THE INFLUENCE OF AGRICULTURE ON GENETIC BIODIVERSITY

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ABSTRACT

Agricultural practices have profoundly modified the genetic biodiversity of indigenous plant species, crop populations, and crop pathogens in the agricultural landscape. The nature and extent of the changes in genetic biodiversity depend on the farming systems in question. Modification of genetic biodiversity increases in magnitude as one moves from extensive grazing systems, which retain much natural genetic biodiversity, through short term leys to arable systems where genetic biodiversity in many crop populations is zero. Reductions in biodiversity of crops have led to the evolution of more aggressive, asexually reproducing pathogen populations which are more difficult to control than those from which they have been derived. Changes in management to encourage the retention of genetic diversity in indigenous plant populations, and to reintroduce genetic diversity into arable crops may have multiple environmental benefits.

INTRODUCTION

Genetic biodiversity may be defined as all those forms of genetic variation found within a species which influence, or could potentially influence, the performance or fitness of individuals (Ennos & Easton, in press). The importance of genetic biodiversity is that it is the raw material required for evolutionary change of populations. The amount and quality of genetic biodiversity within a species or population of that species can be roughly equated with the potential of that population to adapt to environmental change (Fisher, 1930).

Because of our ignorance of the genes responsible for adaptive differences between individuals, there is no simple way of assessing genetic biodiversity from measurements of variation at the DNA level (Lynch, 1996, Ennos *et al.*, 1997). Genetic biodiversity is most readily estimated from traditional quantitative genetic analysis of traits known to be of adaptive significance (Lawrence, 1984). The coefficient of additive genetic variation for a character is a convenient parameter for quantifying the genetic biodiversity for a particular trait (Houle, 1992). In a world subject to continual environmental change, the maintenance of genetic biodiversity is essential for the adaptive adjustments needed by species for their continued survival. Within agriculture, genetic biodiversity is an absolute requirement for the development of improved crops (Simmonds, 1979).

The broad aim of this paper is to review the extent to which agricultural practices have altered and continue to alter the genetic biodiversity of species within the area where they are undertaken. For this purpose we will contrast genetic biodiversity under a variety of types of

agricultural management with the natural situation existing before agriculture was introduced. To limit the discussion to manageable proportions I will concentrate on three aspects of the effects of agricultural practice on genetic biodiversity; the effects of agricultural operations on the genetic diversity of indigenous species whose distributions are largely taken over for agricultural production, the direct influence on crop species diversity, and lastly the indirect effect on genetic diversity within pathogens of the crop.

The paper aims to show the enormous and fundamental changes in genetic biodiversity that occur when agricultural practices are introduced into an area, and emphasises the extent of human control over these changes. The changes brought about have had a range of consequences, some desirable and others less so. The scale of these effects and their consequences must be appreciated in any consideration of biodiversity and conservation within agriculture.

GENETIC BIODIVERSITY BEFORE AGRICULTURAL MANAGEMENT

The populations of plants of any one species existing in Britain before agricultural development would generally have been sufficiently large and interconnected to harbour substantial genetic biodiversity. In large populations the input of genetic variation through mutation is sufficient to ensure a high evolutionary potential (Lynch, 1996). The observed level of genetic biodiversity in this situation is determined by patterns of natural selection operating in populations, and is not materially influenced by random genetic drift.

Certain patterns of selection found in natural plant populations actively favour maintenance of genetic biodiversity above the levels expected in their absence (Ennos, 1982, Hedrick, 1986). For example selection in heterogeneous environments which vary in space and time will tend to maintain genetic variation associated with the different environmental conditions encountered. Interactions with pests and parasites that vary in abundance may also generate selection that maintains genetic diversity for traits such as pest and pathogen resistance (Barrett, 1988, Parker, 1992). These interactions will in turn lead to the evolution of genetically variable and sexually reproducing pathogen populations that are able to exploit their genetically variable hosts. These systems comprising genetically biodiverse plant populations interacting with genetically biodiverse pests and pathogens are commonly found in natural situations unaffected by agricultural practices (Burdon, 1987, Burdon & Jarosz, 1991).

