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Breeding strategy for mixed production systems in sub-Saharan Africa

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Abstract

The strong interaction between the genetic make-up of varieties and environmental conditions calls for breeding strategies to be developed with multidisciplinary and multi-stakeholder approaches. Breeding has been supported by an increasing number of disciplines, such as crop physiologists, statisticians and crop modelers, so as to hasten the processes of crossing, selection and testing. Biotechnological approaches tend to recoil from this ever-widening approach. We argue, however, for a yet further broadening of this wide view, by introducing considerations related to the entire production system within which a crop is cultivated. This approach will better reveal the functioning of species and support identification of the genetic characteristics necessary to enhance productivity in a given context. Special reference is made to sub-Saharan Africa.

Background

Breeding can be a cumbersome activity requiring many resources because of the extensive crossing, selection and testing that takes place in several locations. Breeders thereby select the progenies by their "overall view" of the performance of the crop stand. Due to the large genotype by environment interactions, including the large impact of agronomic practices on crop performance, selection and testing should ideally be done in all target locations, meteorological conditions and cropping systems. In order to accelerate the breeding process and reduce both the number of testing locations and the duration of testing, plant physiologists, statisticians and crop modelers have supported breeders in identifying desired traits, through methods that improve the selection process by understanding genotypes, designing ideotypes and by clustering environments. To further increase the specific adaptation, participatory approaches have proven useful in some countries.

Overall, breeding has contributed about one-third of the yield increase of the major cereals (rice, wheat and maize) during the green revolution (Evenson and Gollin, 2003), while improved agronomic measures were fundamental to the exploitation of the yield potential of the improved crops. Experiments in Europe showed grain yields of wheat varieties from the early 1940's at up to 8 t ha^{1}, while yields for modern varieties were as high as 10 t ha^{1} from the 1970's (at similar application rates of N fertilizer and under optimal temperate growing conditions) (Spiertz, 1982). Actual farmers' yields, however, were lower, at 3 t ha^{1} in 1961 (even at high fertilizer rates), increasing to 8 t ha^{1} only by 2000. The greater difference in yield between old and modern varieties under farmers' conditions as compared to experimental conditions should be ascribed primarily to an improvement in the overall management practice at farms. In addition, crop characteristics such as lodging resistance have prevented modern varieties from topping-over under farm conditions. For allowing older varieties to express their yield potential, they have been physically supported under experimental conditions, such as by fishing nets (e.g. Sayre et al., 1997). The strategy in breeding has been to increase the harvestable proportion of the crop (harvest index) - resulting in a jump from approximately 0.35 before the 1960s to 0.5 in the 1980s (e.g. Austin et al., 1980; Cox et al., 1988; Sayre et al., 1997; Spiertz, 1982) - while also genetically enhancing resistance to lodging, pests and diseases. Both the breeding and agronomic strategies have been geared to raising production efficiency in terms of land, labor and capital, leading to highly specialized systems with sole cropping.

The above demonstrates that the expression of crop characteristics depends heavily on growing conditions. Viewed from the reverse perspective, in designing crops to increase yield and productivity, growing conditions should be prominently taken into consideration. In other words (using the example of lodging), the harvest index was actually *not* the first limiting factor in raising grain yields, but the associated reduction in height may have contributed to reduced lodging and easier crop handling. This calls for a systems perspective on crop performance in recommending breeders as to the characteristics to be altered. It is unlikely, therefore, that advances in single disciplines can address all the issues involved in increasing food production.

