core areas. Peripheral populations are expected to be genetically more variable, since the variable conditions induce fluctuating selection, which maintains high genetic diversity. Alternatively, due to marginal ecological conditions at the periphery, populations there are small and isolated; the within-population diversity is low, but the between-population genetic diversity is high due to genetic drift. It is also likely that peripheral populations evolve resistance to extreme conditions. Thus, peripheral populations rather than core ones may be resistant to environmental extremes and changes, such as global climate change induced by the anthropogenically emitted "greenhouse gases". They should be treated as a biogenetic resource used for rehabilitation and restoration of damaged ecosystems. Climatic transition zones are characterized by a high incidence of species represented by peripheral populations, and therefore should be conserved now as repositories of these resources, to be used in the future for mitigating undesirable effects of global climate change. Preliminary research revealed high phenotypic variability and high genetic diversity in peripheral populations relative to core populations of wild barley and the chukar partridge, respectively.

INTRODUCTION

GLOBAL CLIMATE CHANGE AND ECOLOGY

An Intergovernmental Panel on Climate Change (IPCC) scientific assessment states that emissions resulting from human activities are substantially increasing the atmospheric concentration of "greenhouse gases", which will cause an increase of global mean

temperature of 0.3 °C per decade during the next century, a rate faster than that seen over the past 10,000 years (Houghton et al., 1990). The IPCC predicts that these "rapid changes in climate will change the composition of ecosystems; some species will benefit while others will be unable to migrate or adapt fast enough and may become extinct" (Houghton et al., 1990). Environmental and ecological management problems are likely to emerge due to global warming (Overpeck et al., 1990; Poiani and Johnson, 1991; Mintzer, 1993). Though much uncertainty exists, and more research is required, attempts to predict the ecological effects of possible scenarios of global climate change (GCC), with a focus on ecosystem preservation (Ausubel, 1991), should not wait for unequivocal climatic predictions (Ojima et al., 1991). This is because "The costs of rejecting the greenhouse hypothesis, if true, are vastly greater than the costs of accepting the hypothesis if it proves to be false", and "The greenhouse threat is more than sufficient to justify action now, even if only as an insurance" (Goodland, 1991).

LOCAL EFFECTS OF GLOBAL CLIMATE CHANGE

For the eastern Mediterranean basin, global circulation models suggest a rise of 2–4 °C, similar to the global trend, by the middle of next century, provided that the concentration of greenhouse gases will be equivalent to doubling the current CO_2 concentrations (Cohen et al., 1993). Using paleoclimatic analogues, composite difference or superposed epochs analyses of modern records, and global circulation models, it is predicted that precipitation will exhibit greater spatial variability than temperature. Therefore, reliable regional scenarios are hard to obtain, and result in conflicting projections of precipitation for Israel (Kay, 1993). For example, warmer sea surface temperatures will increase the rainfall over Israel, but possible thermal stabilization will reduce precipitation (Alpert et al., 1993). Potential evaporation due to increased temperatures can compensate substantially for the possible increase in precipitation. Thus, general aridification is expected in spite of a possible increase in precipitation (Cohen et al., 1993).

ECOLOGICAL RISKS

What should ecologists do about global climate change? Besides monitoring ecological responses, they should (a) strive to predict the ecological effects of climate change, (b) identify the risks, and (c) propose risk-aversion strategies and tactics. Though "there is almost no species for which we know enough relevant ecology, physiology and genetics to predict its evolutionary response to climate change" (Holt, 1990), a paramount risk is that of species extinctions. Throughout the past slow changes in climate, spontaneous mutations have occurred and have been selected, and species have evolved and have adapted. In addition, species have dispersed and migrated to regions of favorable climate. Under the predicted fast change (predicted rate of warming of 2.5–5 °C for the next 100 years, compared with 0.05 °C per century during the last 10,000 years; Hinckley and Tierney, 1992), selection will operate on the current genetic structure. Populations with no pre-adaptations, or those unable to migrate through the extensive man-made barriers, may perish (Hinckley and Tierney, 1992). Species extinctions will alter community structure and ecosystem functions, and cascading effects may lead to additional, indirect extinctions.