CHANGES UNDER AGRICULTURE

With the coming of agriculture, dramatic changes have been imposed on these wild populations, altering to a greater or lesser extent their genetic diversity. The degree of change in these systems is dependent upon the type of agricultural practice imposed. I will consider three different agricultural systems spanning the spectrum of effects. The first is an extensive grazing and forage conservation system, the second an intensively managed arable system, and the third an intensively managed grazing and forage conservation system.

INDIGENOUS FLORA

Whichever system is considered, agricultural management of an area brings with it the creation of a distinction between desirable 'crop' plants, and those not involved in the production system. The latter are excluded from the productive area of land either by the actions of grazing stock, or by the regular disturbance, cultivation, fertilisation, crop competition and pest and pathogen control that are associated with arable systems. The consequence is that the indigenous species become restricted in distribution to the margins of the managed land and a less variable set of environments than they would otherwise occupy. The indigenous plant species distributions are fragmented to an extent dependent on the particular spatial pattern of agricultural development. In some cases the populations will comprise many isolated fragments, each of small size, separated by large managed areas from which they are excluded. In other cases they may become restricted to linear but spatially connected habitats such as hedgerows.

Significant changes in genetic biodiversity within these marginalised species are likely to occur as a consequence of the fragmentation and reduction in population size that they have experienced. Where species are excluded from a particular subset of their habitats, the genotypes specifically adapted to those habitats will be lost. In addition within small isolated populations genetic biodiversity will be lost due to random genetic drift in every sexual generation by a fraction that is inversely proportional to the effective population size (Lande & Barrowclough, 1987, Barrett & Kohn, 1991, Ellstrand & Elam, 1993).

This loss of genetic biodiversity and associated adaptive potential will be very serious for species with low rates of pollen and seed dispersal which easily become genetically isolated as a consequence of agricultural development. In species that have effective pollen and seed dispersal, however, gene flow can still take place among spatially separated remnant populations. In such a metapopulation the effective population size is the sum of the population sizes of all remnants, and the rate of loss of genetic variation is very much reduced compared with the rate of loss in a single genetically isolated remnant (Wright, 1951).

As a rule of thumb, loss of genetic biodiversity in marginalised indigenous species will be greatest in annual, inbreeding or outcrossing insect pollinated taxa, and least in perennial, outcrossing, wind pollinated taxa. Where species are vulnerable to loss of genetic variation, the spatial distribution of remnant populations may be of crucial importance in determining the seriousness of the effect. Remnant populations arranged in the landscape in such a manner as to facilitate gene exchange via pollen and seed will retain much higher levels of genetic variation, and a greater potential for adaptation, than the same number of populations of similar size that are completely isolated from each other. Thus sympathetic design of marginal land to promote gene flow among remnant populations, and the retention of a variety of habitat types in the margins of agricultural landscapes may play an important role in maintaining genetic biodiversity and adaptability in the indigenous flora of an area.

CROP AND PATHOGEN POPULATIONS

The above considerations apply to all forms of agricultural systems. I will now consider genetic biodiversity within the crop and crop pathogen components of three specific management systems, contrasting them with genetic biodiversity levels in a non-agricultural situation.

Extensive grazing systems

Consider first an extensive grazing system in which a proportion of the land is devoted to long term pastures and the remainder to long term hay meadows for fodder production. In such a system there will be relatively little manipulation of the abiotic habitat other than the addition of periodic fertilisation. To a large extent the existing environmental heterogeneity will be retained. As a consequence of grazing and cutting different plant species will increase in frequency in the two situations, but a diversity of species will be retained. A number of species, for example ryegrass (*Lolium* spp.) may be encouraged in both situations. In such an extensive system there is no conscious effort to genetically manipulate the crop populations.

Within such an agricultural system extensive genetic biodiversity is expected to remain in the crop species. Genetic biodiversity associated with adaptation to local soil heterogeneity are likely to be retained (Snaydon, 1962), and because there is no control of pest and pathogen populations genetic diversity in resistance characters are expected in the crop. The application of grazing and cutting regimes, however, will also impose quite different selective regimes on populations in the pasture and hay meadows, and genetic divergence between these populations will evolve. Evolution of differences in such characters as tillering ability, flowering intensity and timing are well documented in *L. perenne* (Cooper, 1959), and the rapidity within which these genetic changes take place may be very high (Brougham & Harris, 1967, Davies & Snaydon, 1976, Snaydon & Davies, 1982). Genetically differentiated but biodiverse land races adapted to the particular management regimes imposed will be seen. Such populations have been the raw material for genetic improvement programmes in many forage species.

