Plant Breeding for Agricultural Diversity

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ABSTRACT
Plants bred for monoculture require inputs for high fertility, and to control weeds, pests and diseases. Plants that are bred for such monospecific communities are likely to be incompatible with the deployment of biodiversity to improve resource use and underpin ecosystem services. Two different approaches to breeding for agricultural diversity are described: (1) the use of composite cross populations and (2) breeding for improved performance in crop mixtures.

INTRODUCTION
Monocultural plant communities dominate modern agriculture. Monocultures are crops of a single species and a single variety; hence the degree of heterogeneity within such communities is severely limited. The reasons for the dominance of monoculture include the simplicity of planting, harvesting and other operations, which can all be mechanized, uniform quality of the crop product and a simplified legal framework for variety definition.

Monocultural production supports the design of crop plants from conceptual ideotypes. The wheat plant ideotype is a good example of a plant designed for monoculture. Wheat plants that perform well in monoculture interfere minimally with their neighbours under high fertility conditions, where all ameliorable factors are controlled. The aim of this design is to provide a crop community that makes best use of light supply to the best advantage of grain production (Donald, 1968). This design has produced wheats with a high proportion of seminal roots, erect leaves, large ears and a relatively dwarf structure. This ‘pedigree line for monoculture’ approach is highly successful, but it has delivered crop communities that do best where light is the only, or the main, limiting factor for productivity: therefore the products of this approach to breeding require inputs to raise fertility, and to control weeds, pests and diseases. This breeding effort, coupled to the increasing convenience of monoculture, now dominates modern farming but the restrictions involved have led some people to question the value of this approach to farming and breeding.

THE ECOLOGICAL ROLE OF AGRICULTURAL DIVERSITY
Darwin had a seamless view of population biology, evolutionary biology and ecosystem processes. The advantages of such a view are now being realized. For instance, Tilman (2001) points out two key findings: (1) that a greater number of terrestrial plant species can lead to greater ecosystem productivity and resource use and (2) that greater diversity can lead to greater ecosystem predictability and temporal stability. This links two key concepts: that diversity can underpin productivity and the stability of productivity; and that diversity underpins ecosystem functioning and therefore the ecosystem services required for sustainability.

Biodiversity in agroecosystems provides ecosystem services beyond the production of food, fibre, fuel and income. Altieri (1999) suggests that examples of ecosystem services
include the recycling of nutrients, control of local microclimate, regulation of local hydrological processes, regulation of the abundance of undesirable organisms, and detoxification of noxious chemicals. In addition, agrobiodiversity supports above- and below-ground trophic levels. For instance, Marshall *et al.* (2003) suggest that many arable weed species support a high diversity of insect species, that in turn support several bird species; indicating that weeds have roles within agroecosystems of supporting biodiversity more generally. The restricted biodiversity associated with monocultural plant communities limits the ecosystem services of those production systems, one simple example being the use of herbicides to eliminate all weeds within the crop.

Furthermore, Altieri (1999) recognizes the ecological sensitivity of monospecific communities, stating that nowhere are the consequences of biodiversity reduction more evident than in the realm of agricultural pest management. Altieri explains that the reasons are complex, but he sums up the problem as the loss of inherent self-regulation. Amongst the options that Altieri suggests for utilizing biodiversity to limit pest problems are high crop diversity through mixing crops in time and space, the presence of tolerable levels of specific ‘weed’ species and the deployment of genetic diversity by using variety mixtures or multilines.

The challenge is to link all of these ecological concepts by moving away from monoculture with its biological simplification and consequences for ecosystem services, while simultaneously providing functionality to the diversity incorporated within the crop community.

**EVOLUTIONARY THEORY IN PLANT BREEDING**

The neo-Darwinian view of the process of evolution describes four basic components: (1) the initial generation of variability, (2) the exchange of DNA between chromosomes (recombination), (3) differential reproduction and (4) isolation in space and time. Simmonds (1962) points out that the modern breeding of crops, (or mankind’s pursuit of adaptation of plants to monocultural cropping systems), has seen steps (1) and (2) as important steps only in the initial phases of generating new varieties, but (3) and (4) have come to dominate the process of plant breeding. This breeding effort produces (especially for inbreeding species) homozygous varieties that are adapted (perform well) to the conditions under which they were isolated or selected by the breeder. This process is distinct from providing crop genotypes or populations with a degree of adaptability. Adaptation is the property of a genotype which permits survival under selection; adaptability is the property of a genotype or population of genotypes which permits subsequent alteration of the norms of adaptation in response to changed selection pressures. Hence there has been a tendency to eliminate variability and adaptability in crop varieties and populations, and to pursue the notion that strictly uniform crop populations, adapted to a specific set of circumstances, is a universal ideal.