With biotechnological approaches, the speed of the breeding and selection process can be increased. Much emphasis is placed on issues like insect and disease resistance and herbicide tolerance, and more recently increased nutritional content and reduced allergenicity, etc. These approaches address 'single issues', which may reflect a tendency towards the development of isolated solutions to broader problems, such as concerns for the environment, dietary problems, etc. These approaches are likely to lead the widened perspective on breeding to revert back to breeding strategies that reduce practical problems to narrow and specific crop characteristics. The contribution of breeding during the green revolution has proved this strategy to be successful in the past, but only when the expression of the genetic potential went hand-in-hand with improvements in agronomy. This suggests that an integrated approach may achieve the highest impact. While modifications in crop characteristics may ultimately relate to 'single characteristics', the identification of these characteristics should follow from a broad perspective, and one that complies with local specificities. For those areas that have not benefited from past genetic progress, in particular sub-Saharan Africa, following broad and integrated views are surely to be recommended.

In this paper, we review the current trends in breeding strategies, and argue on the basis of a system-wide perspective for the breeding strategy, including biotechnology, that would most effectively meet the needs of sub-Saharan African agriculture for the coming decades.

Sub-Saharan African agricultural systems

For sub-Saharan African agriculture to prosper, its productivity needs to increase dramatically, in terms of land, but primarily in terms of labor. Over the past four to five decades, yearly labor productivity gains have been minimal or even zero. Labor productivity in sub-Saharan Africa did increase by some 20% between 1960 and 2000, meaning that five people today produce the same amount of food as did six people four decades ago. This stands in stark contrast to Europe, however, where labor productivity increased six-fold and more over the same period, and this over and above the fact that the 1960 productivity levels in Europe were far higher than those in sub-Saharan Africa. The average annual increase in yield over that period has been a fraction of the increases realized in other parts of the world, often not exceeding 10 - 20%. Even for crops important to Africa, such as cassava, banana, millet and sorghum, higher yield gains were realized outside of the continent. Overall, the total volume of food grown doubled, but the availability per person decreased, by 12%, due to the faster rate of population increase (Bindraban et al., forthcoming).

Multiple intervention strategy

Bindraban and colleagues (forthcoming) have showed that other than labor, the use of external inputs as a method of increasing productivity in sub-Saharan African agriculture has been minimal or non-existent. Fertilizer use peaked at some 12 kg ha-1 in the 1980's, but then decreased again due to policies, often imposed by foreign donors, that terminated subsidies for inputs. This failure to employ external inputs is shown to be the prime cause for the negligible growth rates in farming in the sub-Saharan region. The experimental findings in Europe that wheat yield increases have resulted mainly from improved agronomic practices which allowed improved varieties to express their yield abilities is in line with the synergistic effect shown for the entire EU-15 region.

European crop yields remained low at 3 t ha^{-1} in 1960 despite the high application of fertilizers, but had increased to 8 t ha^{-1} by 2000 at similar application rates due to improved genetic yield potential, improved lodging, pest and disease resistance, the use of biocides, more precise application of fertilizers and other inputs attuned to the crops' needs. These synergistic effects that are observed at field scale, and also emerge at a regional level, have their roots in the basic theory presented by De Wit (1992). De Wit argues that 'most production resources are used more efficiently under improving conditions of resource endowment.' This theoretical concept is based on Liebscher's 'Law of the Optimum', which expresses the idea that yields respond more strongly to inputs, the more favorable the crop growth environment.

Species specific to sub-Saharan Africa

Another reason for the lack of increase in productivity in sub-Saharan Africa has been the wide diversity of crops. While in almost all regions in the world, rice, wheat and maize contribute to almost 75% of the food intake (directly and indirectly e.g. through conversion into meat), these staples contribute to less than a third of that in sub-Saharan Africa. Research into these cereals has received much emphasis, because they are also important in industrialized countries. Crops specific to sub-Saharan Africa, such as plantains, roots and tuber crops like cassava and yams, and small cereals such as millet and sorghum have received relatively little attention. At the same time however, the efforts that were given to improving these crops resulted in minimal overall yield improvements, despite a substantial adoption of improved varieties, such as for sorghum (Maredia et al., 2000). These limited gains can be

ascribed to the low usage of other agricultural inputs, which thus prevented the new varieties from expressing their potential. In some instances, over-reliance on a cultivar-alone strategy in order to increase productivity (i.e. single measure approaches) has even led to declining yields, sometimes accompanied by an increased variability of yield (Ahmed and Sanders, 1998). Indeed, whenever a broad package of agronomic measures has been introduced in a production system, successes in yield increase have been reported (Ahmed et al., 2000). In short, the improvement of crops specific to sub-Saharan Africa has not received the attention it deserves, and interventions to enhance productivity through breeding should be accompanied by supplemental agronomic measures to be effective.

