

The role of genetic diversity in sustainable agriculture

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SUMMARY

The depletion of plant biodiversity with the rapid development of agriculture has attracted growing interest in recent years. This paper discusses the evolutionary consequences of monoculture with emphasis on the buffering effects of genetic heterogeneity on disease. The use of host plant resistance and systemic fungicides as disease control measures and their influence on sustainable agriculture are discussed. Three approaches of re-introducing genetic diversity into modern agriculture are indicated. These are composite crosses, multiline varieties, and variety mixtures. It is concluded that the variety mixtures approach holds promise for developing countries where low input cropping systems are practised.

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Introduction

The development of agriculture is one of the greatest relics of man's flair and desire to control his environment. The domestication and development of crop plants have not only given rise to better strains which have sustained great civilizations, but have also helped to disperse the crops from their main "centres of origin". With the onset of systematic breeding, concerted effort have been made by geneticists and breeders to improve crop plants which have opened new horizons for crop evolution. Conventional plant breeding methods have, until recently, normally been used to improve most cultivated crops (Allard, 1960). These methods rely mainly on selecting superior genotypes from either genetically heterogeneous populations such as

RÉSUMÉ

OPPOING-KONADU, E. Y. & ADU-DAPAAH, H. K.: *Le rôle de la diversité génétique dans l'agriculture durable.* L'épuisement de la biodiversité de plant avec le développement rapide de l'agriculture a attiré un intérêt de croissance ces dernières années. Ce papier discute les conséquences évolutionnistes de la monoculture avec l'accent sur les effets régulateurs de la hétérogénéité génétique sur les maladies. L'utilisation de la résistance de plante hôte et les fongicides systémiques comme des mesures de contrôle de maladie et leur influence sur l'agriculture durable sont discutés. Trois façons de la re-introduction de la diversité génétique dans l'agriculture moderne sont indiquées. Celles-ci comprennent: 1) Les croisements composites 2) Les variétés multilignes et 3) les mélanges de variétés. La conclusion est tirée que l'approche des mélanges de variétés tient une promesse pour les pays en voie de développement là où les systèmes de culture ayant peu de facteurs de production sont pratiqués.

landraces, or from the progeny of segregating populations (pedigree breeding), and/or on substituting specific new genes into already well-adapted genotypes. The selection of plants for improved resistance to diseases is one of the earliest objectives of plant breeding. To date, the possibility of improving on the performance and/or dependability of disease-resistant crop cultivars is a major concern of plant breeders.

This paper discusses the evolutionary consequences of genetic homogeneity and emphasizes the buffering effects of genetic heterogeneity on crop diseases. With examples taken mainly from cereal breeding, it also provides an understanding of genetic diversity from the standpoint of optimizing current and future progress and/or gains in breeding programmes.

The evolutionary consequences of plant breeding on cultivated crops

The significant increase in crop yields over the last half century can, in part, be attributed to breeding (Fehr, 1984). The advent and progress in plant breeding has, however, had serious implications on the amount and range of genetic diversity in crops (Eyzaguirre & Iwanaga, 1996). This is because as favourable alleles are selected and fixed, genetic variability is reduced. Thus, in crops that have a long history of improvement, the genetic gap between elite gene pools and unimproved pools or germplasm collections is growing larger with each breeding cycle (Martin, Blake & Hockett, 1991; Rasmusson & Phillips, 1997).

The selection of varieties for higher yield, uniformity in performance, and other qualities which are dictated by the industrial requirements of modern agriculture often reduce the number of different genotypes of a crop. This, according to Harlan (1976), is analogous to the reduction in the number of species used by man as compared to when agriculture first evolved. The joint effects of species monoculture and regional variety monoculture in reducing the genetic base of crops are further aggravated by the exchange of breeding material between breeders in different countries. International agricultural research institutes such as the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) and the International Institute of Tropical Agriculture (IITA) provide breeders with a wide range of materials from which they can make their selections. An outstanding line, therefore, has a high probability of being selected and used across continents.

