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Original article

# Cereal variety and species mixtures in practice, with emphasis on disease resistance

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**Abstract** – Variety mixtures can provide functional diversity that limits pathogen and pest expansion, and that makes use of knowledge about interactions between hosts and their pests and pathogens to direct pathogen evolution. Indeed, one of the most powerful ways both to reduce the risk of resistance break-down and to still make use of defeated resistance genes is to use cereal variety and species mixtures. The most important mechanisms reducing disease in variety and species mixtures are barrier and frequency effects, and induced resistance. Differential adaptation, i.e. adaptation within races to specific host genotypic backgrounds, may prevent the rapid evolution of complex pathotypes in mixtures. Mixtures generally stabilise yields and yield losses due to disease; abiotic stresses are also better buffered than in pure stands. When mixture components are carefully put together, product quality can be enhanced or at least equal that of the pure stands. Mixture use in practice worldwide is reviewed.

**functional diversity / induced resistance / differential adaptation / yield stability / evolutionary plant breeding**

**Résumé** – **Les mélanges de variétés et les mélanges interspécifiques de céréales dans la pratique.** Les variétés en mélanges, de par leur diversité génétique, limitent le développement des épidémies et des ravageurs. Cette diversité peut être organisée selon notre connaissance des interactions hôte – agent pathogène pour influer sur l'évolution des

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Plant Genetics and Breeding

populations parasites. La culture de variétés en mélange ou de mélanges interspécifiques est une des méthodes les plus efficaces à la fois pour limiter le risque de contournement des résistances, et pour utiliser avec bénéfice des résistances déjà contournées. Les principaux facteurs de réduction de la sévérité des épidémies dans les mélanges sont les effets de barrière, la proportion de plantes sensibles et la résistance induite. L'adaptation d'isolats de même race au fond génétique d'un hôte, ou adaptation différentielle, pourrait ralentir la sélection de races complexes dans les mélanges. D'une façon générale, les mélanges stabilisent les rendements. Le risque de pertes de rendement dues aux stress biotiques et abiotiques est plus limité dans un mélange que dans une culture pure. Un choix judicieux des composants du mélange peut permettre d'obtenir une qualité du produit de récolte équivalente ou supérieure à celle d'une culture pure. L'utilisation des mélanges au niveau mondial est discuté.

**diversité fonctionnelle / résistance induite / adaptation différentielle / stabilité du rendement / amélioration génétique**

## 1. Introduction

Up to the last two hundred years, agricultural systems were based on crop varieties and landraces that were genetically heterogeneous. Some of the heterogeneity would have been selected consciously, but much of it would have arisen through natural selection or random events. It is impossible now to gauge the extent to which the overall heterogeneity would have been useful as a buffer against the effects of diseases, pests, weeds and other environmental variables. Monoculture may have been common but only at the species level. For example, the major rotation in European agriculture was wheat – barley or oats or beans – fallow.

During the agricultural revolution of the 17th and 18th centuries, there were major developments that included an increase in diversity among crop species, the introduction and development of clover-based cropping systems, and directed selection and multiplication of superior plant genotypes. By the middle of the 19th century, Charles Darwin [23] was able to report:

"It has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case. The same has been found to hold good when one variety and several mixed varieties of wheat have been sown on equal spaces of ground."

But the reason(s) for the mixture advantage were not known.

From the mid-nineteenth century on, plant breeding, mechanisation and other factors such as inorganic fertilisers and pesticides evolved rapidly, allowing for and leading to a massive concentration on monoculture and all contributing to weed, pest and disease problems in different ways. 'Monoculture' refers usually to the continuous use of a single crop species over a large area. However, with respect to plant pathogens and pests it is important to differentiate between monoculture at the level of species, variety or resistance genes [29]. For example, within a species there may be many different genotypes with different resistances to a specific pest or pathogen and great variation with respect to competitiveness with weeds and other crops. Within modern varieties there is usually little diversity for resistance or morphological traits.

Resistance gene monocultures are more difficult to conceptualise. Many different varieties may exist, but with the same resistance (or susceptibility) gene(s). For example, in the late 1960's, virtually all hybrid maize varieties in the southeastern US possessed the cytoplasmatically inherited Texas male sterility. Unfortunately, this trait is closely linked to susceptibility to certain strains of the pathogen *Cochliobolus carbonum* (syn. *Helminthosporium maydis*). The monoculture for susceptibility (even though different varieties had been planted) led to selection for these strains and in 1970 the pathogen caused more than 1 billion (=$10^9$) $US in losses [90].

As a consequence of the use of large-scale resistance gene monocultures, varietal resistance, particularly to air-borne plant pathogens, has to be renewed continuously because of the strong selection for pathogen genotypes able to overcome resistance [11, 46, 48, 71, 85, 94]. Routine applications of synthetic inputs, including multiple fungicides, have become necessary in cereal production in Europe and the US.

Starting in the 1920s, some breeders and pathologists maintained and developed the notion that the disease problems caused by monoculture could be avoided or alleviated by retaining functional diversity within the cereal crop. This means, the diversity that limits pathogen and pest expansion and that is designed to make use of knowledge about interactions between hosts and their pests and pathogens to direct pathogen evolution [67, 84]. Indeed, there is a whole array of genetic and ecological interactions among plants and their pathogens that play a role in disease reduction in diverse populations (for details see e.g. [5, 6, 10, 12, 15, 51, 67, 79, 92, 96, 99]):

(1) Increased distance between host plants possessing the same resistance;

(2) Restriction of pathogen spread by resistant plants that act as barriers. These effects are reciprocal, i.e. plants of one host genotype will act as a barrier for the pathogen specialised to a different genotype and vice versa. Together, (1) and (2) effectively reduce the infection efficiency of the pathogen (i.e. the numbers of successful infections relative to the number of pathogen propagules). In addition, autoinfection (i.e. infection of the same genotype) is effectively reduced;

(3) Selection in the host population for more competitive and/or more resistant genotypes can reduce (or sometimes increase) overall disease severity;

(4) Competitive interactions among host plants may affect plant susceptibility;

(5) Pathogens non-virulent on a host genotype may induce resistance reactions that work against virulent races;

(6) Interactions among pathogen races (e.g. competition for available host tissue) may reduce disease severity.

Diversification can be achieved at the species, variety and gene level (Tab. I) with effects on pathogens, insect pests and weeds [25, 28, 29, 71]. Examples for early within-crop diversification strategies are the barley Composite Cross populations [38, 87], and the mixture or multiline concept [12, 13, 41].

Because of the framework of legal protection built up for plant breeders and their varieties, development of population breeding became illegal in Europe. Multilines were also not accepted generally by breeders because of the conservative nature of the breeding approach involved. For these and other reasons, Wolfe and Barrett [98], and later, other workers, chose to concentrate on the analysis and use of mixtures of varieties for air-borne disease control in cereals. Nevertheless, the

**Table I.** Possibilities for diversification at three levels of uniformity on which monocultures are commonly practised: species, variety and resistance gene.

| Level of uniformity | Diversification possibilities |
|---|---|
| Species: Individuals may differ in genetic make-up (resistance, morphology, etc.) | Arrangements among and within species, varieties and resistances using inter-cropping |
| Variety: Usually genetically uniform, the same gene(s) in the same genetic background | Arrangements among and within varieties and resistances - includes variety mixtures, multilines and populations |
| Resistance gene: the same gene may exist in different genetic backgrounds | Arrangements among resistances - multilines and populations |

use of the club wheat multiline 'Rely' in Washington State in the northwestern USA represents a current highly successful application of the intra-crop diversification principle. In the 1998–99 season, 76% (= 62 000 ha) of the winter club wheat area was planted to this multiline [39].

During the late 1970's in the UK, there was initially a rapid uptake in the use of variety mixtures, particularly in wheat and barley. Unfortunately, as the acreage expanded, mixture production became strongly discouraged by maltsters and millers who did not want to buy mixed grain, despite the possibility that the components might have complementary quality characteristics. Nevertheless, by 1981, wheat mixture development was sufficiently effective for Mr. Gordon Rennie to gain the world record wheat yield at the time (13.99 t·ha$^{-1}$) with a mixture grown in Scotland (Guinness Book of Records, p. 152, 1994; [73]). Furthermore, interest in the use of mixtures for restricting mildew on barley spread to the former GDR, where, during the 1980's, the whole spring barley acreage was eventually sown to a range of mixtures. This strategy led to an 80% reduction in the national mildew level with a consequent massive saving in fungicide use [97]. It is important to note that the mixtures that were used commercially were put together by agreement among breeders, pathologists and maltsters, thus ensuring that a high quality of malt for export was maintained during the period of mixture cultivation.