Mixed farming systems

In its strategic plan for enhancing agricultural development in sub-Saharan Africa the InterAcademy Council (2004) identified another systems characteristic that might have hampered the adoption of green revolution solutions (see Bindraban and Rabbinge, 2003). Productivity enhancing measures have led to a worldwide specialization of cropping systems with single crops of narrow genetic diversity grown in a field which facilitates cultivation practices through mechanization. Most farmers in sub-Saharan Africa, however, cultivate up to 10 to 15 food and cash crops in a wide array of mixtures, often in combination with animal husbandry. Moreover, even within the crops, a multitude of genotypes are grown, each with its own characteristics and uses (Seboka and van Hintum, 2006). Mixed-cropping systems tend to diminish risk by reducing crop losses from pests, diseases, and abiotic stresses, and allow the effective use of farm labor to ensure food availability (e.g. Lhoste and Richard, 1993; Sissoke, 1998). These farming systems are a coping strategy to survive the harsh biophysical conditions, including low and highly variable soil fertility (Eswaran et al 1997; Voortman et al 2000), severe pest and disease pressures including lethal animal diseases (Asiema 1994), and highly erratic rainfall. A low population-to-land ratio provides only a modest capability to intensively control biophysical conditions per unit area - e.g. by practicing intensive weeding or by specializing production, as for instance in inundated rice cultivation in densely populated Asian countries. Consequently, an extremely wide range of interspersed crops and cropping systems has developed across sub-Saharan Africa (Dixon et al 2001). Diverse socio-economic, institutional and cultural factors, such as family circumstances, communal use or private land rights, and distance from the household compound to the field or market, further shape the complex characteristics of the farming systems.

A diversified development pathway

Strategies for enhancing the productivity of sub-Saharan African agriculture should take these complex systems as a starting point, as it is unlikely that the transformation towards specialization will occur within a single generation for the almost 90 percent of African farmers who are currently engaged in diversified farming systems. Stepwise upgrading and improvement of the productivity of diversified systems should be aimed at, by exploiting ecological synergies - such as reduced pest and disease dissemination, optimal exploitation of soil water and nutrients, and the provision of nutrients by legumes to non-legume crops. This strategy would take Africa along a more diversified path of modernization than was pursued during the green revolution. Whereas the enormous diversity may have constrained progress in productivity in the past, it could turn out to be an asset in designing resilient agricultural production systems.

Plant breeding, as a major contributor to productivity enhancing technologies, will have to develop an appropriate strategy to comply with the needs of agriculture in the region. Advancements within the breeding discipline in isolation are not likely to solve the complex challenges of increasing agricultural productivity in sub-Saharan Africa: they will have to be aligned with views and insights generated in multi disciplinary and multi stakeholder approaches.

Developments in breeding

General progress in increasing the yield potential of cereal crops during the green revolution has been substantial, primarily based on an increased harvestable proportion of the total biomass rather than an increase in total biomass itself. From the 1990s onwards progress has declined, suggesting that the easy gains have been exhausted. Breeding strategies have moved towards an improvement of specific characteristics in order to safeguard yields, primarily by increasing resistances to pests and diseases, by enhancing lodging resistance and by raising drought tolerance.