Suneson (1956) described a “new” method of plant breeding. He suggested that it is important to recognize the value of evolutionary fitness in plant breeding. Evolutionary change is based upon the interaction between populations and their environments, where environmental interactions are both abiotic and biotic. Suneson describes a process of assembly of seed stocks with diverse evolutionary origins, recombination by hybridization, the bulking of F1 progeny, and subsequent prolonged natural selection for mass sorting of the progeny in successive natural cropping environments. Therefore, Suneson promoted a method of plant breeding that moves away from the notion of strictly
uniform crop populations and towards populations with a high level of heterogeneity, thereby repeatedly harnessing all components of the neo-Darwinian view of evolution.

COMPOSITE CROSS POPULATIONS
The bulk population breeding method described by Suneson (1956) depends upon the nature and outcome of mass trials by artificial and natural selection acting on a heterogeneous mixture of competing genotypes. This is distinct from pedigree selection schemes where early and continuous individual selection begins in the F2 generation. In composite crosses a large number of carefully chosen varieties are intercrossed and all the hybrids are bulked together for propagation. The basic idea of the composite populations is that the introduction of genetic diversity may a) allow the isolation of superior individual lines in a cost effective manner, and b) that diverse populations may offer better performance than pure lines. These lines and populations are the result of adaptation to those selection pressures imposed during the breeding process, both natural and artificial, providing improved fitness to given environmental conditions. Indeed, the evidence from barley composite crosses, is that directional and stabilizing selection over a number of years tends to produce agronomically superior crops.

Composite cross populations also provide the option of farmer participation in the process of selection; this may be important since low input production systems are difficult to characterize, and all require slightly different emphases in the interactions between crop vigour, disease resistance, weed resistance, fertility scavenging and pest resistance. But also, importantly, with populations or lines with a broad genetic base there should be some capacity for a genetic response to selection, or adaptability. There are advantages to producers of providing a compromise between adaptation and adaptability, especially for low input production systems, because predicting the range and intensity of limiting factors year on year is impossible.

EFRC, in collaboration with the John Innes Centre, have produced six composite cross populations that are growing in trials across the UK. This work is part of a DEFRA-funded project ‘Generating and evaluating a novel genetic resource in wheat in diverse environments.’

BREEDING COMPONENTS FOR MIXTURE PERFORMANCE
Following an effective crop rotation, the simplest step forward for introducing diversity into cropping systems is to grow variety mixtures, followed by species mixtures. However, components are very rarely selected for performance in variety mixtures. Decisions on mixture composition are often based on yield in monoculture. But the underlying assumption may be incorrect: yielding ability, which is required for high monocultural performance, is not necessarily the same as competitive ability in mixtures (Hill, 1996).

Hill (1996) calls for an approach to breeding for mixtures that selects for good general and specific combining abilities with other varieties/species. Hill suggests two possible strategies, either focusing on one component of a mixture only, ‘the passive approach’, or focusing on both components using alternating cycles of selection, ‘the active approach’. In the passive approach a number of genotypes from one component could be assessed in all possible binary combinations against a set of testers drawn from the other component. In the active approach the roles of tester and tested are reversed in alternate cycles of selection. The active approach permits a degree of coevolution of components; the
passive approach should deliver varieties that are better suited to mixing with a particular crop type than varieties bred for monocultural communities. Breeding for mixture performance is especially important for organic or low input systems where the predictability of important variables is less certain than in conventional systems, and therefore the need for a crop community to buffer against the risks of these variables is more important.

CONCLUSIONS
Monocultural plant communities have different demands from plant breeding than cropping systems based on diversity. The ability of diverse cropping systems to provide inherent buffering against both biotic and abiotic variables without resorting to synthetic inputs is clear. As a consequence, the potential for biodiverse cropping systems to contribute to important ecosystem processes is greater than for monocultural communities. Composite cross populations are a way of producing crop communities with a higher degree of heterogeneity, as is breeding varieties for good ecological combining abilities in mixtures. However, any adoption of breeding for agricultural diversity requires shifts in legal and administrative frameworks and an improvement in the market acceptability of heterogeneous crops.

REFERENCES