In recent years, interest in the concept of crop mixtures grew in many countries, which led to the establishment of the COST (European Cooperation in the Field of Scientific and Technical Research) working group on cereal variety mixtures. The aim was to encourage collaboration, research and further development of the concept in practice. The resulting range of field experiments and computer simulation studies has helped to elucidate further some of the mechanisms of disease restriction in mixtures.

The objectives of our paper here are: (1) to summarise results of ongoing research on the ecological and genetic interactions in diversified host populations, divided into effects on disease (part 2), yield (part 3), and quality (part 4); and (2) to present information on the practical use of cereal mixtures in the countries where we are aware of their use (part 5).

## 2. Ecological and genetical interactions in mixtures

Recent mixture research has focussed on the elucidation of ecological and genetical interactions in mixtures with respect to the effects of proportion and level of resistance among the host cultivars, and induced resistance. There has also been interest in the evolution and selection of pathogen populations on host mixtures, and in practical issues such as yield effects, buffering against abiotic stress, and quality aspects of mixtures.

### 2.1. Effects of resistance level and the proportion of resistance on disease in mixtures

An important question is whether disease reduction in a mixture can be predicted from the number and proportions of resistant components in the mixture and their resistance levels.

Early work on stem rust of oats (caused by *Puccinia graminis*, f. sp. *avenae*) related the rate of pathogen increase to the log of the proportion of susceptible plants in a mixture [53]. In contrast, a direct relationship between disease severity and mixture composition was found in an experiment involving different sets of mixtures of four near-isogenic barley lines differing in resistance to barley powdery mildew (caused by *Erysiphe graminis*, f. sp. *hordei*) [49]. The powdery mildew levels in the mixtures were reduced most when the mean resistance of the pure stands was intermediate. This translated into a linear relationship between the effect of mixing on disease and the mean resistance level. In a more detailed follow-up experiment with two-way mixtures composed of different ratios of one fully susceptible and one completely resistant component, a curvilinear relationship for disease severity (Fig. 1a) and a clear linear

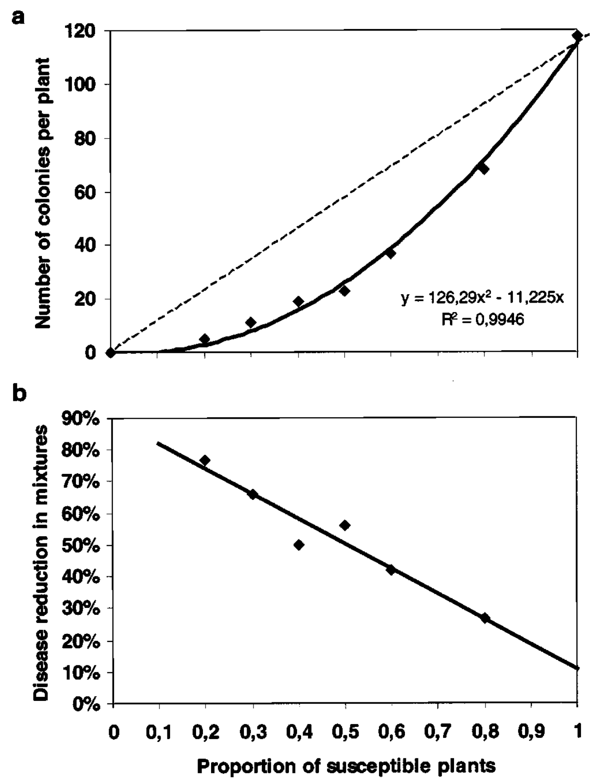



**Figure 1.** Effects of the proportion of susceptible plants in two-way mixtures of near-isogenic barley lines with different proportions of susceptible and resistant plants. (a) Observed powdery mildew levels. The equation shows the quadratic relationship between frequency and disease severity. The dashed line indicates the expected levels of mildew if the relationship were linear. (b) Disease reduction in mixtures relative to the mean disease on the pure stands (Data from Munk et al., 1998).

relationship between disease reduction and resistance level was found [70] (Fig. 1b).

In mixtures composed of components resistant to only part of the pathogen population, further mechanisms such as induced resistance, may contribute to disease reductions (see Sect. 2.2). In mixtures composed of more than two components with differing resistance, other levels of mixing effects may be expected. However, the basic relationships are still expected to be valid.

In line with these results are data from 16 experiments in Poland in which all possible two- and three-way mixtures of sets of usually five barley varieties were compared. In 13 cases, reductions in powdery mildew were greater in three-way than in two-way mixtures (statistically significant in six cases) [30].

In addition to powdery mildew restriction, a significant decrease in disease with an increase in component number from two to five in mixtures, was observed for the splash-dispersed scald disease (caused by *Rhynchosporium secalis*) [76].

These results have two implications. Firstly, the performance of a mixture with respect to disease reduction can be predicted from a knowledge of the resistance level of the components in pure stand. Secondly, it is not so much the number of components in a mixture but rather the mean level of resistance of all components with respect to the actual pathogen population that determines the performance of the mixture.

While these results appear straightforward, some important factors that may affect the performance of mixtures are often overlooked or ignored. Firstly, in mixtures, not only the frequency but also the density of the mixture components changes with changing composition (see Sect. 2.1.1). Secondly, the overall inoculum pressure should influence mixture performance (see Sect. 2.1.2). Thirdly, the effects of mixtures on disease are likely to change with changes in the scale of mixture use in practice because of changes in inoculum pressure (see Sect. 2.1.3).

#### *2.1.1. Differentiation between frequency and density effects in mixtures*

When changing the densities of barley plants in a growth chamber experiment with potted plants, powdery mildew infection was reduced with reduced density [14]. In contrast, when conditions favoured epidemic development in a field experiment, reducing the density of susceptible pure stands of barley plants led to an increase in powdery mildew [31]. No density effects could be observed when epidemics were short. If, however, the density of susceptible pure stands was reduced by replacing susceptible plants with resistant plants, i.e. the density and the frequency of the susceptible plants was changed simultaneously, disease severity on the susceptible plants was

**Table II.** Powdery mildew levels (Area Under Disease Progress Curve (AUDPC) and disease relative to the mean of the pure stands in two and three-component barley variety mixtures exposed to low and high inoculum pressure[a] in four trials conducted between 1994 and 1997 in Scotland (Newton, unpublished data).

| | Trial 1 | | Trial 2 | | Trial3 | | Trial4 | |
|---|---|---|---|---|---|---|---|---|
| Inoculum pressure | AUDPC | relative disease | AUDPC | relative disease | AUDPC | relative disease | AUDPC | relative disease |
| low | 226 | 0.53 | 353 | 0.64 | 105 | 0.30 | 161 | 0.65 |
| high | 295 | 1.00 | 355 | 0.77 | 108 | 0.42 | 140 | 0.76** |

[a]Plots were either surrounded by the susceptible variety Golden Promise or by the resistant variety Derkado (*mlo11*).
**Difference between high and normal inoculum pressure was statistically significant at $P < 0.05$.

significantly reduced [31]. An important difference between the laboratory and field experiment was that in the laboratory, available resources for the plants were kept constant as they were potted, while in the field reducing the planting density invariably increased the available nutrient and water resources for the plants. This is known to lead to higher susceptibility to powdery mildew [72]. In addition to changes in nutritional status, plants in the less dense stands produced more tillers, probably increasing the role of autoinfection. In experiments with yellow rust on wheat, Garrett and Mundt (unpublished) also found variable effects of density on disease severity in pure stands, though mixtures were always most effective at an intermediate planting density.

### 2.1.2. Effects of inoculum pressure on mixture performance

It is logical that the effectiveness of variety mixtures for disease control varies with epidemic severity. From a practical standpoint, a larger impact in more severe epidemics would be desirable. In one study where plots were artificially inoculated in the centre with wheat stripe rust, disease reduction increased with increased epidemic severity [1]. The effectiveness of oat multiline varieties developed to control crown rust in Iowa, USA, remained effective even under extremely harsh and prolonged epidemics in southern Texas [13].

Mechanistically, many associations between mixture efficacy and epidemic severity are possible. If a severe epidemic results from early initiation, then mixtures may perform well because of a large number of pathogen generations [53, 96]. Given equal generation number, it has been suggested that mixtures will be less effective against faster epidemics due to the increased rate of approach to the host's carrying capacity for disease [65]. However, if disease increase is discontinuous, as is often the case, then the saturation influence may have little or no impact on mixture performance [34]. Finally, a given level of exogenous inoculum will account for a larger proportion of infections in a slow epidemic, thus potentially masking the mixture effect. On the other hand, larger amounts of outside inoculum may be produced during seasons that are favourable for epidemic development, resulting in less effective disease control in severe epidemics (Tab. II).