We can conclude that for those species retained in the extensive grazing situation, genetic biodiversity within populations may remain as high as that within unmanaged populations, but as a consequence of management the genetic biodiversity between populations will actually be increased above that found in the natural situation. Thus, in this instance, agricultural practices positively enhance genetic biodiversity within the crop species.

Since the species diversity of the pasture and meadow populations remains high, and genetic biodiversity within them are relatively unaffected by management, we anticipate that pathogen populations adapted to crop species will be as genetically biodiverse as those in the natural situation, and will be predominantly sexually reproducing. Our rather sketchy knowledge of this area, derived predominantly from studies of endophytic fungi of grasses, suggests that this conclusion is justified (Leuchtmann & Clay, 1990).

Intensive arable systems

At the other end of the spectrum of agricultural practices are intensive arable systems. Here large inputs involving cultivation, fertilisation, irrigation, and control of competitors, pests and pathogens are applied to an area of land to produce a completely homogeneous and optimal environment for crop growth. Introduced into this environment is a monoculture of an exotic crop species which has been adapted through the process of crop breeding to produce maximum yield of harvestable product under these conditions.

In Britain the vast majority of crops raised in this manner are the products of line breeding (inbreeding cereals) or clonal reproduction (potatoes) (Simmonds, 1979). These methods of breeding produce crop varieties that are genetically uniform for important economic and harvest traits, but have the side effect of generating genetic uniformity at all other loci in the genome. Each variety comprises a single genotype and contains no genetic biodiversity. Thus when an arable crop is introduced into a new area the substantial genetic biodiversity originally existing in the indigenous populations is reduced to zero.

In such a crop population there is no potential for evolutionary change. Evolution of arable crop species of this type is confined to plant breeding stations which also harbour the readily useable genetic biodiversity upon which future evolution will be based. Changes in the genetic composition of crop populations over space and over time are entirely governed by the range of varieties available, and the policy of deployment of these varieties by man.

Thus in the arable crop situation, which covers roughly one third of the agriculturally managed land in Britain (Anon, 1996), the genetic biodiversity of populations is entirely under human control. Deployment of diversity is almost always as populations of single genotypes, with genetic biodiversity being confined to variation between varieties planted in different fields or regions. It should be remembered that these varieties may themselves be closely related genetically. These points serve to emphasise the enormous control and responsibility that man has for determining genetic biodiversity of plants within Britain.

Having acknowledged the profound effect of arable agriculture on plant biodiversity, we can explore the indirect effect that this has had on biodiversity in associated pathogen populations. The environment available to an arable crop pathogen differs very markedly from that available to a pathogen of indigenous plants. Pathogens on indigenous plants exploit a resource at relatively low density, relatively long lived and stable, which displays heterogeneity as a consequence of both environmental and genetic variation. In such a situation transmission probabilities between host plants are relatively low. Pathogen genotypes showing slow pathogen development with minimal deleterious effects on the host are expected to evolve, and genotypes practicing sexual reproduction capable of producing genetically variable offspring will be favoured (Ennos, 1992).

In a crop situation, on the other hand, the hosts are at high density, are short lived and show little environmental and genetic heterogeneity. In such circumstances there will be selection for pathogen genotypes that rapidly exploit and reproduce on the crop host since the probability of transmission to a new host is very high. Because of the genetic uniformity of

the crop the pathogen may rely on asexual reproduction which can ensure early propagation and reproductive rates since the necessity for producing variable progeny is removed (Ennos, 1992). Thus we anticipate the evolution of more damaging, asexually reproducing pathogens in the crop situation, which themselves have low genetic biodiversity.