The quest for specific plant characters by growers and breeders has led to the pursuit of these goals without due regard for the ecosystems which incorporate crop plants. In most industrialized agriculture, the over-extension of the pure-line theory has resulted in a few genetically homogeneous varieties being used in large-scale monocultures. This practice has increased the vulnerability of crops to diseases and pests. The

southern corn leaf blight epidemic in the United States in 1970 (Ford-Lloyd & Jackson, 1986), for example, resulted from the over-use of the cytoplasmic male-sterility factor (*Tms*). The "boom-and-bust" cycles on certain pure line varieties, resulting from the evolution of the pathogen to overcome the resistance of the host cultivars, is a direct consequence of deployment of cultivars in large-scale monocultures.

Barrett (1981, 1988) states that the two immediate effects of successful plant breeding are the reduction in the genetic diversity of crops and genetic erosion. The latter is caused by the loss of native varieties through abandonment and/or replacement with introduced commercial cultivars. With the onset of the "Green Revolution" in the 1960s, and the steady spread of the use of high-yielding and genetically uniform varieties across the world (Simmonds, 1979), the problem of erosion of genetic diversity worsened. This raised major concerns because the long-term success of plant breeding depends upon the availability of a pool of diverse genetic material. The global awareness about the rate of loss of germplasm led to efforts aimed at preserving what is left of exploitable genetic variation (Brown, 1978; Frankel & Bennet, 1970).

Plant diseases and methods of control

The devastating effects that pathogens have on crop production are apparent, both as pandemics that occasionally ruin large areas of crops (e.g. the southern corn leaf blight in the USA in 1970), and as modest losses arising from epidemics of limited spatial and temporal severity. As a direct response to the effects of diseases on crops, breeding for disease resistance is one of the most important objectives of plant-breeding programmes. Plant breeders are constantly searching for sources of resistance to diseases of crops. Strategies have included the use of single major genes (vertical resistance) and pyramiding several genes (horizontal resistance) (Pedersen & Leath, 1988). Whenever possible, durable resistance, i.e., resistance that can protect the crop

over several years (Johnson, 1978, 1984) is also sought and incorporated into genetically desirable backgrounds.

Fungicides/pesticides, whenever available, have been used in disease control where genetic sources of resistance are unavailable. The fate of fungicides have, however, been similar to that of resistant varieties; pathogens have evolved tolerance with increased use of fungicides, albeit the rate of evolution of tolerance has not been as rapid as that for virulence to resistant varieties. The slower rate of evolution of sensitivity of diseases to chemical fungicides is due to two main reasons. Firstly, chemical treatments are not as readily adopted as resistant varieties because there are tradeoffs between costs and benefits. Fungicides are an extra cost to the grower, and to justify its application, growers must be satisfied that the increase in yield will more than offset the cost of application. Secondly, no matter how they are applied, fungicide treatment does not act throughout the growing season; and so selection on the pathogen population is not as constant as that applied by resistant cultivars (Barrett, 1981).

The widespread use of effective resistance genes, however, puts an intense selection pressure on the pathogen population. This usually leads to the evolution of virulent pathotypes and hence "breakdown" of the resistance. For instance, barley cultivation in Europe has in the past been sustained largely by single major genes at the *Mlg* and *Mla* loci for resistance against the most economically important disease of barley, the powdery mildew, caused by the fungus *Erysiphe graminis* f. sp. *hordei*. However, selection pressure on the pathogen population has led to the evolution of appropriate virulences against the various *Mlg* and *Mla* alleles, rendering them ineffective (Wolfe & Schwarzbach, 1978). According to Wolfe (1992), barley cultivation in Europe is currently being sustained by only a single major gene for resistance, the *mlo* gene, and the fungicide, triazole. The widespread use of the *mlo* gene can, therefore, be assumed to be putting a strong selection pressure on the