### 2.1.3. The effects of scale on mixture performance

Experimental studies of mixtures are almost always prohibitively expensive on a large spatial scale. However, observations suggest that disease control is greater in commercial fields than in experimental plots [66, 96]. More recent data from commercial mixture use supports this view. The percentage of the barley crop sown to variety mixtures in the former East Germany increased from 0 to 92% during the period from 1980–1990, while mildew incidence declined by 80% and fungicide use also declined by 80% [97]. Similar reductions of mildew severity were not observed in neighbouring countries, where mixtures were not widely used. More recently, rice variety mixtures have been planted in contiguous rice fields containing

812 and 3342 ha in 1998 and 1999, respectively. Pure stand controls replicated throughout the region of diversification indicated that variety mixtures decreased blast severity on susceptible varieties by an average of 94% [101].

There are several possible explanations for the effect of spatial scale on mixture performance. First, and perhaps most important, is that the effects of interplot interference (i.e. the influence of neighbouring plots) are more severe for mixtures than for pure stands [96], and interplot interference can sometimes obliterate the impact of mixtures on disease [66, 96]. Such observations are logical, since the major impact of mixtures is to reduce the infection efficiency, while the effect of interplot interference is to increase the actual population size of the pathogen through inoculum immigration into a plot. This contrasts with studies of quantitative resistance, for example, where the effects of reduced sporulation and lengthened latent period would not be affected directly by interplot interference. Secondly, excessive amounts of artificial inoculum used to initiate epidemics in experiments can reduce the effectiveness of mixtures [34, 96]. Finally, the spatial dynamics of epidemic spread at different spatial scales may cause mixtures to be more effective when planted over larger areas [34].

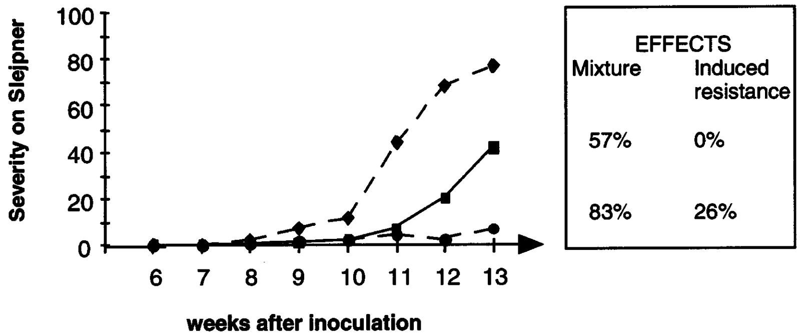
### 2.2. The effects of induced resistance

The main factor accounting for disease reduction in variety mixtures is the increased distance between susceptible plants. However, induced resistance caused by avirulent pathotypes can also contribute to the mixture efficacy. Induced resistance (IR) enhances resistance of plants and protects them against subsequent infection by normally virulent pathotypes. The protection is based on the stimulation of defence mechanisms and metabolic changes that speed up recognition of pathogens, and it has been argued that IR should be durable in the same way as the *mlo* resistance gene in barley against mildew (for review see [58]). Overall, IR results in reductions in epidemiologically important parameters such as infection efficiency, lesion growth and sporulation rate. These effects should become even more important at the polycyclic level in the field [86].

IR has frequently been observed for rusts and powdery mildews of small grains in laboratory as well as field studies (e.g. [17, 40, 43, 62, 91]). However, few field studies have been conducted to assess the effect of IR in varietal mixtures. In one field study [19] IR was estimated to be responsible for a 24% mildew reduction in barley varietal mixtures. A 50% reduction in incidence of powdery mildew and *Drechslera avenae* that occurred in field investigations with mixtures of spring barley and oats was attributed to IR by Villich-Meller and Weltzien (1989, in [86]). IR was also suggested as a possible mechanism for disease reductions in a wheat mixture against yellow rust [26].

To determine the extent to which induced resistance could be a factor in controlling yellow rust epidemics in wheat varietal mixtures, large (9 × 18 m) field plots of different combinations of three different wheat varieties were heavily inoculated with a challenger virulent race (isolate J89108) and an inducer avirulent race (isolate J89101) of *P. striiformis*. The three treatments were: the variety Slejpner (yellow rust resistance *Yr9*, susceptible to J89108) in pure stand, Slejpner mixed with Arcane (Yr6, susceptible to J89101) (1:2), and Slejpner mixed with Estica (resistant to both races) (1:2). Significant field protection due to IR was obtained two times, during two years. In the first year, after two months, disease on Slejpner in mixture was reduced by 57% when not exposed to avirulent inoculum, i.e. when mixed with Estica. When mixed with two thirds Arcane and thus exposed to large amounts of avirulent inoculum, however, disease reduction was 83%, indicating that an additional 26% disease reduction was due to induced resistance (Fig. 2). In the second year, the mixture effect was 63%, 46% due to reduced density of the susceptible host and 17% to induced resistance. Thus, induced resistance accounted for 31% and 27% of the total disease reduction in variety mixtures in the two years, respectively. Because of resistance induced by the prevalent avirulent race (produced by Arcane) epidemics on the susceptible variety were delayed by two weeks,

**Figure 2.** Evolution of wheat yellow rust severity on field plots of variety Slejpner (*Yr9*) in pure stand (diamonds), of Slejpner mixed with the totally resistant variety Estica (1:2) (squares) and of Slejpner mixed with Arcane (*Yr6*) (1:2) (circles), 6–13 weeks after inoculation with the yellow rust isolate J89108 (race 232E137, virulent on *Yr9*, avirulent on *Yr6*) and the inducer isolate J89101 (race 45E140, virulent on *Yr6*, avirulent on *Yr9*). Each point was the mean of 75 notation points (15 tillers each) and 4 replicates. The mixture effect was calculated on the area under the disease curves (AUDPC) as the relative AUDPC differences between Slejpner in the mixture and in pure stand. The induced resistance effect was the difference between the Slejpner:Estica mixture effect and the Slejpner:Arcane mixture effect (de Vallavieille-Pope and Goyeau, unpublished data).




an effect that remained throughout the season (de Vallavieille-Pope and Goyeau, unpublished).

Reductions of the same order of magnitude were observed in previous studies with yellow rust [26] and barley powdery mildew [19, 20, 62]. However, in another study mixture effects on barley powdery mildew disappeared when plants were treated with a yeast-derived resistance elicitor indicating that the elicitor might have been even more effective than avirulent inoculum [80].

Varietal variation in induction has been reported for several plant-pathogen systems. The extent of protection by induced resistance was dependent on the host variety and was correlated with the presence of known resistance genes with respect to the pathogen population [17, 20, 62, 80]. Thus, to maximise the role of induced resistance in variety mixtures it would be worthwhile choosing mixture components on the basis of their inducibility for resistance.

While IR can be local or systemic in plants, in the examples of foliar diseases of small grains, IR seems mainly to have local effects. However, computer simulations indicate that even locally induced resistance can be effective in reducing the severity of disease in varietal mixtures [52].

### 2.3. Pathogen evolution in mixtures

The consequences of the large-scale use of variety mixtures need to be considered in terms of the ability of pathogens to develop new virulences. Whether or not selection in mixtures is for complex pathotypes that accumulate many virulences is largely unknown and has been subject to much theoretical discussion. Until recently, such discussions concluded that to prevent such selection there has to be some kind of selection against unnecessary virulences, a notion that was first raised by Vanderplank [92] and confirmed by later studies [56, 61]. Several theoretical models have attempted to define the conditions under which selection against unnecessary virulence is effective enough to maintain an equilibrium between simple races (carrying a single virulence) and complex races (carrying several virulences) in the pathogen population [6, 7, 37, 55, 61, 79].

Virulence genes determine whether infection will be successful or not, but many other genes are involved in the infection process and it is likely that selection also occurs with respect to these genes. Quantitative differences in the ability to infect a variety can be detected among isolates carrying the same virulence genes. As a consequence, when a virulent race causes an epidemic on a cultivar, there may be selection within the pathogen population for the individuals best adapted to their host genetic background. In host mixtures, simple races always reproduce on the same host genotype, whereas complex races develop successive generations on different host genotypes. Differential adaptation to the host genetic background could then result in an increase of the reproduction rate for simple races but not for complex races. Such an effect was suggested for *Puccinia graminis* f. sp. *avenae*, [54] and for barley powdery mildew [19]. Differential interactions between isolates and varieties have been demonstrated for several pathogens, such as *Erysiphe graminis* f. sp. *hordei* [63], *E. graminis* f. sp. *tritici* [81], *Puccinia recondita* [50, 89], *P. striiformis* f. sp. *tritici* [44], *P. graminis* f. sp. *tritici* [57], *Phytophthora infestans* and *P. hordei* [45].