AVERTING THE RISKS OF EXTINCTION

If global change is perceived as an increase in environmental stress, will all populations across the geographical range of a species respond similarly, or would some suffer critically while others endure and persist? Should the latter be the case, then under climate change, the persistent populations could serve as sources for recolonizing areas previously occupied by the less tolerant populations. If unifying principles exist by which these two types of populations can be delineated, then populations of potential resistance and persistence should be treated as "biogenetic resources". Consequently, the areas in which they occur should be strongly protected against development which causes physical destruction and reduction of their habitats; such habitats should be urgently preserved as repositories to be used for future rehabilitation and restoration of other areas and ecosystems damaged by GCC effects.

GENETIC STRUCTURE AND POPULATION PERSISTENCE ACROSS THE RANGE

Persistence of a population under environmental change such as GCC can be attained if the population includes genotypes which are resistant, due to specific adaptations or pre-adaptations, or to high phenotypic plasticity. In either case, the genetic variability of the population can be low (most individuals are resistant or phenotypically plastic), or high (resistant and nonresistant genotypes are common). A combined genetic-demographic mathematical model predicts enhanced population persistence with an increase in genetic variance (Pease et al., 1989). It is rather unlikely that most individuals of a species will be resistant to the same extent, either through adaptation or through phenotypic plasticity, to conditions that rarely occur within most of the distributional range. It is therefore more plausible that genetic variability, with respect to resistance and plasticity, varies across the species' distributional range. Specifically, we envisage that populations at the boundary of the species' geographical range ("peripheral" sensu Brussard, 1984) are in some ways different from those away from the boundary ("core" populations). The questions to be addressed are, therefore: (a) Are there differences in responses to environmental changes between peripheral and core populations of species? and (b) Do these differences result from differences in genetic variability?

WORKING HYPOTHESES

CORE AND PERIPHERY HYPOTHESES

The relative persistence under novel changes such as those associated with GCC, of core vs. peripheral populations, is determined by micro-evolutionary mechanisms which operate differently, depending on the size and spatial patterns of these populations, and their interaction with the environment. Population densities often decline from core to periphery, due to reduction in habitat favorableness, environmental stability, and predictability (relative to the best performing and most frequently held strategies or phenotypes found across the species' range; Brussard, 1984). This decline in density may result in increasing patchiness and isolation of local populations from core to periphery (Lawton, 1993). Alternatively, core and periphery do not always differ much with respect

to densities and spatial patterns. This happens when the distribution is abruptly terminated due to competitors or predators which attain superiority or effectiveness, respectively, under the environmental conditions which prevail over the boundary region (Pielou, 1979).

In either case, population persistence is enhanced through the occurrence of genetic combinations (a) resistant to stress, or (b) having a wide range of tolerance, which is somewhat wider than the currently prevalent range of conditions, and covers further deterioration likely to result from GCC. The question is whether core and peripheral populations differ with respect to these two features. Accordingly, peripheral populations will persist either better or worse than core populations, or no differences are to be expected. In the following, we elaborate on each of these alternatives.

1. Core will persist better than periphery. Because the core is environmentally more favorable, it harbors dense and contiguous populations, whereas peripheral populations are small and isolated (Mayr, 1965; Lewontin, 1974). Environmental favorableness is expressed in the number of types of exploitable ecological niches, and is, thus, greater in core than periphery (da Cunha and Dobzhansky, 1954). Populations at the core are highly heterozygous and heterotic. Thus the same genotypes can perform better in the variety of niches available in the core, and the load of producing less fit homozygotes is balanced by the large size of these populations and their high degree of outcrossing (Carson, 1959). Soule (1973) proposed that heterozygosity is also advantageous in the periphery, but peripheral populations frequently become extinct, so that the required level of heterozygosity is rarely reached there. To conclude, core populations are expected to undergo balancing selection and therefore they maintain high additive genetic variance, whereas peripheral ones are smaller and isolated and have lower additive variance. This we call the "Carson" hypothesis, which implies that under GCC, core populations are more likely than peripheral ones to respond to the novel selection pressure and to persist. Accordingly, measures against habitat destruction and major conservation efforts should now be directed toward core distributional areas of species.