pathogen, and it can be predicted that the resistance this confers may soon be overcome by the pathogen. Similarly, the heavy selection exerted by triazole on the pathogen population may be expected to render it ineffective. Thus, the environmental impact of the use of resistance genes and fungicides is to constantly change the genetic composition of pathogen populations, and also to increase the number and range of chemical fungicides that is added to the agro-ecosystem. The apparently short life expectancy of new varieties, coupled with the recent global concern on environmental degradation partly through the use of agricultural chemicals, has accelerated the need for strategies of crop breeding and/or use that minimize over-reliance on these methods. The re-introduction of genetic heterogeneity into agricultural practices is an environmentally friendly and sustainable way of reducing disease levels in cultivated crops without sacrificing yield.

Genetically heterogeneous populations and modern agriculture

The dwindling level of genetic diversity in plants bred and cultivated by man has prompted an increasing emphasis on the protection of the remaining diversity in crop plants (Simmonds, 1979). As concerted efforts are being made to capture and preserve the remaining genetic heritage for use in breeding, more innovative ideas about methods of deploying such genes are being proposed. It is expected that an approach to breeding which considers the fact that cultivated crops were extracted from complex ecosystems in which plants grew in association with others in an ecologically compatible way will ensure the establishment of a proper equilibrium between the plant and its agro-ecosystem. Allard & Hansche (1964) have provided some evidence that genetically diverse populations under the agricultural environment are frequently higher yielding over a range of environments than genetically homogeneous populations. They contend that optimal yield may depend on breeding varieties in which the appropriate

compromise is found between the demands for uniformity and the advantages of diversity.

The underlying principle of the idea of re-introducing variability into cultivated crops is mainly derived from the recognition of the role of diseases in host evolution, and the evolutionary relationships of host-pathogen systems. The observation that genetic variation in a host population reduces the impact of parasites on the population has been recorded (Haldane, 1949). There is also some evidence from natural populations that genetic variability results in lower disease levels (Burdon, 1978; Burdon, Oates & Marshall, 1983). Haldane (1949) formulated a mechanism by which hosts and pathogens would co-evolve, each acting as a selective agent on the other. Theoretical investigations have shown that such a mechanism could maintain genetic diversity in the host and pathogen (Leonard, 1969; Clarke, 1976; Groth & Person, 1977).

In populations that are less disturbed, i.e., in natural populations, the ability of host and pathogen to evolve together, and the consequent maintenance of genetic diversity in both, can create a dynamic equilibrium between host and pathogen. Plant breeding, as man-directed evolution, disturbs the dynamic equilibrium with the introduction and the use of crops in monocultures. In addition to shifting this dynamic balance, plants established in pure stands do not benefit from the merits of intergenotypic synergism which sometimes occurs in heterogeneous environments. The co-existence in a given environment of different genetic stocks, in contrast to homogeneous genetic populations, frequently leads to beneficial interactions between different genotypes, through competition. Allard & Bradshaw (1964) have proposed two mechanisms by which the performance of crop varieties is stabilized:

- 1) individual buffering, which results from the developmental and physiological flexibility of individuals in a population; and
- 2) populational buffering, which is the result of the coexistence and interaction of different

genotypes in the population.

Whereas genetically homogeneous populations rely on only individual buffering to stabilize yield, heterogeneous populations draw on the advantages of individual and populational buffering for higher and stable yield (Marshall & Brown, 1973). Genotypes grown in heterogeneous stands can also have such higher and stable yield through intergenotypic complementation and/or compensation. This causes the mixture population to yield greater than the sum of its parts, leading to higher yield even though the various parts may vary in their individual contributions (Wolfe, 1985). Schutz & Brim (1967) and Schutz, Brim & Usanis (1968) have proposed intergenotypic overcompensation, which results in the enhanced reproductive ability of one genotype while depressing the reproductive value of the other competitor by a lesser amount, as the reason for the yield advantage of mixtures over genetically homogeneous varieties. They also recognize that there can be intergenotypic undercompensation, albeit this is rare. Similarly, in rare instances, genotypes that are lower-yielding suppress the higher-yielding components, resulting in a lower total mixture yield. This is called the Montgomery effect (Montgomery, 1912). The positive effects of intergenotypic interactions have been shown to contribute to higher grain yield in mixtures of wheat and barley (Allard & Adams, 1969).