The effects of differential selection on pathogen evolution in variety mixtures were tested with a simulation model (Lannou et al., in preparation). The model was used to study the consequences of intra-race diversity on the pathogen evolution in a two-component variety mixture. It was assumed that, within a race, a proportion of isolates would have an infection efficiency greater or lower than the average on a given host genetic background. Two situations were investigated in which the pathogen multiplication rate could have either dependent or independent values on two different cultivars. In the first situation, it was considered that, if a pathogen genotype was a little more fit on one of the host genotypes than the average, it had to be a little less fit on the other host. In the second situation, a pathogen genotype could have a higher infection efficiency than the average on one cultivar, and maintain a mean spore efficacy on the other cultivar. The initial frequency of the complex race was set to be low (1 in 1000) compared to simple races, in order to simulate a situation where complex races emerge in a simple race population. In the simulations, 20% of the spores were allowed to produce autoinfections [51].

In the case of independent values of the multiplication rate on both cultivars, the effect of differential selection was similar or greater than the effect of a 10%-cost of virulence. For dependent values, the increase in complex race frequency was much slower (Fig. 3). Within each race, genotypes with a higher multiplication rate tended to replace the less fit genotypes (Fig. 4). This was faster, however, for simple races, which always reproduced on the same host genotype.

These results suggest that the genetic diversity within the pathogen races and the interactions between individual isolates and host cultivars could be as important as the cost of virulence in pathogen race dynamics in mixtures.

In an attempt to confirm these theoretical results, a field experiment was performed in 1997 and 1998 to measure differential adaptation in a wheat powdery mildew (*E. graminis* f. sp. *tritici*) population (Villareal and Lannou, unpublished). The experiment was designed so that the pathogen produced successive and discontinuous generations on wheat cultivars Orkis (resistance genes *Pm2+Pm8*) or Etecho (resistance gene *Pm4b*), either grown as pure stands or in a mixture. Infection efficiency was measured as a fitness component of the pathogen, relative to the host genotype. Initial infection occurred naturally, and initial populations (in April) were not different in aggressiveness on the two cultivars. After seven

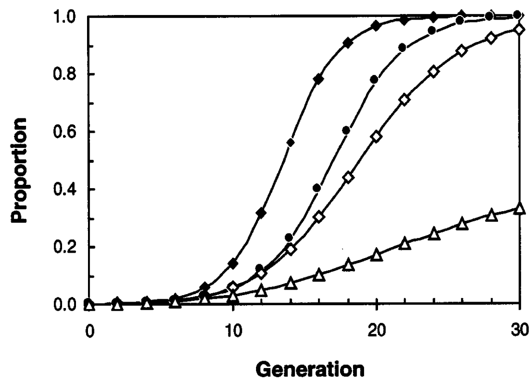



**Figure 3.** Frequency of the complex race for 30 pathogen generations in a two-component mixture (1:1). Black symbols are for simulations of single-genotype races, either with no cost of virulence (diamonds) or with a 10%-cost of virulence (circles). White symbols are for simulations with intra-race diversity for spore efficacy with either dependent (triangles) or independent (diamonds) values of spore efficacy on both host genotypes (data from Lannou et al., unpublished).

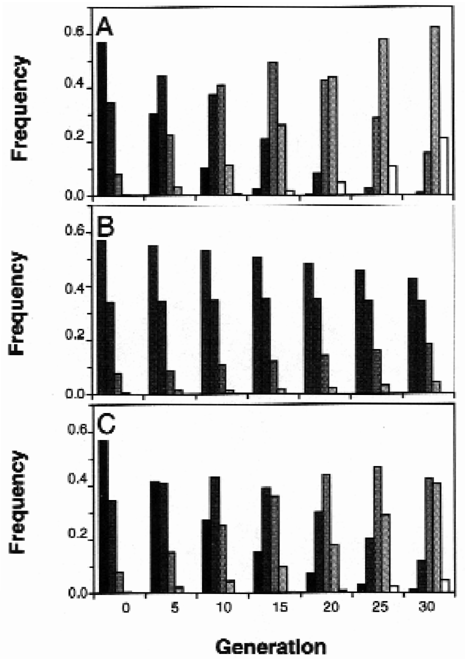



**Figure 4.** Genotype frequencies within the different races reproducing in a two-component mixture. The simulations are the same as in Figure 3. **A**: simple race; **B**: complex race with dependent values of the spore efficacy on the mixture components; **C**: complex race with independent values for spore efficacy. For each race, genotypes with a mean spore efficacy are in black and genotypes with the highest spore efficacy are in white. Intermediate values are in grey. Genotypes with a spore efficacy lower than the average are not represented. Genotype frequencies are shown every 5 pathogen generations (data from Lannou et al., unpublished).

generations (in July), isolates reproducing in pure stands had a better infection efficiency (+20%) on their host of origin than on the other one. This was attributed to selection within the pathogen population for a better spore efficacy with respect to the host genetic background. This selection was found to be independent of the virulence genes carried by the isolates. For isolates reproducing in the variety mixture, infection efficiency remained constant, on average, during the epidemic. This could have important consequences for pathogen evolution in host mixtures, since simple pathotypes can only reproduce on the same host, whereas complex pathotypes may reproduce on different host genotypes in different generations.

It was estimated that, in the absence of selection for simple races (e.g. due to a cost of virulence) these should theoretically have disappeared from the Orkis-Etecho mixtures. Since no fitness reduction was detected related to the number of virulences in the isolates, it seems that an increase in frequency of the complex isolates in the variety mixture was effectively counteracted by differential selection.

These theoretical and experimental results suggest that differential selection by the host genetic background is a selective force, acting without a need for a cost of virulence, that contributes to the advantage and maintenance of simple pathogen races within pathogen populations developing in host mixtures. Two conditions are required for this selection to be effective: genetic heterogeneity of the host population, which is realised in variety mixtures, and genetic diversity in the pathogen population.

### 2.4. Effects of mixtures on abiotic stresses

For the practical use of mixtures, their performance with respect to stresses other than diseases, to yield and to quality is critical.

The unpredictability of the weather makes varietal choice for winter cereals especially difficult for growers because the more popular varieties may not be the most winter hardy. Mixtures offer a possibility to the grower to insure against excessive losses in cold winters. Thus, wheat farmers in Oregon often use mixtures of more and less winter hardy varieties, together with drought resistance to minimise losses to cold and drought (Mundt and Finckh, personal observation). In addition to compensation effects, nurse plant effects could also play a role. For example, in Poland, a cold sensitive winter barley variety had markedly better survival rates when grown with a cold tolerant variety than when grown alone (Nadziak et al., unpublished). In Switzerland, many farmers sow spring wheat in late autumn, mainly because of quality considerations. A way to protect spring varieties from unexpected cold winters was demonstrated by Maillard and Vez [60]. In a mixture of a spring (cv. Kolibri) and a winter wheat (cv. Zenith) both sown in autumn, the strong overwintering effect on

Kolibri in 1979 was compensated by the mixture partner Zenith (Fig. 5).

Reductions in lodging are also commonly observed (Merz and Wolfe, personal observation) but only rarely have these been systematically measured (e.g. [35]). In barley variety mixtures in Switzerland, lodging was reduced to 10% from an expected 32% (mean of two pure stands) (Merz, personal observation**),** and in a Polish trial lodging was significantly reduced by 15% below the mean of the pure stands (Newton and Nadziak, unpublished data). Wolfe (personal observation) noted that in different three-way variety mixtures of barley, there was little lodging in the mixture overall if two components were resistant to lodging. However, if two of the components were susceptible to lodging, they tended to drag down the third, standing component.

## 3. Effects of mixtures on yield

One of the most important criteria for the success of mixtures in practice is their yielding ability. It has been argued that mixtures present greater yield advantages in low-yielding environments than in high yielding environments. This notion appears not to be generally valid as demonstrated in a series of mixture trials over 11 years in Poland.

More than 40 different barley and several wheat cultivars were evaluated for their performance in mixtures in a series of 13 experiments, conducted at several locations over several years each, resulting in a total of 78 trials. Each experiment included pure stands of four to seven cultivars or breeding lines and all possible three-way mixtures.

The relative yield of mixtures ranged from 0.92 to 1.11 with a mean of 1.02 (Fig. 6) [30]. There was no effect of the overall yield potential of the environment on the performance of the mixtures.