Breeding the green revolution

The Consultative Group of International Agricultural Research (CGIAR) has played a prominent role in variety improvement. A first wave of 'modern' rice, wheat and maize varieties was released in the late 1960's, drawing from prior research work carried out in developed countries. This latter benefit could not be applied to crops like cassava and beans. Progress also remained slow because of the low research priority that was given to these crops both in North and South. Moreover, for a rapid adoption of varieties a two-step breeding approach was necessary. Breeders at CGIAR centers would breed productive plant types specific to major agro-ecological zones, which would subsequently be further bred for location-specific traits, such as resistances to diseases, pests and abiotic stresses. This two-stage breeding necessitates an effective breeding infrastructure at national level, in the national centers for agricultural research, in order to make the second step. These conditions were met in Asian and Latin American countries, but not in sub-Saharan Africa. Evenson and Gollin (2003) feel relieved to note that recent evidence shows yield gains in sub-Saharan Africa to have started to come from improved varieties after 1980. They omit to state, however, that in these recent two decades or so the contribution from agronomic practices to yield gains has actually been negative, due to reduced use of inputs. Their own data reveal virtually all yield gains from 1960 to 1980 to have resulted from increased use of inputs, and almost none by variety improvement. Overall yield gains after 1980 decreased to only *one-third* of that prior to this decade.

Crop Physiology

Breeding efforts cannot, therefore, be based on single intervention strategies to increase agricultural productivity, and indeed, the need to support breeding efforts with work from other disciplines in order to improve breeding efficiency and effectiveness was recognized some time ago (e.g. Jackson et al., 1996). Declining progress in the increase of yields, both real and potential, called for input from new disciplines, such as plant and crop physiology. However, while plant and crop physiology could elucidate relationships between traits and performance for specific environmental conditions, it has rarely resulted in straightforward improvements of breeding efficiency or improved varieties. This can be partly ascribed to large uncertainties caused by the variability of climate and agronomical practices. Rees and colleagues (1993), for instance, did report a positive relation between photosynthesis and yield, but it depended strongly on the timing of the measurement. It also remained unclear whether the relation was causal or not, as no relation was found with growth rate. Only rarely have positive relations been found between photosynthesis and yield potential, while selection for high photosynthesis has actually resulted in a *decreased* yield in some crops (Evans, 1990). These particular counter-intuitive results may stem from trade-off effects with other traits due to competition or pleiotropy. For instance, photosynthesis is also found to be negatively correlated to leaf size (Evans and Dunstone, 1970; Rees et al., 1993) which alters the radiation regime in the canopy and ultimately canopy photosynthesis. Regardless of explanations for negative effects of photosynthesis on production, however, the point remains that any contribution which photosynthesis can make to yields is not one that is simple and direct, which exemplifies the difficulties found in utilizing plant and crop physiology for the purposes of breeding efficiency or variety improvement.

Crop modeling

Crop modeling has the quantitative ability to integrate reductionistic knowledge from soil science, crop physiology and meteorology in order to assess whole crop performance on the basis of crop specific characteristics (Boote et al., 2001). This approach balances negative and positive impacts of specific crop traits in relation to environmental conditions, enabling a more holistic view. The crop modeling approach is thus more in line with breeders' perspectives in judging the overall performance of lines and varieties. Modeling approaches have been used to design ideotypes such as those used in rice breeding programs (e.g. Dingkuhn, 1991). Bindraban (1997) applied this modeling approach to identify required traits in order to break through the apparent upper limit in yield potential of wheat grown under optimal conditions. The modeling approach that attempts to unravel the interactions between traits in widely varying environmental conditions can assist in a more precise identification of the determining genetic traits. Yin and colleagues (2002; 2004) evaluated the capacity of a model to identify the quantitative trait loci (QTLs), one which both determined the desired trait(s) across a wide range genotypes and environments, and explained their interactions (GxE). Along with improving statistical methodologies to more precisely assess GxE interactions (e.g. Cooper et al., 1999), the contribution from disciplines other than breeding thus opens up possibilities for more effectively design and target crop improvement, in particular for harsh conditions requiring specific trait combinations.