Strategies for re-introducing genetic diversity into modern agricultural practices

The composite cross approach

Ever since the awareness of the use of genetic heterogeneity as a means of controlling disease, increasing and stabilizing yield was established, several approaches have been proposed to re-introduce genetic heterogeneity into agricultural crops. Harlan & Martini (1929) proposed the "composite cross" method of breeding which was later called "an evolutionary plant-breeding method" (Suneson, 1956). In this approach, many genetically diverse varieties are intercrossed to

produce a genetically heterogeneous population consisting of new recombinant genotypes and parental types. This population can then be grown under normal agricultural conditions for several years in the region where new and/or adapted varieties are needed. Natural selection is expected to act on the genetic variation and to sort out and increase the frequency of new genetic combinations that are most adapted and higher yielding. According to Mak & Harvey (1982), this method also preserves genetic variation in an exploitable form besides the original objective of producing new genetic variation.

Unfortunately, the usefulness of the evolutionary plant-breeding method in producing varieties for agriculture cannot in any way compare with conventional plant-breeding techniques. Firstly, the process is too slow. The process of natural selection in evolving new locally adapted genotypes is far slower than the artificial selection pressure that the breeder is capable of imposing. Although the method requires less skill and financial investment, the time required to produce commercially usable varieties is too long to be an economically viable approach for large-scale commercial breeding. Secondly, the loss of certain apparently less fit genotypes during the long selection period (Muona, Allard & Webster, 1982) also defeats the supposed additional role of composite crosses in preserving usable variation.

The multiline approach

Jensen (1952) and Borlaug (1953, 1959) were the earliest to propose the use of multilines as an alternative strategy to introduce genetic variability into cultivated crops. The principal objective of this concept in breeding is to control diseases of crops through heterogeneity of resistance without sacrificing yield. Multiline varieties are developed through modifying the conventional backcross method of breeding. The end product of this technique would be a mechanical mixture of several phenotypically similar (near-isogenic) lines which would be different for their specific disease resistance genes. Commercially important varieties

are chosen as recurrent parents, and crossed to a large group of donor parents. The latter group is chosen by its reactions to a particular disease. The segregating material from these crosses are handled by the pedigree method. F1 plants are classified for resistance to the reference disease, and backcrossing is continued for as long as necessary to recover lines phenotypically similar to the recurrent parent.

The epidemiological effectiveness of this approach has been established empirically (Borlaug & Gibler, 1953; Browning & Frey, 1969). For instance, one of the first multiline cultivars for commercial production, Miramar 63, was released from the Colombian wheat-breeding programme mainly for the control of wheat stripe and stem rust. To develop it, the Brazilian wheat Frocor was crossed with some 600 varieties and lines. Over 1,200 lines, similar phenotypically to Frocor but with resistance from the 600 non-recurrent parents, were produced. Miramar 63 was a mechanical mixture of equal parts of 10 of the best lines giving resistance to stripe and stem rust. In some of the yield trials, Miramar 63 had yields that were more than double the yield of some renowned higher-yielding pure line varieties (Rockefeller Foundation, 1964). However, the many backcrosses sometimes involved in developing multilines make the breeding procedure slow. Browning & Frey (1969) estimated that it takes 5 years from the time Breeders' Seed of individual isogenic lines is increased to the time farmers sow Certified Seed. In addition, multiline is usually bred for resistance to a target disease, and it is also possible that by the time that a suitable multiline variety is developed, the recurrent parent might have been outclassed.