Just as with disease reduction, the number of mixture components also appears to influence the yield performance of mixtures. For example, increasing the number of components in mixtures of winter barley resulted in significantly increased yield benefits above the mean of the monoculture components. This was partially attributable to a corresponding increase in control of the splash-dispersed pathogen *Rhynchosporium secalis* as component number increased (see also Sect. 2.4.2.2), but the trend was also observed in the absence of disease [76]. Similarly, yields of three-way mixtures of barley in Poland were on average higher than for two-way mixtures (significant in six out of 18 comparisons) [30]. The yield benefit correlation with mixture component number has been noted previously in barley [78] and wheat [66] and can be explained in terms of better resource exploitation above and below ground, but there has been little experimental or theoretical work carried out to specify these interactions. The contribution of individual components of the mixtures to either yield or disease reduction can be assessed by stepwise regression analysis and varies considerably [76].

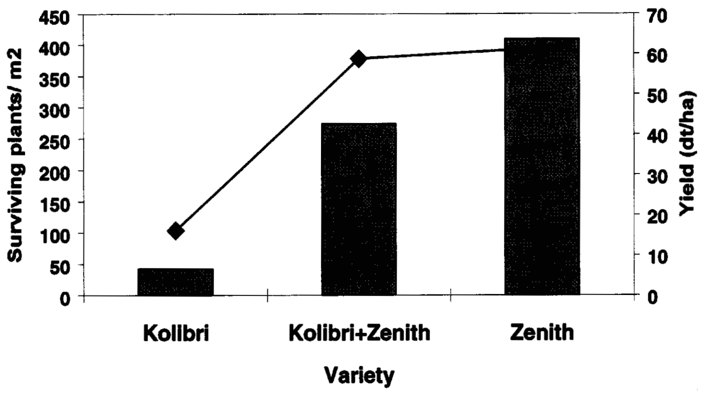



**Figure 5.** Survival (bars) and yield (diamonds) of the spring wheat variety Kolibri and the winter wheat variety Zenith in pure stands and in mixtures in Switzerland (data from Maillard and Vez, 1983).

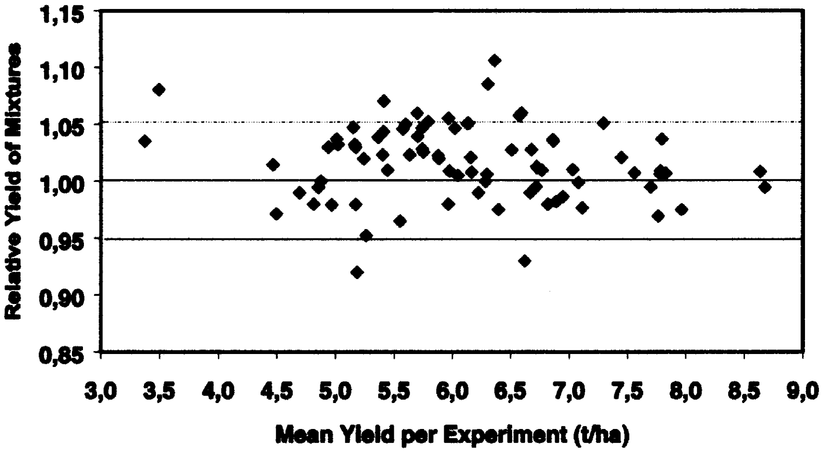



**Figure 6.** Effect of the overall yield potential of a site on the relative performance of barley variety mixtures in 78 trials in Poland involving four to seven cultivars. Trials were conducted between 1987 and 1996 at various trial sites. The relative yield of 3-way mixtures as compared to the mean of the pure stands (=1) is plotted. Each data point represents the mean of the relative performance of all mixtures in a given trial.

### 3.1. Yield stability in mixtures

Reliable and thus stable yield is of major interest for growers. While in a given year and location a variety in pure stand may be the highest yielding entry in a mixture trial, it is usually impossible to predict which variety will be the highest. To assess the yield stability of the mixtures and pure stands, the Polish trials were analysed using regression analysis [24] as modified by Mundt et al. [68]. Here, an example is given for a trial encompassing seven barley cultivars in pure stands and the 35 possible three-way mixtures grown in seven different environments in Poland (Fig. 7, Tab. III). The

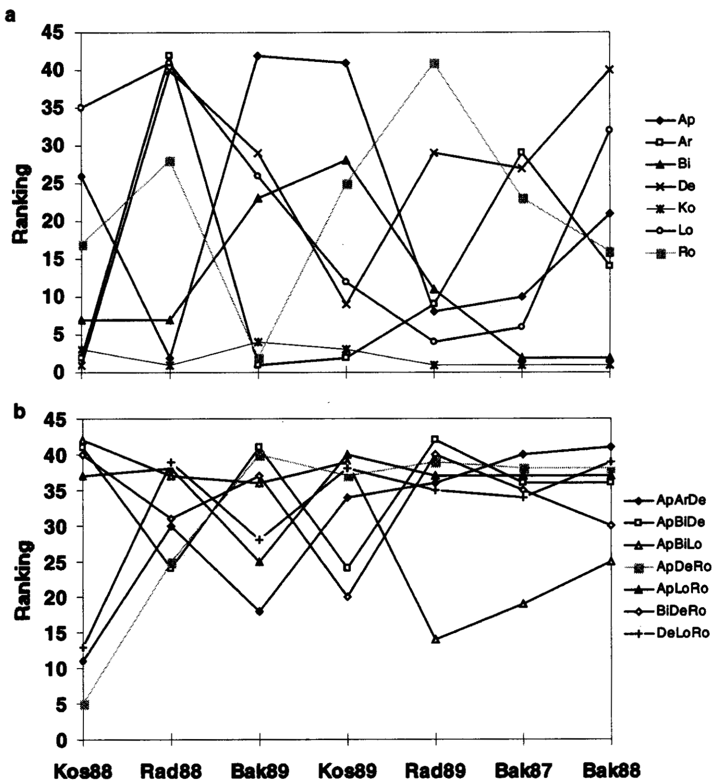



**Figure 7.** Ranking by yield of seven pure stands of barley (a) and the seven best three-way mixtures (b) in seven different environments (location/ year combinations) in Poland between 1987 and 1989. In each environment there were a total of seven pure stands and 35 three-way mixtures. The highest yielding treatment was given rank 42, the lowest yielding rank 1 (Finckh, Gacek, Nadziak and Wolfe, unpublished).

**Table III.** Mean rank and range of rankings for yield, yield per ha (kg) and residual mean square error (MSE) of rank over: seven environments of the seven highest yielding mixtures; and the pure stands of a yield trial involving seven pure stands and 35 three-way mixtures of barley in Poland. It is indicated if the slope was statistically significant (*) and if it was positive or negative. A positive slope means that yield increases with increasing conduciveness of the environment for yield. Numbers in parentheses give the mean yield of all mixtures containing a given cultivar. (Data from [30]).

| Mixtures and Cultivar(s) | Rank | MSE | Range | Mean | Yield | Slope |
|---|---|---|---|---|---|---|
| ApBiDe | 34.9 | 61 | 24-42 | 6019 | | + |
| ApLoRo | 35.9 | 24 | 25-40 | 5965 | | + |
| BiDeRo | 31.7 | 50 | 20-40 | 5961 | | + |
| ApDeRo | 31.7 | 165 | 5-40 | 5931 | | +* |
| DeLoRo | 32.3 | 87 | 13-39 | 5906 | | + |
| ApArDe | 30.0 | 130 | 11-41 | 5879 | | +* |
| ApBiLo | 30.3 | 119 | 14-42 | 5869 | | – |
| Dema (De) | 25.0 | 220 | 1-40 | 5734 | (5745) | + |
| Roland (Ro) | 21.7 | 145 | 2-41 | 5724 | (5733) | + |
| Apex (Ap) | 21.4 | 253 | 2-42 | 5678 | (5770) | + |
| Lot (Lo) | 22.3 | 221 | 4-41 | 5672 | (5709) | – |
| Ars (Ar) | 14.1 | 248 | 1-42 | 5488 | (5635) | + |
| Bielik (Bi) | 11.4 | 104 | 2-28 | 5408 | (5666) | – |
| Koru (Ko) | 2.0 | 2 | 1-4 | 4820 | (5547) | – |
| Mean | | | | | | |
| pure stands | 16.9 | 170 | | 5503 | | |
| mixtures | 22.4 | 96 | | 5686 | | |

yields of all pure stands and mixtures in the trial were ranked and regressed on the mean yield of the environments in which the experiment was conducted. A high mean rank with low mean square error (MSE) and a non-significant, or at least positive slope is the most desirable combination. While the ranks of the mixtures, with one exception, did not range below 10, the ranks of the pure stands ranged over a much larger amplitude (Fig. 7). The MSE of the mixtures were overall much lower than for the pure stands. The seven best mixtures and the pure stands are listed in Table III.