2. Periphery will persist better than core. R.A. Fisher (Fisher, 1930a,b) postulated the maintenance of substantial geographic differentiation by a weak selection pressure, when a cline in genotype frequencies exists. If the environment of core populations is perceived as stable, and hence selection is stable, genetic additive variance and heritability are low. At the periphery the environment is fluctuating, which induces fluctuating selection, and therefore additive variance and heritability are larger than in the core. Thus, as favorableness and predictability decrease from core to periphery, selection changes from one for high average fitness, to one promoting genetic flexibility (Brussard, 1984). In the periphery many genotypes are maintained, each adapted to cope with a specific environmental state. GCC is expected to make some climatic states more common than they are now; thus, the frequency of genotypes that can cope with these states will increase, while others may perish. However, the population will persist. Even if novel, more extreme states occur, genotypes adapted to somewhat less extreme conditions are likely to be pre-adapted to somewhat more extreme conditions by having a wide enough norm of reaction. In the core, on the other hand, genotypes adapted to rarely occurring environmental states may not be maintained. Consequently, rather than just undergoing genetic change as in the periphery,

the core populations are more likely to perish under GCC. This we call the "Fisher" hypothesis. It does not address the issue of whether peripheral populations are small and isolated, or quite large and contiguous, similar to core ones. If peripheral populations are small and isolated, the question is whether they are mainly subjected to random or to nonrandom selective forces. In both cases they can be more resistant to climate change than core ones, but through different mechanisms.

Small and isolated populations, either colonizing populations (Baker and Moeed, 1987), or those that are often expected at the periphery, are subjected to strong random evolutionary forces such as drift, inbreeding, and founder effect (Holt, 1990; Heywood, 1991). They can also be virtually cut off from gene flow from other populations of the periphery or the core. Also, though random mutations occur less frequently when the number of individuals is small, when a mutation does occur in a single individual, it represents a relatively large proportion of the population and will be more likely to increase to fixation due to genetic drift. Under these conditions, in the periphery, the within-population genetic variability will be low, but the between-population genetic variability will be high. This is why peripheries are the sites of much genetic innovation (Mayr, 1965), and even genetic "revolutions" (Tempelton, 1980), and can be viewed as the engines of evolutionary change and the primary source of speciation. At least some of the innovations are likely to be resistant to GCC-induced changes. Therefore, these populations, with their novel genetic combinations, should be conserved for their significance with respect to GCC, and also because they have great evolutionary potential.

Under many conditions prevailing at the periphery, random evolutionary forces will not swamp out selection. If environmental conditions at the periphery are indeed unstable, with frequent extremes, each population may either evolve several genetic combinations, adaptive for a given environmental state (specialists), or all populations may evolve genotypes with high phenotypic plasticity (generalists). Especially in the latter case, overall genetic variability in the core will be higher than in the periphery, but peripheral populations will have higher chances of persistence under GCC. Indeed, Whittaker and Goodman (1979) suggested that core populations are large, stable, and undergo "saturation selection", i.e., selection for competitive ability. Peripheral populations are small and experience favorable conditions only rarely, hence they undergo "adversity selection", evolving means of surviving unfavorable conditions. An examination of the metabolic costs of multiple environmental stress resulted in the conclusion (Parsons, 1990) that "populations from ecological margins are likely to have been selected for environmental stress resistance, and so are expected to contain genotypes useful in countering stressful periods". Parsons concludes that "conserving populations from the more benign habitats may be a strategy of restricted use, when the primary aim is the maintenance of high levels of stress resistance to ensure survival against future environmental changes".