Biotechnological approaches

At present, biotechnological approaches (genetic modification) allow 1) the incorporation of highly specialized characteristics that are determined by single genes, and 2) the acceleration of the breeding process. In developed nations, such as in Europe, consumer desire increasingly drives research efforts, in contrast to the more supply-driven approach in the past. Consumer desire is increasingly related to concerns about health and safety issues, and more broadly to the broad concept of sustainability. Plant genomics is believed to make a valuable contribution to these concerns as it facilitates identification and improvement of the adaptability of existing crops and trees to the needs of different users. Wheat varieties, for instance, are altered to the specific requirements of the bread, biscuit and starch industries. The nutritional content of food crops is adjusted, as is the functionality of crops in general. This strategy will be pursued through forthcoming research funded by the European Community (see www.plantTP.com).

For developing countries, 'single bullet approaches' such as nutrition-enhancing characteristics and resistances to pests and diseases are being implemented - for instance, through Bt cotton, Bt maize and Golden Rice - with varying results. Some introduced characteristics, such as those derived from the insecticidal microbe, *Bacillus thuringiensis* (Bt-gene), increase resistance to certain classes of insects, which is important for crops like cotton and maize. Extensive surveys in farmers' fields in China and India show cotton yields to increase when Bt varieties are used, while pesticide use and the associated occurrence of poisoning among farmers decrease dramatically; all this leading to a major increase of economic gross margins, even at the higher seed costs (Huang et al., 2003; Morse et al., 2005). For more extensive systems of cotton production such as in South Africa, however, Bt-cotton does not show the same positive results as it does in China and India: there is only a slight yield increase and a limited reduction in labor requirement, while relatively high levels of pesticide use continues - resistance appeared to be low, probably due to the greater diversity in insect population (Hofs et al., 2006).

Golden Rice (GR) has higher contents of ß-carotene in the endosperm and may contribute to alleviating Vitamin A deficiency. Currently in the R&D stage, GR is expected to provide a high financial rate of return for the investment costs. It will not be able to completely eliminate the problems of vitamin A deficiency, and should be considered as a complement rather than a substitute for alternative micronutrient interventions (Dawe et al., 2002; Zimmerman and Qaim, 2004). For successful dissemination and use by farmers of GR, institutes in Europe are collaborating closely with international and national research institutions, in order to create a national sense of ownership and breed appropriate lines adapted to the production area (Al-balili and Beyer, 2005).

Clearly, many of the current initiatives in biotechnological improvement in Africa result from spill-over effects of activities developed outside the continent, rather than being initiated from desires and needs coming from within. An overview of developments on resistance for abiotic stresses (Thomson 2003) reveals, for instance, that most attention has been paid to tobacco, with some also on rice and potatoes. An example of where a targeted single trait improvement could have a large effect on African agriculture is described by Toenniessen and colleagues (2003). This concerns the Cassava Mosaic Disease (CMD), the most prevalent cassava disease in Africa, causing reductions in yield of 20 - 90%. Host plant resistance appears to be the most effective means of control, as farmers cannot afford insecticides to control the white fly vector. Some resistance has been detected in an interspecific backcross progeny of a cross between cultivated cassava and the wild relative. Recently, a novel dominant gene that confers resistance to CMD was detected in a Nigerian variety which was shown to be qualitative in nature and stable across environments. In order to develop resistant varieties for Africa, through either conventional breeding or biotechnology, it is important that particular attention be given to issues relevant and specific to the continent itself.

Breeding strategies to enhance the productivity of sub-Saharan African agriculture

In developing breeding strategies for agricultural systems in sub-Saharan Africa, the characteristics of the mixed-farming (intercropping) systems should be factored into the design process for plant types. The land and labor productivity of farming systems can be increased by a more systematic arrangement of the various crops grown in a field (Mkamilo, 2004). It is found that farmers will pursue mixed cropping despite evidence that higher land and labor productivity can be attained when crops are grown singly: apparently, other criteria are also considered by farmers in determining their strategy. Therefore, the identification of required crop characteristics should be based on a participatory approach with local farmers.