### 3.2. Correlation between disease severity and grain yield in mixtures/multilines

While yield benefits in mixtures have been observed in the presence and absence of disease on many occasions [99], knowledge about the relationship between disease severity and yield in mixtures is limited. The reason for this is that in most trials only diseased mixtures are compared to the mean of the diseased pure stands. To determine the effects of disease reduction on mixture yield, non-diseased controls need to be included in the trials, doubling trial size and complicating experimental design because of problems with interplot interference.

In an experiment with winter wheat [26], there was a strong negative correlation between yellow rust severity and yield of pure stands, but no such correlation was observed in mixtures (Fig. 8). It appears that with increasing disease severity, relative yield losses were reduced in mixtures as compared to pure stands (Fig. 8b). In a similar way, in the study of mixture effects on yield and *R. secalis* infection in barley [76], the correlation between disease and yield was 0.63 in the pure stands but only 0.08 in the mixtures (Newton et al., unpublished). Clearly, plant-plant interactions in mixtures are affected by disease and competitive relations have been shown to be strongly affected by disease (e.g. [16, 26]).

To avoid ambiguous effects of plant-plant interactions in mixtures, Kølster et al. [49] studied mixtures of near-isogenic barley lines (NILs) differing only in race-specific resistances when infected with barley powdery mildew. In the absence of disease the expectation is that a mixture of NILs should perform equally to a single line and NILs should not differ in competitive ability. In the presence of disease, however, the performance of different NILs may be affected differently and consequently compensation could occur. There was a significant negative correlation between disease and yield for the 19 NIL pure stands. However, for the thirteen four-way mixtures, the correlation between disease and yield was not significant. As in the study with winter wheat [26] (Fig. 8), the tendency was that yield losses in mixtures were

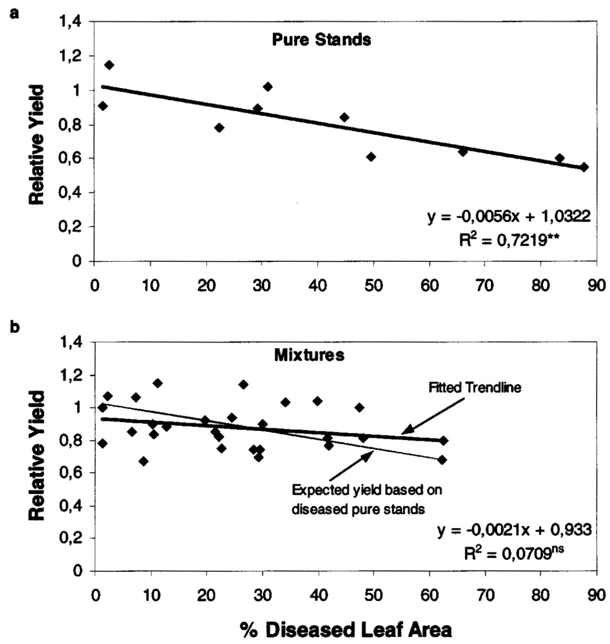



**Figure 8.** Correlation between severity of wheat yellow rust and yield relative to the mean of the healthy control plots in pure stands (a), and various two-way mixtures (b), of five winter wheat cultivars grown in two locations in the western USA in 1989. For pure stands, relative yield = yield in diseased plot divided by the yield in the healthy plot. For mixtures relative yield = yield in the diseased mixture divided by the mean of the yield of the healthy pure stands, weighted by the proportion of the cultivars that were grown in mixture. Trend lines were fitted and the equations are given in the graphs. For pure stands, the correlation between disease and relative yield was significant at $P < 0.01$ (**), the correlation was not significant in the mixtures (ns). The expected relative yield for mixtures based on the effect of disease on pure stands is added to (b). Based on Finckh and Mundt [26].

relatively lower at higher than at lower disease severities, in comparison to pure stands.

The same effects were observed even in the absence of major gene resistance in the field when barley cultivars with low disease resistance (high yield loss in monoculture) that differ in partial resistance to powdery mildew were mixed together. Again, yield losses due to powdery mildew were less in mixtures than in pure stands and there was a positive correlation between the yield advantage in mixtures and the yield loss due to powdery mildew in monoculture [74, 75].

The increase in relative yield advantage of mixtures with increasing disease severity in the pure stands points to the great benefits in terms of yield stability and buffering from unexpected calamities that growers could reap by adopting within-crop diversification.

## 4. The effects of mixtures on the quality of the product

### 4.1. Mixtures, fungicide use and product quality

There is increasing concern among consumers about pesticide residues in food and consequently an increasing demand for reduction of pesticide use. This is reflected by the Swiss 'Extenso' scheme (see Sect. 3.2) that subsidises production without fungicide, insecticides and growth regulators. 'Extenso' products are successfully marketed under a special label indicating the consumers' willingness to pay for perceived quality advantages. Much of the 'Extenso' cereals are produced as mixtures.

Because of the great ability of mixtures to buffer against yield losses due to disease (see Sect. 2.4.2.1 above) yield increases in mixtures through the use of fungicides are often low, making the use of fungicides less attractive [99]. In recent trials in Scotland, fungicide-treated mixtures consistently gave yield responses similar to untreated mixtures compared with their respective monoculture components, demonstrating that agronomic attributes of mixtures need to be considered at least as important as reduction in disease (Newton, unpublished data). An interesting interaction with the environment was observed in Switzerland in field trials with winter wheat using five varieties and five two- or three-component mixtures where the effect of fungicide treatment was investigated in three subsequent years at three locations (= 9 environments). The yield data showed that in high-yielding environments the mixtures' performance was best and that there was hardly any advantage from fungicide use (Merz, unpublished data), in line with results with barley mixtures [100].

### 4.2. Taste and processing quality

There is no doubt that the uptake of variety mixtures has been limited by the uncertainty among farmers of their ability to sell their grain to industrial end-users. However, this uncertainty should not apply to farmers wanting to use their crops for feed, either as whole crop silage or as grain. Indeed, variety mixing represents a particularly valuable tool for organic farmers who do not have access to fungicides for disease control. For the non-organic farmer, mixtures will often have the advantage of more economical production than from pure varieties with fungicide treatments. Winter barley variety mixtures are grown in Scotland as a 6-row high yielding feed quality variety mixed with a 2-row to increase the specific weight, i.e. to increase quality [73].

In the north-western USA, varieties within the same market class are not segregated at the elevator. Thus, it makes no difference for grain customers if varieties are grown in pure stand or in mixture. In general, there is probably more variability for end-product quality among grain from different fields of the same variety than there is among crops of the same varieties grown together in the same fields. Thus, marketing of grain from variety mixtures has not been an issue, to any degree. Even when considering produce for which quality has to be exact and high such as malting barley or bread wheat in Europe, the obstacles can be overcome. For example in the former GDR all malting barley was produced in variety mixtures that had been composed in collaboration between breeders, growers and maltsters with no reduction in product quality [97]. In fact, Baumer and Wybranietz [8] compared the variability in malting quality of pure stands and variety mixtures of malting barley cultivars that belonged to the same quality class over eight locations. They found that the variability in quality due to location effects was significantly higher for the pure stands than for the mixtures.

More recent trials confirmed these findings [77]: growing both winter and spring barley cultivars in combinations of different malting quality did not affect malting quality significantly except for decreases in homogeneity of cell wall modification. A particular mixture of three winter malting cultivars even gave higher hot water extracts than the component cultivars in pure stands, with no adverse effects on homogeneity [77].

When two sets of spring barley germplasm, from cultivars grown either in the UK or in Poland, were grown on one UK site at two levels of nitrogen fertilisation, laboratory scale malting revealed three mixtures with extracts equal to, or significantly higher than, those of all of their components [88]. Increased nitrogen fertilisation gave higher diastatic power, but reduced hot water extract in mixtures and component cultivars. Polish mixtures and their component cultivars showed a higher Kolbach index but a slower rate of filtration, following malt extraction, than their UK counterparts. Further, it was concluded that, overall, the malting performance of the mixtures was largely determined by the nature of the germplasm from which they were constructed and the conditions under which they were grown rather than whether they were grown in mixtures or monocultures. Importantly, there was potential for selecting mixtures of superior malting quality which retained all the other beneficial attributes of mixtures [88].

In general, flour made from high class wheat produced under the Swiss 'Extenso' scheme offers the same quality as 'conventional' material and is used by major food suppliers and bakeries to produce specially labelled bread. This has helped to increase wheat mixture cropping, now up to 10% of the total wheat area.