The variety mixture approach

Cultivar diversification schemes, through the development of varieties in mixtures, is the most recent approach to introducing genetic variability in agriculture (Wolfe, 1985; Wolfe & Barret, 1976, 1980). This method is based on the mechanical mixing of genetically different varieties, each

possessing different, 'specific disease resistance genes. As well as drawing on the advantages of diversity, it also offers a wider scope for the maximum use of current varieties and extending their usefulness without changing current breeding practice. The effectiveness of this approach in controlling the most economically important diseases in different environments, and in increasing overall grain yield has been well established (Simmonds, 1962; Trenbath, 1974; Wolfe & Barrett, 1976, 1980; Barrett, 1981; Mahmood, Marshall & McDaniel, 1991; Browning, 1988; Wolfe, 1985, 1992; Wolfe, Minchin & Slater, 1983, 1985). For instance, consistent reductions in the incidence of disease of the order of 50-70 per cent have been reported relative to the mean of the components grown as pure stands. Yield increases of the order of 6-10 per cent have also been recorded which compared favourably with results from the use of fungicides to control disease (Barrett, 1981; Opong-Konadu, 1994).

In studies in Poland during 1983-1985, three-cultivar (1:1:1) mixtures of various cultivars each with different genes for resistance showed 15-70 per cent less infection of barley with *E. graminis* than pure stands of the cultivar, and 3-17 per cent higher yield than the mean of the components of the mixture (Gacek & Nadziak, 1988). In a 4-year trial of four European spring barley varieties, Claret, Egmont, Goldmaker and Triumph, the mixtures equalled or yielded more than their pure stands in 15 out of 16 comparisons by an overall mean of 8 per cent ($P < 0.001$); the mean yield (6.94 t/ha) was equal to that of the highest yielding component, Triumph (6.96 t/ha). Overall, the yields of the mixtures were also less variable than those of the pure stands (Wolfe, Minchin & Slater, 1983). In a trial of five other varieties, Apex, Klaxon Kym, Natasha and Vista, the result was similar. In this trial, which compared the pure lines with the 10 three-component mixtures that could be derived from them, the average yield of the mixtures of 7.05 t/ha was significantly different ($P < 0.001$) from that of the pure stands of 6.22 t/ha. The yields of the 10 mixtures had a narrower range, 6.67 to 7.41

t/ha, compared to a range of 5.70 to 7.24 t/ha for the five pure stands. Furthermore, all the 10 mixtures exceeded the mean yield of their components, and six exceeded the yield of all of their components (Wolfe, Minchin & Slater, 1985).

In a multilocational study of five pure line sorghum cultivars and 14 of their mixtures in northern Ghana, Mercer-Quashie (1979) showed that mixture yields were not significantly different from the best component. He further showed that the yields of mixtures were higher than the means of their components and more stable over different environments than the individual cultivars grown separately. Barrett (1981) states that using a mixture, the most recent varieties could be incorporated, and by the judicious choice of varieties, resistance to a range of diseases could be combined in a mixture. Wolfe (1985) adds further that it is uncommon for a mixture to yield less than the mean of its components, and even rare for it to be as low as or lower than the worst component.

In barley breeding, the use of variety mixtures to control foliar disease is partly based on the recognition that in the natural ecosystems of Israel, where the progenitors of cultivated barley abound, they are attacked by the same array of pathogens that plague the crop in agroecosystems, yet epidemics are rare (Browning, 1988). These co-evolved populations have reached a dynamic balance and crop traits, such as multiple disease resistance, that are highly desired by breeders, have evolved. Such populations possess polygenic general resistance in which are embedded major genes for specific resistance in different spatial and/or genetic combinations. The mode of disease control in variety mixture populations is similar to that in natural ecosystems. The components of a genetically heterogeneous population, each possessing a major gene for resistance, provide a buffering effect on the entire plant population by reducing the rate of spread of the disease.