3. There will be no differences in persistence between core and peripheral populations. This occurs when gene flow from the core is stronger than selection in the periphery. Mayr (1965, 1970) proposed that near the species border environmental conditions are marginal and selection is severe, hence, only a limited number of genotypes is able to survive. Mayr suggested that gene flow from core to periphery becomes an increasingly one-way inflow,

whereas core populations are in the midst of a stream of a multidirectional gene flow. Thus, they harbor at all times a large store of freshly added immigrant genes, and peripheral populations, therefore, often have lower genetic diversity than core populations. However, there could be cases of peripheral populations replenished by a steady stream of immigrants from a more favorable portion of the species range; peripheral populations are thus merely "sinks" while core ones are the "source" (Lawton, 1993). In addition, though each of the relatively isolated peripheral populations loses variability due to drift, all of them combined retain the same variability of the far less isolated core populations. Mayr cites the peripheral population of *Drosophila subobscura* from Israel, which is chromosomally polymorphic to the same degree as core populations of this species (Goldschmidt, 1956). This null hypothesis of virtual equality of core and periphery we call the "Mayr hypothesis." It implies that no differences in persistence under GCC are expected between core and peripheral populations. If this hypothesis is not rejected, no preferential allocation of conservation effort can be prescribed, and the core-periphery distinction is irrelevant for environmental deployment with respect to GCC.

THE CORE–PERIPHERY HYPOTHESES AND CLIMATIC TRANSITION ZONES

If the Carson hypothesis is favored (cores are likely to persist better than peripheries), then a GCC-oriented conservation strategy for a species of interest (i.e., a wild relative of a cultivated plant, or a species of aesthetic value or of a major ecosystemic function) should concentrate on the core area of distribution, by protecting it from current development leading to habitat destruction and other man-induced population reductions. On the other hand, if the Fisher hypothesis is favored (peripheral populations are more resistant than core ones), the same strategy should be directed to the periphery region of this species' distribution. The Fisher hypothesis is of particular interest, as its validation permits a highly cost-effective conservation strategy. This is because species boundaries often coincide with climate transition zones, which are therefore rich in peripheral populations. For example, the desert/nondesert transition zone in Israel borders on three biogeographical provinces — the Saharo-Arabian desert at its northern edge, the Asian steppes at the southwestern edge, and the Mediterranean province at the southeastern boundary. As a result, this narrow transition zone exhibits a high density of distributional boundaries and is inhabited by a large number of species represented by peripheral populations (Danin and Plitmann, 1987). On a larger scale, most species occurring in Israel, except for endemics, can be considered as represented by peripheral populations, while their cores are elsewhere. Thus, several species of conservation interest are likely to have geographically overlapping peripheral populations within the climatic transition zone of Israel. But each will have a core population in a different area. Under the Carson hypothesis, for conserving several species of interest, several different reserves have to be established in the core area of distribution of each species. Under the Fisher hypothesis, all these species can be conserved in one reserve, located at a climatic transition zone. The Fisher hypothesis and its ramifications, therefore, have the most practical applications, since if it is valid, the regions requiring protection now, to serve as repositories to be utilized later, can be easily defined. Resources invested in their preservation will be cost-

effective in an environmental deployment for a GCC risk-aversion. Due to its significance in the applied context, we will now elaborate on the hypothesis that peripheral populations will persist better than core ones, and should therefore receive attention.

STRUCTURAL AND GENIC DIVERSITY IN CORE AND PERIPHERY

In many *Drosophila* species, polymorphism for chromosomal inversions but not genic heterozygosity decline from core to periphery (Brussard, 1984). Core–peripheral decline in genic heterozygosity is predicted by the Carson hypothesis, and its absence in *Drosophila* species is attributed to migration (Gillespie, 1975), and to the fact that their peripheral populations are not small enough, and grow quickly following bottlenecks. The decline in structural diversity, however, is more in line with the Fisher hypothesis.