Identifying crop traits for mixed systems

To illustrate the desired breeding strategy for Africa, we will look into intercropping, using the comprehensive description by Davis and Woolley (1993) in order to appreciate the extent to which crop varieties react differently to being grown with other crops in the same field.

Basically, net gains from intercropping relative to sole cropping can be expected if 1) ground cover is provided over a longer period of time, and 2) as a result of reduced water, agrochemical (e.g. fertilizer) and pesticide requirements due to a more efficient exploitation (of water and agrochemicals) and reduced pest and disease pressures. Significant cropping-system based genotype interaction occurs particularly in the dominated crop (and less in the dominating crop). Gains through intercropping can generally be obtained by minimizing the competitive strength of the dominant crop and increasing its harvest index and, for the dominated crop by better exploiting the niche left.

As dominant crops tend to be more successful in extracting mobile nutrients and water, even far away from the roots, they respond more strongly in terms of vegetative growth and ultimately compete with and reduce the growth of the dominated crops - as is the case, for example, in the relationship between maize (dominant) and beans (dominated). This phenomenon is particularly important under conditions of low nutrient and water availability, with competition reducing as availability increases. Thus there are several potential variables in intercropping systems: not only may planting arrangements differ, but also the root morphological requirements and production conditions (high under or low), calling for specific rooting designs. There are species suitable for intercropping as their complementary rooting patterns do not compete for immobile nutrients such as P.

As a general rule, increased diversity of crop species leads to systems that are less prone to disease and pest infestation due to obstructed spreading and the diluted effects of non-host plants. However, pest and disease incidence and severity levels are not always suppressed by intercropping. A systematic search for optimal combinations is required. Recently, Skelsey and colleagues (2005) developed a model to systematically assess the impact of crop combinations on disease dissemination and infestation. The systematic design of cropping patterns through such modeling could be very successful: for example, the employment of patterns that use species which reduce infestation combined with improving the genetic resistance of crops might result in a significant reduction in pesticide use.

When considering intercropping, crop height, and even height relationships within a plant, is another factor to be taken into consideration. The height of crops may have to be adjusted to optimize light adsorption and utilization (Wubs et al., 2005). For a maize-bean intercropping, Davis and García (1983) found that the maize cultivar characteristics which best favored bean growth - because of reduced light interference - were a less-tall plants with relatively long internodes and narrow leaves.

As mixed cropping is commonly used by resource-poor farmers under conditions of low-inputs and stress tolerance, efficient uptake mechanisms should be incorporated into breeding efforts. Mutsaers and colleagues (1993) for instance, found real biological advantages to occur in intercropping over sole cropping for the cassava-maize combination only when maize yields did not exceed 3.5 t ha-1. Sorghum varieties can be selected for genetically determined higher levels of iron and/or can the iron contents be increased through specific agronomic practices. Tolerance in maize to low-N tends to result from improved N partitioning within the plant rather than improved uptake. Genetic differences in P-utilization efficiency have been reported for beans.

Crop modeling can reveal the better options of the endless combinations that are possible in mixed systems. Models need to be further developed however, in order to be able to more fully assess the specific characteristics of inter- and mixed cropping systems. A particular weakness of existing models is their inability to simulate plant morphogenesis. A plant's adaptive ability to adjust to specific conditions, such as to fill a gap due to a stand loss, is an essential component to be included in models. Current developments in three-dimensional crop models could be applied to complement current models and make good this current shortcoming (e.g. De Visser et al., 2006).

Selection for suitable varieties under intercropping is not necessarily incompatible with selection for sole cropping, but additional characteristics do need to be taken into account. Selection should take place in early generations for specific traits, rather than in advanced stages based on yields only. Due to the complex interactions of intercropping, which are more pronounced the greater the number of species involved, model analyses should support the search for specific characteristics. By utilizing the ecological synergies of intercropping combined with appropriate crop characteristics, primarily resistance, resilient production systems may be designed that optimally exploit available resources and require minimal agro-chemical inputs. Crop physiologists should look specifically into these characteristics to support breeders in their efforts. While attempting to minimize input use, nutrient inputs and outputs of the systems should, of course, always be balanced, to prevent soil degradation. It should be emphasized that the use of external nutrient inputs remains essential to raise total production: attempts to improve productivity without external inputs, either organic or inorganic fertilizers, are highly unlikely to achieve very much.