An important aspect is interactions between nutrient supply and grain quality, and the effects of mixing under low and high input conditions. In an attempt to improve the baking quality of wheat under low nitrogen fertility conditions, Sarandon and Sarandon [83] found that a 1:2 mixture of a low-yielding high quality wheat and a high-yielding lower quality wheat, yielded as much as the high-yielding variety alone, but with the high quality of the low-yielding variety. The mixture effects on grain protein content disappeared under high nitrogen input. This result is significant in view of the current efforts of organic farmers to improve bread-making quality under lower nitrogen fertility in organic systems. Under organic conditions, varieties with lower molecular weight gluten often have better quality than the high molecular weight gluten varieties that are bred for high input agricultural systems (Völkel, personal communication).

Consumers would be unlikely to notice the difference between flour or malt derived from pure stands versus mixtures. However, the same might not be true for rice, where the consumer can see individual grains in the final product. In the Philippines, it is general practice to mix rice varieties before selling them to customers. Also, the widely popular Basmati rices that are sold all over the world usually contain only some percentage of real Basmati (Finckh, personal observation). We are aware of only one study where the quality of grain from rice mixtures has been studied [18]. In this case, grain from a three-component variety mixture was compared by a consumer panel with grain from the three components grown separately in pure stand. The panel detected no difference between rice from the mixture or the pure stands for taste, aroma, or stickiness. Further, members of the panel did not recognise that rice from the mixture was, in fact, a mixture. In terms of overall consumer acceptability, the mixture was equal to two of the component pure stands and superior to the third. Tests of physical and chemical characteristics for the mixture were intermediate between those of the best and worst component pure stand.

## 5. Mixtures in practice

The use of mixtures and multilines is popular in many different areas of the world especially for wheat and barley. An informal survey conducted by the COST working group revealed that, in addition to mixtures in wheat and barley, the concept is also being applied successfully in Colombia, where coffee is produced mostly in multilines to protect the crop from coffee leaf rust (caused by *Hemileia vastatrix* [28, 29, 64] (Fig. 9).

The results of this survey can only be viewed as an indication of mixture use because there are no data available on the use of mixtures from many parts of the world . An important result , however, is that, in addition to variety mixtures, species mixtures are widely used especially as forage mixtures (grass species and clover) and for feed cereal production. An impressive example is in Poland, where since the 1950s, official advice and encouragement was to grow pure stands. Despite this advice, many growers chose to grow mixtures of cereals (barley-wheat, barley-oat) or cereals with legumes and the area under species mixtures increased from 400 000 ha in 1970 to 1.2 mio ha in 1993 [22]. In Pakistan, wheat and sugarcane are inter-cropped to save labour costs in protecting the

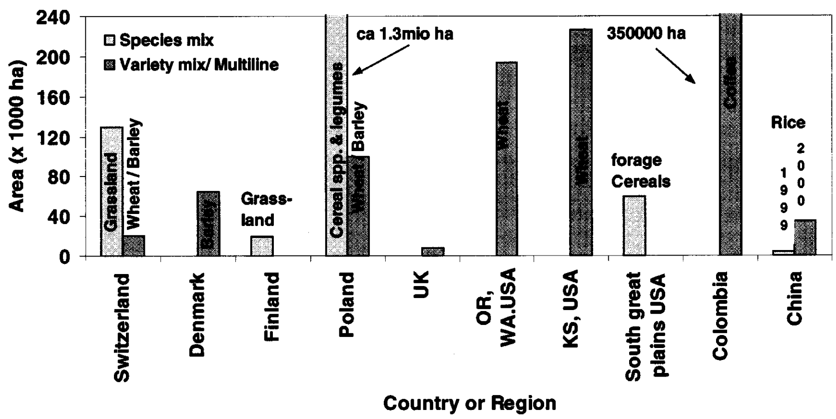



**Figure 9.** Multilines, variety and species mixtures grown in various countries of the world. Data from an informal survey conducted between 1996 and 2000 by the authors.

sugarcane from frost injury (Aslam, personal communication).

### 5.1. Legal restrictions

In the Pacific Northwest of the USA, where most of the U.S. research on mixtures is currently being done, there have been no legal restrictions on the sale of mixed seed for either sowing or end-product use. Seed of variety mixtures is currently being sold by the two largest seed companies in the state of Oregon, as well as by many smaller seed companies. In addition, many growers produce seed of mixture components and do their own mixing. The most common practice is to grow a mixture population for 3 or 4 years before reconstituting or changing the mixture.

Attempts have been made by Swiss wheat breeders to screen breeding line combinations for their mixing ability and performance in numerous environments. They finally selected the best three-component winter wheat mixture and proposed that it should be registered in the national variety catalogue in 1996. Although uniformity was a selection criterion, the committee responsible refused to register it because of concerns over the definition of 'purity' and the production of seed.

Selling of seed mixtures was generally not allowed in Denmark (although labelled mixtures can be traded within member states of the EU according to legislation introduced in the 1970s). However, because of the continuous break-down of powdery mildew resistant barley varieties in Denmark, interest in mixtures grew in the 1970's (see [93]) and, from 1979, seed companies were allowed to produce and sell mixtures of spring barley and, from 1988, winter barley mixtures. Between 5 and 15% of the area grown with spring barley has been planted to mixtures since 1984 (62 000 ha in 1996) [69]. Winter wheat mixtures were allowed for the first time in the autumn of 1998.

In order for a seed company to produce and sell variety mixtures, the mixtures have to be approved by the Danish Plant Directorate of the Ministry of Food, Agriculture and Fisheries. Mixtures can be approved according to the following criteria:

1) Production of mixtures within spring barley, winter barley and winter wheat is allowed. Only varieties from the Danish National List of Varieties or the EU variety list can be chosen as components;
2) Mixtures should be composed of equal amounts of the varieties by weight;
3) Mixtures can be composed of 3 or 4 varieties;
4) When composing mixtures, resistance to important epidemic diseases (powdery mildew, yellow rust, scald, net blotch and Septorias) as well as agronomic traits (grain yield, maturity time and length) should be taken into consideration.

The criteria concerning resistance level is fulfilled if the average level of disease severity is below a certain maximum value. This value changes from year to year and is calculated from disease assessments made on the five most widely grown varieties per crop in the disease observation plots at the Danish Agricultural Research Station for Plant Improvement. Resistance criteria were updated in 1997. Before that, one of the criteria was that the mixtures should be composed of four varieties with at least three different race-specific resistance genes.

The criteria concerning agronomic traits are fulfilled if the grain yield on average over five years is 95% (relative to standards). For new varieties with fewer years in trials the figure is 97%. The varieties may vary no more than 5 days in maturity time or by 20 cm in straw length.

For the season 1999/2000, 4 winter barley mixtures and 13 winter wheat mixtures have been approved. Also 46 spring barley mixtures have been approved for sale in the year 2000.

### 5.2. Practical breeding, extension, and research aspects

In Poland, variety mixtures are tested in multi-location field trials and the best mixtures from all trials are selected each year for recommendation to the growers. Recommended mixtures are tested each year in large (1 ha) demonstration field plots. In these plots, between 1984 and 1993, the best mixtures yielded on average 10% more than the mean of their component pure stands [22]. In the barley breeding programme, varieties and breeding lines are evaluated for performance in mixtures [22] applying simple combining ability and yield stability analyses [32, 33], because it is not possible to extrapolate from the performance of a variety in pure stand to its performance in mixture.

The ‘Extenso’ scheme (see Sect. 2.4.3.1) was introduced in 1992 by the Swiss government to reduce the oversupply in cereals. Wheat or barley produced with these rules was entitled to a state contribution of SFR 800·ha$^{-1}$ (circa 500$ US). This subsidy made ‘Extenso’ very attractive to farmers: about 60% of the barley crop and 35% of wheat are now produced under this scheme. As variety mixtures fit perfectly into the ‘Extenso’ scheme, their importance has also increased since 1992. About 20% of the barley area and 12% of the wheat area (both mainly winter crops) in Switzerland are now cropped with mostly 2-component mixtures.

Baking quality was a restricting factor in Switzerland until the early 1990s for growing wheat mixtures. Wheat prices are based on quality classes and there were only 1–2 high quality winter wheat varieties available (90% of wheat area is cropped with winter wheat). However, because of changes in breeding and selection practices, and also to make reduction in pesticide inputs possible, six winter wheat varieties with a high baking quality and four two-component mixtures are now available and are recommended by the research station extension service (for more information see www.admin.ch/sar/fal/sorten/gbwwd.html and www.admin.ch/sar/fal/sorten/gsmwd.html). In addition, many regional seed suppliers offer premixed seed – all two-component mixtures of registered varieties – which helped to promote mixture cropping. As mixture cropping in Switzerland is closely related to the ‘Extenso’ scheme, it’s future is unsure. Up to now the government reduced the premium stepwise (1999: about SFR 300·ha$^{-1}$) and current plans are to make ‘Extenso’ part of the direct payments for integrated production by 2002. So far, the farmers have discovered the advantages of mixtures but if there is no longer a clear economic advantage to produce under the ‘Extenso’ scheme, then they may prefer another form of production.