Following da Cunha and Dobzhansky (1954), Brussard suggested that since traits on which selection is most likely to act are quantitative, and determined by polygenic inheritance, selection for these traits is stabilizing in the core. In order to minimize production of individuals with extreme phenotypes, linkage arrangements that combine alleles of opposite effects and an inversion that "congeals" the supergene will be favored. In the periphery "exploitation selection" prevails, whereby the common fluctuations in numbers select for maximum flexibility and generality with respect to adaptations to variable densities and environmental stress. The reduced structural polymorphism may therefore indicate a higher genetic flexibility in the periphery, given that inversions "lock" genome segments and reduce their recombinability.

Brussard (1984) concluded that peripheral areas exposed to stressful and unpredictable conditions do not favor average phenotypes (e.g., tolerance to desiccation stress may be irrelevant in optimal core environments, but is important in the periphery). Hence, free recombination enabling resistant phenotypes to be produced will be selected for, and inversions that retard recombinations will be selected against. Therefore, different core populations will have the same resistance to stress, irrespective of the ecological setting of their environments. But peripheral populations are expected to have higher resistance, and to display more variations in additive traits.

GENOTYPIC TOLERANCE AND PHENOTYPIC PLASTICITY

In spite of their high tolerance, peripheral populations are unable to expand beyond the distributional boundaries and increase their species' range, probably because the acquisition of increased stress resistance has a metabolic cost which precludes acclimation (Parsons, 1991). For example, selection in *Drosophila melanogaster* for desiccation resistance has lowered the phenotypic plasticity as expressed in acclimation to desiccation (Hoffmann, 1990). Parsons (1991) concluded that range expansion into more stressful habitats is precluded by the concomitant metabolic cost of adaptations to stress. Thus, species margins can be related to climatic extremes, where metabolic costs may be sufficient to preclude major range expansions even though variability may be high. Peripheral populations should have both high genetic variability and phenotypic plasticity. But extreme peripheral ones will be devoid of phenotypic plasticity, which prevents them from producing founding populations in even more extreme conditions outside the current range.

CORE–PERIPHERY IN PLANTS

Annual plants of arid regions exhibit large variability in size, features of life-history (Went, 1949; Aronson et al., 1990), and high phenotypic plasticity (Bradshaw, 1965; Schilchting, 1986; Sultan, 1987). This is considered adaptive in unpredictable environments (Levins, 1963; Jain, 1979). Genetic differences between peripheral and core populations of plant species depend markedly on the dimensions of gene flow. Levin (1981) concluded that although gene flow in plants is weak, it permits substantial local differentiation. Loveless and Hamrick (1984) reviewed the literature extensively and concluded that, at least in outcrossing species, gene flow is sufficient to continually introduce novel alleles into widely separated populations. A more recent review (Heywood, 1991) suggested that gene dispersal via pollen is more extensive than previously thought. This should reduce genetic variability in peripheral populations of outcrossed species, but autogamous species display remarkable levels of local genetic differentiation (Heywood, 1991). Finally, a recent study (Zanetto and Kremer, 1994) of the European oak *Quercus petrea* (Matt) Lieb. across its range, discovered higher heterozygosity in the core than in the periphery, but a higher number of alleles per locus in the periphery than in the core.