These predictions are borne out by what we know of the evolution and genetic biodiversity of crop pathogens (Barrett, 1981). There is good experimental evidence that crop pathogens evolve earlier reproduction and greater aggressiveness over time where crop densities are high (Kolmer & Leonard, 1986, D'Yakov & Gorlenko, 1989, Holguin & Bashan, 1992). A much greater prevalence of asexual reproduction and lower genetic biodiversity in crop pathogens compared with their counterparts on wild hosts can also be seen (Brown *et al*, 1991, Kohn, 1994). Indeed evolution in crop pathogen populations is often modelled as evolution in a mixture of clones, and as the spread of new mutations occurring in a clonal, asexual population. Thus the profound changes in species diversity, density and genetic biodiversity in crop populations have an enormous indirect effect on the genetic biodiversity of their pathogens. An understanding of these effects is required to understand arable crop pathogen impact and control of arable crop pathogens.

Short term leys

In terms of the intensity of agricultural management, and the extent of changes in genetic biodiversity, short term leys for pasture and hay/silage lie somewhere between extensive grazing and arable systems. Modification of the soil environment to increase homogeneity and fertility is practiced. Semi natural vegetation is replaced by selectively bred forage varieties of a limited number of the species that are present in the original vegetation. These forage varieties are often selected from land races evolved under more extensive grazing systems.

During the selection of these outbreeding crops, there is a reduction in genetic biodiversity for a number of agriculturally important traits such as leaf size, growing period and digestibility. However the population improvement method of breeding based on crosses among a number of different genotypes ensures that genetic biodiversity is retained for many other characters (Simmonds, 1979). The extent of remaining genetic biodiversity within populations is much closer to that found in wild populations than in arable crop varieties. On the other hand the widespread use of the same variety over large areas will reduce the genetic biodiversity between populations compared with the situation for extensive grazing.

From the point of view of crop pathogens, the density of crop species is increased over that found in extensively managed pastures and conditions for transmission of pathogens are increased. An increase in pathogen aggressiveness may evolve. The crop population is still, however, genetically variable for resistance traits and there remains an advantage to sexual reproduction in the pathogen. Thus genetic biodiversity in the pathogen is not expected to decrease, as in the case of arable crop pathogens, nor is an entirely asexual reproductive system likely to evolve in the pathogen.

CONCLUSIONS AND IMPLICATIONS

This survey of different agricultural management systems emphasises that each has effects on the genetic biodiversity of its component crop and pathogen populations, but the extent and nature of these effects can be very different. However a number of general conclusions can be drawn. The first is that a reduction in the genetic biodiversity of indigenous species is anticipated wherever agriculture is practiced as a consequence of the fragmentation and isolation of their populations. The impact of this is crucially dependent on the extent of genetic exchange that is possible between the remnant populations

The second is that crop populations show a huge range of genetic biodiversity from zero in most arable crops to levels comparable to those in wild populations under extensive grazing management. Because of the concentration of particular farming systems in different regions, there will be huge geographic differences in genetic biodiversity of crops populations (and their pathogens) throughout Britain.

The third general conclusion relates to the way we grow our crops, and the level of genetic biodiversity which they contain. This can have profound effects on the genetic biodiversity of the pathogens with which they interact. Arable crops comprising monocultures of single genotypes lead to the evolution of aggressive, asexual pathogen populations with low levels of genetic biodiversity. These are very different from populations of pathogens on non agricultural hosts.

Recognition of the undesirable effects of single genotype monoculture on pathogen evolution have stimulated moves to introduce genetic biodiversity into arable crop populations through the planting of varietal mixtures carrying different resistance alleles, as well as genetic diversity at other loci. Significant reductions in pathogen damage have been achieved in experimental trials, though the planting of such varietal mixtures has not been widespread (Wolfe, 1985).

This review has illustrated the enormous influence that agricultural practices can have on the level of genetic biodiversity in many components of the agricultural landscape. This implies that changes in management can make a real difference to genetic biodiversity levels which may underpin increases in biodiversity at higher levels. Thus planning to facilitate gene flow among native vegetation remnants in an agricultural landscape will help to maintain the genetic biodiversity and adaptive potential of the native species in these remnants, and may ensure their retention in the face of environmental change. Inclusion of greater genetic biodiversity in arable crops may limit the evolution of increasingly aggressive crop pathogens, and reduce the need for chemical control of these pathogens. This in turn will help to reduce pesticide use and increase local species diversity. Agricultural landscapes represent some 80% of the land area in Britain. Sympathetic changes to their management to promote the conservation of indigenous genetic biodiversity, and the wise deployment of crop genetic biodiversity could have major beneficial environmental impacts for the country.

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