Wolfe & Barrett (1980) have proposed three main mechanisms for controlling disease in variety

mixtures:

- 1) decrease in the spatial density of the susceptible plants, thus limiting the amount of susceptible tissues per unit area, and hence the extent to which the pathogen can increase;
- 2) the barrier effect produced by the resistant plants in the mixture; and
- 3) the resistance induced by non-pathogenic spores, thus limiting the normally pathogenic spores in their infectivity or preventing them altogether.

From the epidemiological point of view, these mechanisms encompass the advantages to be derived from race-specific and race-nonspecific resistance, as well as complete, incomplete, and partial resistance. Such epidemiologic resistance thus uses many types of genetic resistance and population structures. The use of varieties in mixtures protects their resistance from intense selection pressure for the appropriate virulence genes in the pathogen population. Scott *et al.* (1978) state that, with mixtures of varieties, combinations of pathogenicity characters may then be selected less rapidly. In some form, therefore, this is a way of genetic protection of an extensively used cultivar. As Browning (1988) puts it, "with the ease of mixing genotypes rather than breaking linkage groups, combining many polygenic systems, or pyramiding major-effect genes, diversity is also an easy and effective way of effecting future adjustment. Diversity also offers a means to confront exotic pathogens with high hitchhiking potential and to ensure against an epidemic following their introduction".

Nonetheless, arguments have also been raised by antagonists of the mixture idea, that variety mixtures may lead to the evolution of pathogen "super races" or complex races capable of infecting all or most of the components. Wolfe & Barrett (1980) argue that the evolutionary dynamics of a pathogen in a mixture can lead to increases or decreases in the frequencies of the different pathogen genotypes during the season, but there will not necessarily be a constant increase or

decrease in any one genotype. A mixed host stand may select simple, intermediate, or complex races, but how this selection is done and the resulting array of race(s) is not easily predictable (Barrett, 1978, 1980; Barrett & Wolfe, 1978; Wolfe & Barrett, 1976; Groth, 1976); therefore, the fear of the appearance of complex races is unfounded. Wolfe & Barrett (1980) again state that "an essential part of the disease-control approach in mixtures is that no one mixture be used for an extended period of time; this reduces the possibility of the complex pathogen genotypes being selected". They further argue that even if a mixture would lose its ability to control disease, such a loss in a judiciously constituted mixture is more likely to be a gradual process.

Conclusion

The depletion of plant biodiversity with the rapid development of agriculture has, in recent years, attracted growing public and scientific interest. The most glaring example of the consequences of this problem is the difficulty and cost of controlling major diseases of crop plants and maintaining the usefulness of newly bred varieties. The last three decades have witnessed a period where the major defence against plant diseases, host resistance, has been augmented by the use of systemic fungicides to allow further intensification. The two immediate effects of the dependence on only two forms of plant disease control is the increase in the cost of variety and crop production, arising partly from the efforts needed to continually breed and introduce new varieties, and also through the elevation of fungicide use to a common farm practise.

The pathological consequence of diseases on crop plants is the rapid loss of genotypes with "ephemeral" resistance, leading to the need/search for durably resistant varieties. In the same way, the rapid reduction in the effectiveness of fungicides leads to the need for replacement with more durable forms. The variety mixture approach offers an excellent opportunity for maintaining and/or prolonging the usefulness of varieties of

crops, to protect their resistances more robustly and to do so more cheaply than continuous breeding for resistance and/or increased use of fungicides. Mixtures of varieties of temperate cereal crops such as barley have been successfully grown on a commercial scale in many parts of Europe including UK, Denmark, Czechoslovakia, and the former East Germany. The advantages they have over pure line cultivation in disease control and overall yield output is well documented (Chin & Wolfe, 1984; Bruckner, 1987; Wolfe, 1990, 1992; Wolfe, Minchin & Slater, 1983, 1985; Wolfe & Barrett 1986; J. H. Jorgensen, pers. comm.), although the individual, specific, disease-resistant genes of the components of the mixtures were no longer effective in controlling the most prevalent European barley disease. The variety mixture approach could be especially useful in the developing world and in many low-input agricultural systems as a reliable and environmentally friendly cropping system.

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