CORE–PERIPHERY AND THE CLIMATIC TRANSITION ZONE IN ISRAEL

Aronson et al. (1990) found that 8 plant species were more abundant and more variable in plant size in the core than in the periphery within Israel. They suggested that the peripheral populations might have been selected for the very specific conditions at the desert edge, which have reduced their genetic variability. In a theoretical review, on the other hand, Nevo and Beiles (1988) proposed a positive correlation between genetic and environmental variation caused by "diversifying selection". Variable selection over space and time is responsible for the maintenance of extensive genetic variation, and the restrictions on the maintenance of stable polymorphism decline in regions with spatio-temporal climatic unpredictability. Oscillatory changes in the environment induce oscillatory microevolutionary responses (Holt, 1990). These notions are supported by evidence from Israel, where a significant distinction in genetic variability between arid and mesic populations of 38 species was detected (Nevo, 1983; Nevo and Beiles, 1988). Among the plants were 28 populations of *Hordeum spontaneum* C. Koch analyzed for 28 loci, and 22 populations of *Triticum dicoccoides* (Ascherson et Graebner) Aaronsohn analyzed for 42 loci. Five loci were more diverse in mesic populations, and 10 loci and all other genetic indices showed higher diversity in xeric populations. Peripheral populations at the desert edges (e.g., *H. spontaneum*) exhibited higher levels of polymorphism and heterozygosity than core populations, and the trend was more pronounced in sedentary animal species (e.g., in land snails). Average heterozygosity and gene diversity were positively correlated with rain-fall variations (Nevo and Beiles, 1988), strongly in sedentary land snails, but weakly in *H. spontaneum*. We envisage that since populations in the transition zone of Israel have evolved in unstable environments and have high genetic diversity, some of their genotypes will survive GCC, whereas in core populations of same species genetic diversity is low, and no genotypes resistant to even milder changes exist. That peripheral populations of annual plants are highly opportunistic as compared

with core populations, can be implied from the study of Boeken and Shachak (1994) carried out in the climatic transition zone of Israel. Species represented there by peripheral populations, both those with the core in the Mediterranean region and those with the core in the desert, responded to man-made disturbances that increased local soil moisture much more strongly than species represented there by core populations.

CASE STUDIES — PRELIMINARY RESULTS

PHENOTYPIC VARIABILITY AND PLASTICITY IN WILD BARLEY

Wild barley, *H. spontaneum*, is a widespread Irano-Turanian-Mediterranean annual grass (Harlan and Zohary, 1966). It grows in regions with between 100 and 1000 mm mean annual rainfall, and its distribution is limited by low winter temperatures and extreme summer drought (Nevo, 1993). Several thousand spikes were collected from 12 Turkmenian and 6 Israeli populations in the spring of 1992 and 1993, and sampled using a mixed or clustered sampling strategy (Marshall and Brown, 1975)following Mendlinger's (1980) protocol. Seeds from each of 30–50 plants spaced 1–2 m apart along a transect were collected into separate bags. Five of the Israeli populations were at the southern periphery of the species distribution (Negev and Judean deserts), and one Turkmenian population was at the northern periphery of the distribution, whereas the other 11 Turkmenian populations (foothills of Kopet-Dag chain and Badhis Highland) and one Israeli population represented core ones.

The collected seeds were germinated in a greenhouse and each plantlet was planted in a sterile sand garden in the Blaustein Institute for Desert Research at Sede Boker, (100 mm mean annual rainfall), in a completely randomized block design. The plants were grown between November 1993 and May 1994, under two water treatments, with 8–10 replicates per treatment per population. The water stress treatment added 37 mm, and the nonstressed one added 75 mm to the natural rainfall of 47 mm in that winter. At each watering, 0.25 g fertilizer NPK 20:20:20 for each plant was applied in the intervals between successive rainstorms. After establishment, the plants were monitored every second day until the appearance of awns, and daily thereafter. At senescence the spikes were harvested, and measured in the laboratory.

Phenotypic variability in 18 phenological and morphological traits of the plants, expressed in coefficient of variation, CV, (standard deviation divided by mean of values over all populations), ranged between 3.9% and 74.1% (for days until awn appearance, and number of reproductive tillers, respectively, in peripheral populations under stress). Mean CV was 4–75% higher in nonstressed peripheral populations compared with nonstressed core populations, in 14 traits. The mean CV in core populations was higher than in peripheral populations, in only four traits. Variability increased under stress in core populations in all traits except for two vegetative ones (number of vegetative tillers and vegetative tillers' height). In peripheral populations, variability increased in 9 traits and decreased in 9 other traits (Table 1). Thus, peripheral populations not only are phenotypically more diverse, but are less affected by stress.