The Danish Agricultural Advisory Service started long-term trials with spring barley mixtures in 1979. Between 1979–1991 at least 230 spring barley mixture trials, and in addition, trials with winter barley, winter wheat and peas, were conducted all over Denmark [69]. A standard variety is included in all variety trials (cereals and other crops) but, since 1983, the standard variety in spring barley trials has been a mixture – changing almost every year. Later, the winter barley and winter wheat trials also had a mixture as standard. Every year, a detailed report is published (in recent years the editor has been Carl Åge Pedersen) on all the trials and the report is distributed to the extension service and to others.

In Oregon, USA, research on mixtures and extension of that knowledge to farmers has been part of an integrated approach to crop production. Critical to adoption of mixtures has been interactions of research and extension personnel with farmers. Initial studies are often done in small plots at experiment stations, with promising treatments being moved to larger plots in farmers’ fields. University personnel recognise that farmers are attempting to produce grain, not just green leaves. Thus, disease control is just one aspect of variety mixture research. Yield stability in the face of unpredictable variety × year interactions, caused by disease or not, is a more important factor for many farmers. The value of mixtures has not been overstated, i.e. mixtures have not been proposed as a cure for all production problems, so most growers who have experimented with mixtures have been pleased with the results.

### 5.3. Breeding and analytical tools

Cereal mixtures have been constructed from either near-isogenic lines or cultivars bred for exploitation as monocultures. In neither case have they been selected for overall performance in mixtures. There is a considerable literature on the analysis of genotypes for their mixing ability ([29] for review). Analysis of mixing ability requires experimentation with pure stands and mixtures, and conclusions about the mixing ability of one set of cultivars cannot be extended to cultivars that have not been tested. Instead of expensive experimentation, breeding of varieties with functional diversity for resistance and high yield performance, for example via bulk selection, composite [38] or top-crosses [59], could reduce costs and increase genetic diversity without sacrificing other advantages of modern high-yielding varieties.

For a composite cross, diverse varieties or lines are intercrossed in all combinations. The $F_1$ plants are then grown as a bulked hybrid population for subsequent generations without conscious selection. This has been termed an "evolutionary plant breeding method" [38, 42, 86]. Yield synergies among genotypes that had co-evolved in a barley composite cross over 18 years were significantly higher when grown in mixtures than they were in a mixture of cultivars that had not co-evolved [4]. In addition to greater ease of selecting for good mixing ability, composite crosses and subsequent bulk selection can play an important role in genetic resource conservation [3]. Other methods available are simple bulk selection and top crosses or the bulking of breeding populations after fewer back crosses than usual [28]. For the future improvement of variety mixture performance, there is a need to expose breeding lines to the same conditions that they will be exposed to later, i.e. to diverse neighbouring plants.

Molecular markers offer the opportunity to select for attributes that are not easily identified as single gene expressions. Yield and quality parameters, for example, have many quantitative components. Some will need to be homogeneous, whilst recent work on barley malting quality indicates that heterogeneity at certain loci is beneficial for obtaining good extract [88]. QTL (quantitative trait loci) mapping analysis can identify markers closely linked to loci involved in beneficial mixture interactions. QTLs can also be used to design mixtures for particular purposes, such as barley mixtures with low glycosidic nitrile or high diastase for whisky distilling. Such specialist attributes may not justify the breeding of new cultivars, so mixtures offer a practical way of combining the attributes of the most advanced cultivars with other desirable traits.

Molecular markers can also be used to accurately quantify the components of mixtures. For example, all cultivars of barley tested can be identified using four simple sequence repeats (SSRs) [37, 82]. This could be carried out by sampling leaves from the growing crop, harvested grain, or perhaps even from the malt. This technology can be used not only to determine whether a mixture comprises the declared cultivars, but also whether there is any contamination with other cultivars, what the contamination is, and in what proportions the components (and contaminants) occur. This has both practical advantages for processors so that they can fine tune their conditions, and for authenticating mixture composition claims. This may remove several of the objections raised by legislative authorities about enforcing standards.

## 6. General discussion and conclusions

Variety mixtures are being used with success in many parts of the world, reducing diseases and stabilising yields. One of the main constraints to mixing is often the lack of suitable components because they have to be agronomically similar for quality and maturity but different for resistances to diseases and other stresses. Targeted research and breeding for mixtures could improve mixture performance considerably.

The use of mixtures is not the answer for all farming needs, but could make a significant contribution, which is often neglected for the wrong reasons. Mixtures have tended to be consigned to the 'alternative technology' box along with 'organic' agriculture and other 'environmentally friendly' or 'politically green' approaches. On the contrary, mixtures are applicable to many agricultural situations. There are many potential benefits for their use in low input and 'organic' situations where there is a lack of alternative approaches for controlling disease. Their potential and economic impact is likely to be as great, however, in mainstream agriculture, where the yield and reliability of the best products of modern breeding programmes could be further enhanced.

Biodiversity provides insurance against unforeseen environmental effects. The use of variety mixtures is an approach that builds this protection into agricultural practice rather than keeping it in store for use in the event of disaster. Mixtures may not remove the requirement for pesticides but they may enhance their durability and reduce the level of active ingredient required for reliable effect.

An important aspect that has been noted but not fully explored (see [28] for a review), is the advantage that mixtures can bring in terms of simultaneous resistance to several diseases combined with buffering against unpredictable environmental variation. For example, Wolfe and Meyer (unpublished) noted that, in a winter barley mixture grown for restriction of powdery mildew, incidence of both net blotch (*Helminthosporium teres*) and scald (*Rhynchosporium secalis*) were also reduced significantly in relation to the mean disease levels on the component varieties grown as pure stands. For each of the three diseases, it happened that a different component of the mixture was the most resistant. Similarly, recent observations with wheat mixtures in variety trials indicate simultaneous reduction of at least three diseases (Wolfe, personal observation). On a much larger scale, it was noted in the former GDR during the period of extensive use of mixtures selected for mildew control, that leaf rust infections were also reduced significantly. Complementation could also occur for product quality as demonstrated elsewhere for baking quality of wheat [83].

From such observations, it is clear that mixtures can be designed to complement the efforts of the plant breeder by bringing together positive characteristics that would otherwise be deficient in the component varieties.

The use of variety mixtures for disease control is particularly valuable for low input and sustainable agricultural systems, including organic agriculture. To improve the scope and reduce costs still further, farmers have made simple adaptations of seed hoppers, augers and seed drills allowing them to design and apply their own mixtures for specific uses on the farm [47]. On farm experimentation also allows the farmer to determine, for a specific situation, the number of generations for which a specific mixture might be grown before a new seed mixture is required.

For systems in which fungicide inputs are used, there are also options to integrate the use of the fungicides with variety mixtures. This could have the advantage of both limiting the amount of fungicide required and restricting selection of pathogen genotypes adapted either to the varietal resistances in the mixture or to the fungicides. Wolfe [95] demonstrated this approach by investigating mixtures in which the seed of only one of the three variety components was treated with a fungicide applied to the seed. Such a mixture limited disease to the same amount as that with a full fungicide treatment, while limiting selection for fungicide resistance to only one-third of the plants in the crop population. However, the amount of disease on the untreated mixture and the yield of that mixture, were not significantly different from the treated mixtures, which raised the question of the value of the fungicide treatment.

One criticism of mixtures in practice that remains common is that the highest yield is always obtained by growing the highest yielding variety, and not from mixtures. This is an incorrect view because, among competing varieties, it is usually impossible to predict which will be the highest yielding in a future season in a specific location (see e.g. Fig. 7). For a safe bet, it is sensible to grow several leading varieties at the same time, and, better still, to grow them in a mixture. Also, experience shows that a mixture of competing varieties with similar yields in pure stand is likely to produce more than the mean of the components which means that it is likely to outyield all or most components.

The activities of the COST Working Group on Cereal Variety Mixtures have been restricted to the control of air-borne diseases on temperate cereals. Much is now known about the effectiveness of such mixtures and how they work. In our view, it is important to extend this view, not only to all cereals, but to all arable crops, to build on initial work with, for example, rape, soybeans, potatoes and beans. Moreover, the variety mixture system represents only one aspect of inter-cropping: we need to undertake further analysis and development of other forms of inter-cropping, including species mixtures and the many possible combinations of row- and strip-intercropping [9, 21].

In the longer term, there is a strong argument to be made for incorporating into breeding programmes the possibility of selecting varieties for mixing or ecological combining ability, that is, for their ability to perform well in different inter-cropping systems.

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