A breeding program

A breeding program specific to intercropping systems can only be realized when the high costs of breeding can be recovered. A program will be economically justifiable if it leads to (a combination of) higher yields, improved quality, reduced risk of crop failure and/or reduced production costs. Although projected returns are likely to be lower for intercropping than for sole breeding - most obviously because part of the potential of one crop tends to be conceded so as to make a gain in that of another - other criteria may have to be considered when assessing investment returns. Instead of evaluating the yield of a single crop under optimized conditions (as in most current breeding) the yield, quality, risks and costs of realistic production systems need to be evaluated. The support of appropriate models might be necessary in this approach, since the range of variables is much broader than that used in standard contemporary breeding programs. An example of the kind of variable specific to intercropping that might need to be considered would be a case in which breeding for one crop leads to gains in the accompanying crop without that crop itself undergoing a genetic improvement i.e. these gains would have to be added to the benefits. Also, stability of production can be of greater value to poor farmer families than total production (e.g. in order to be able to cope with harsh conditions). Most breeding efforts in the past have concentrated on the 'understorey crop', with the objective of selecting understorey crops that are more tolerant to intercropping stress, while less attention has been paid to the dominant crops. This has left unused the opportunity of breeding for reduced dominance, for instance to allow for more light penetration to the understorey crop. These systems characteristics ought to be integrated into breeding strategies in the quest for appropriate varieties for the complex farming systems found in sub-Saharan Africa.

Hauggaard-Nielsen and Jensen (2001), for instance, identified required crop traits for peas in intercropping with barley and demonstrated that conventional breeding programs are not sufficient for adaptation to intercropping. The pea cultivar by cropping systems interactions indicated that cultivars may perform differently in sole and intercropping. Determinate pea varieties, for instance, are generally more compatible than indeterminate varieties, and allow barley to better exploit soil nutrients while they contribute to the system through N-fixation (in low-N environments).

The total monetary value of the intercrop may have to be considered rather than the total produce in optimizing the systems, as total income may be important to farmers. Also, farmers may apply wider criteria in using varieties, such as labor requirement, compatibility with other activities in terms of labor requirement, consumption preferences and risk. Therefore, and also because experimental stations can be poor predictors of elite line performance on farms, adaptive variety testing should be undertaken through farmers' participation. Farmers' preferences for varieties can feed back into scientists' research on desired traits for further improvement.

Suggestions for breeding programs specific to intercropping have been made already, since during the 1970s, but to our knowledge hardly any such programs have been put into practice. Some initial findings of intercropping breeding and breeding strategies for intercropping are provided by Davis and Woolley (1993), but this is about as far as it has gone.

The role of biotechnology

Once desired traits of crops to be grown in mixed cropping systems are identified, biotechnological approaches could be applied to speed up the breeding process. When traits are related to single or few genes, as with the introduction of resistance to herbicides, disease and insects, quick gains could be made. For instance, more erect leaves, i.e. a different leaf angle, allow deeper penetration of radiation to understory crops (Hauggaard-Nielsen and Jensen (2001). The vast majority of agronomic traits are quantitative and are controlled by a number of genes simultaneously, which calls for more complicated and advanced biotechnological approaches, such as QTL analyses and marker assisted breeding (Daniell and Dhingra, 2002). Also, the first successes of polygenic transfer, such as the development of the Golden Rice, have now been obtained.