Two-way ANOVA revealed significant interactions between water treatment (stressed

Table 1

Periphery/core ratio of coefficients of variation, CVs, of 18 traits in all plants of all 12 core populations combined, and plants of all 6 peripheral populations combined, and CVs of all plants from peripheral populations, of water-stressed and nonstressed populations of *Hordeum spontaneum* from Turkmenistan and Israel, grown in a garden experiment in Sede Boker, 1993 (arranged in decreasing order of nonstressed populations)

Trait	Nonstressed		Stressed	
	Ratio	CV*	Ratio	CV
Awn length	1.75	40.0	1.52	37.0
Days until awn appearance	1.70	6.7	1.74	1.7
Number of nodes	1.60	24.3	1.30	23.1
Number of spikelets in a spike	1.42	23.6	0.88	19.8
Spike length	1.42	18.2	0.88	15.5
Culmen length	1.42	41.2	0.91	36.7
Total height	1.38	31.9	0.83	25.9
Penultimate leaf length	1.34	39.2	1.39	50.0
Days until anthesis	1.29	5.2	1.48	6.9
Height of vegetative tillers	1.24	42.0	1.26	41.0
Number of reproductive tillers	1.23	70.7	1.11	74.1
Internode length	1.20	33.3	0.89	33.7
Flag leaf length	1.05	45.3	1.17	51.6
Number of vegetative tillers	1.04	39.1	1.54	45.4
Days until tillering	0.99	33.5	0.96	35.5
Seed weight	0.99	28.8	0.84	26.3
Spike weight	0.83	29.1	0.59	28.7
Spikelet weight	0.75	21.5	0.72	26.7

*CVs of stressed plants are significantly different ($p < 0.01$) from those of nonstressed plants, Wilcoxon matched-pairs signed-ranks test.

vs. nonstressed) and geographical source (core vs. periphery) in 8 of the 18 examined traits, indicating differences between core and peripheral populations with respect to their phenotypic plasticity. These 8 traits exhibited mean population reduction in values under water stress, as compared to nonstressed populations (except for number of nodes in peripheral populations). Core populations exhibited a significantly stronger reduction than peripheral populations (Table 2), suggesting a weaker phenotypic plasticity in peripheral compared with core populations (Schlichting, 1986; Aronson et al., 1992). Thus, peripheral populations of *H. spontaneum* are phenotypically more diverse but less plastic than core populations of this species.

These preliminary results of the *H. spontaneum* study support Bradshaw's hypothesis (Bradshaw, 1965) of antagonistic selection for phenotypic flexibility and genetic diversity, and the proposition of Parsons (1991) that increased stress resistance could reduce phenotypic plasticity if the same mechanism controls the plastic response and the genetic

Table 2

Mean values for phenotypic traits of *Hordeum spontaneum* of 12 core and 6 peripheral populations
from Turkmenistan and Israel, and the effect of experimental water stress, in a garden experiment
at Sede Boker, Negev Desert, Israel, growing season of 1993/94. Lengths are in cm. Displayed traits
are those demonstrating significant interaction between geographical category and treatment
(2-way ANOVA), arranged in a decreasing order of % reduction in stressed core populations

	Core		Periphery	
Trait	Values in nonstressed populations	% reduction in stressed populations*	Values in nonstressed populations	% reduction in stressed populations
Culm length	49.2	33.2	41.6	20.0
Flag leaf length	7.4	32.5	7.5	14.8
Internode length	10.8	31.8	11.1	22.5
Total height	68.8	28.2	60.8	15.5
Penultimate leaf length	14.4	26.5	14.8	9.3
Number of spikelets in a spike	29.6	25.5	24.6	1.0
Spike length	19.6	15.5	19.2	5.7
Number of nodes	4.6	2.4	3.7	−4.0

*Difference between core and peripheral populations in percent reductions in trait values under
stress is significantly different, $p < 0.01$, Wilcoxon matched-pairs signed-ranks test.

variation in stress resistance. It therefore remains to be evaluated which of the two
strategies contributes more to persistence under GCC.