The multi genic nature of many stress tolerance mechanisms certainly calls for multi disciplinary approaches. It might, for instance, be possible to estimate the phenotypic effects of polymorphisms once biochemical pathways are established that relate processes at cellular, organ and plant levels, integrated through modeling approaches (Wollenweber et al., 2005). Attempts to improve salt and drought tolerance by way of conventional breeding have, to date, had rather limited success, and nor have biotechnological approaches yet been successful, though various efforts in these areas are underway. For example, Pereira (personal communication) has developed a transgenic rice with much less stomata, which is less susceptible to drought stress.

Though increasingly emphasis is being placed on characteristics that appear to be determined by a complex of genes, the ultimate phenotypic expression is strongly influenced by G*E interactions. The generally multi genic nature of stress tolerance may therefore favor conventional breeding approaches over biotechnological. However, biotechnology might help to unravel the mechanisms behind stress tolerance, test hypotheses about the function of genes in these mechanisms, and accelerate conventional breeding by applying marker assisted breeding.

Concluding remarks

Improving the productivity of complex production systems is likely to be beneficial only at relatively low levels of production, while further productivity increase will necessitate the transition from mixed cultivation to sole cropping. Under current low productivity levels in farmers' fields in sub-Saharan Africa, and because of the need to ensure food security while attempting to incorporate cash crops in order to enter the market economy, the development of productivity enhancing approaches to mixed systems is essential. This is particularly so as the rural poor are being pushed into ever more marginal areas because of population growth, habitat destruction and claims by wealthier and foreign farming communities on the better lands. It cannot be expected that crop cultivation will be very successful under such marginal conditions or that high levels of production per unit area will be attained. Therefore, a strategy should be selected that will enhance the resilience of the system.

The complexity of the mixed production systems calls for support from multiple disciplines to identify the appropriate crop traits required for specific cropping systems and growth environments.

Over the past decades the tools available to support plant breeding have become stronger. A more holistic view of the eco-physiological performance in intercropping can be provided by modeling that integrates soil science, crop physiology and meteorology, and reveals the competitive ability of the species and varieties involved. Modeling supports the search for desired cropping systems under prevailing environmental conditions, facilitates the specification of the most promising of the endless combinations of crops in intercropping systems, and hastens the search for genes related to certain crop traits, importantly, those specific to the needs of intercropping systems. Along with biotechnological methods that allow testing of hypotheses and increase the speed of breeding, an approach to intercropping and other complex systems ought to be developed that is specific to sub-Saharan Africa. With current biotechnological initiatives, a narrow approach is again gaining in importance. We feel that breeding and biotechnological strategies aimed at modifying crop characteristics should be derived from a wider systems perspective if it is to make an effective contribution to increasing the productivity of African agriculture.

In plant breeding, it is widely assumed that the best varieties for sole cropping could be equally well used for other cropping systems. Moreover, in describing the genetic adjustments made to crops (e.g. Sharma et al., 2002), even those specific to Africa (e.g. Thomson, 2003), no relation between the genetic make-up of the crop and the cropping system is made, nor is the importance of the production system considered. The genotype-by-cropping system interactions reveal, however, the need for system-specific characteristics. While some attention had already been paid to breeding strategies for intercropping in the 1970's, to our knowledge few breeding efforts have emphasized these complex production systems.

In the search for the specific characteristics of new varieties that can increase the productivity of African agriculture, the most advanced technologies should be applied because of the complexity of the production systems. Multi stakeholder approaches should be implemented to identify required characteristics, to participate in selection and testing. It should be appreciated that many transgenic technologies have been released by public research institutions, and that several of these, notably in China, India and Brazil, play an important role complementing and supplementing the efforts of the private sector, which, currently at least, only concentrates on a handful of profitable crops. The African continent may again be all too easily left behind due to its lack of scientific and institutional capacity (e.g. Toenniessen et al., 2003; Al-Babili and Beyer, 2005), and remain a user of externally developed technologies. Renewed investments are needed to develop breeding programs for the specific conditions of mixed systems in order to support the transition of the majority of the farmer population in sub-Saharan Africa to higher productive, sustainable and resilient agricultural practices.

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