GENETIC VARIABILITY IN THE CHUKAR PARTRIDGE

The chukar partridge *Alectoris chukar* (J.E. Gray) is a ground-dwelling Phasianid bird.
It ranges from China and the Himalayas in the east to the Near East and Bulgaria in the
west (Cramp and Simmons, 1980). The deserts of Israel and Sinai delineate its southwestern
geographical distribution border (Watson, 1962; Randi et al., 1992). In Israel, the
distribution is contiguous across the mesic Mediterranean habitats in the north to the xeric
region in the south, and becomes patchy in the extreme hot desert in the far south (Pinshow
et al., 1983; Paz, 1987).

In 1993 five populations of chukars were sampled in Israel along a geographical
periphery-to-core gradient of the continuous distribution range: Ramat David, Ben-
Gurion Airport, Yattir, Nevatim, and Sede Boker. The northernmost population sampled
of the Mediterranean region, at Ramat David in northern Israel, represented a core
population, while the southernmost population sampled, of Sede Boker in the Negev
Desert, represented a peripheral population. Approximately thirty birds were sampled
from each population. Tissue samples were transported in dry ice to the laboratory and
polyacrylamide gel electrophoresis was used to resolve 32 genetic loci, according to the
method of Randi and Alkon (1994).

Of the 32 loci examined 14 (43.75%) were polymorphic over all five populations. A
monotonic trend of increasing genetic diversity, moving from the core toward the

Table 3

Genetic variability estimates for 32 loci of chukars sampled in 1993, across a gradient from core (Ramat David) to periphery (Sede Boker)

Location	Mean number of alleles per locus	Percentage of polymorphic loci	Observed mean heterozygosity ± SE	Expected mean heterozygosity* ± SE
Ramat David	1.4	28.1	0.062 + 0.023	0.082 + 0.029
BG airport	1.4	28.1	0.078 + 0.026	0.084 + 0.030
Yatir	1.5	37.5	0.090 + 0.031	0.090 + 0.030
Nevatim	1.5	37.5	0.094 + 0.030	0.101 + 0.030
Sede Boqer	1.6	40.6	0.104 + 0.037	0.101 + 0.033

*Hardy–Weinberg expected mean heterozygosity.

periphery, was consistent for all examined variability measures: number of alleles per locus, expected (Hardy–Weinberg) heterozygosity, observed heterozygosity, and percentage of polymorphic loci (Table 3). The trend was also consistent with the trend revealed by Randi and Alkon (1994), who sampled three of these populations three years earlier. The most extreme differences in genetic diversity were found among the two furthermost populations of Ramat David (core) vs. Sede Boker (periphery). For example, the percentage of polymorphic loci and observed heterozygosity for the core population were (respectively) 28.1% and 0.062, compared with 40.6% and 0.104 at the periphery.

We did not sample the most peripheral populations in the extreme arid region, which are probably smaller and more isolated, and where genetic variability may therefore be relatively low. But our results pertaining to the contiguous distribution support the Fisher hypothesis: environmental favorableness and predictability for the chukar are expected to decrease, and the number of maintained genotypes and the levels of polymorphism and heterozygosity increase, from core to periphery.

CONCLUSIONS

Our preliminary results indicate higher phenotypic (wild barley) and genetic (chukar partridge) variability in peripheral than in core populations. Though our partridge data pertain to comparison of core with southern periphery only, the barley study included both southern and northern peripheries of the species distribution. Thus, the observed trend is not just an aridity cline, but is likely to reflect a core–periphery dichotomy. The barley and the partridge, a plant and a bird species, are sufficiently divergent in the taxonomical sense, so as to confer generality to the proposed ecological dichotomy. The peripheral populations of both the barley and the partridge co-occur in the Israeli climatic transition zone between the desert and the Mediterranean regions. Further research on the genetic variability of the barley and phenotypic variability of the partridge, as well as on the heritability of drought resistance in peripheral populations of other plants in Israel, is underway. But the preliminary findings reported here may already point at an urgency for

habitat conservation of the Israeli climatic transition zone, as an effective environmental deployment for mitigating GCC ecological effects.

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