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Agricultural Water Management 80 (2006) 241–261
Agricultural water management
www.elsevier.com/locate/agwat

Past, present and future criteria to breed crops for water-limited environments in West Africa

M. Dingkuhn [a,*], B.B. Singh [b], B. Clerget [c], J. Chantereau [a], B. Sultan [d]

[a] *Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), TA40/01 Ave. Agropolis, 34398 Montpellier, Cedex 5, France*
[b] *International Institute for Tropical Agriculture (IITA) Kano Station, PMB 3112, Kano, Nigeria*
[c] *ICRISAT/CIRAD Sorghum Ecophysiology Project, BP 320, Bamako, Mali*
[d] *Laboratoire d'Oceanographie Dynamique et de Climatologie (LODYC), Boite 100, 4 Place Jussieu 75252, Paris Cedex 5, France*

Available online 15 August 2005

Abstract

Asia's Green Revolution of the 1960s and 1970s has largely bypassed West Africa, and "modern" (high-yielding, input responsive) germplasm for staple crops has found comparatively little adoption, except for systems that are have good access to markets and sufficient water resources. It is unlikely, however, that breeding objectives conserving traditional crop characteristics as found in extensive systems would have been more successful. The authors identify systems caught in the agricultural transition from subsistence to intensified, market-oriented production as the most important target for crop improvement, and provide examples of new breeding objectives for cowpea, sorghum and upland rice. In each of these cases, breeders, with the help of physiologists, have developed innovative plant-type concepts that combine improved yield potential and input responsiveness with specific traditional crop characteristics that remain essential during the agricultural transition. In the case of cowpea, dual-purpose varieties were developed that produce a good grain yield due to an erect plant habit, then produce new leaves enabling a second harvest of green foliage. For upland rice systems that are limited by labour (mainly needed to control weeds that abound due to shortened fallow periods), a weed competitive plant type was developed from *Oryza sativa* × *Oryza glaberrima* crosses. Lastly, sorghum breeders who had previously deselected photoperiod sensitivity are now re-inserting sensitivity into plants having "modern" architecture, in order to allow for flexible sowing

* Corresponding author. Tel.: +33 467 61 55 64; fax: +33 467 61 71 19.
E-mail address: dingkuhn@cirad.fr (M. Dingkuhn).

doi:10.1016/j.agwat.2005.07.016

dates while maintaining an agro-ecologically optimal time of flowering near the end of the wet season. The ecophysiological basis of these plant types, their place in current and future cropping systems, as well as the problem of under-funding for their realisation, are discussed.

Keywords: Selection criteria; Plant types; Sorghum; Cowpea; Upland rice; Dual-purpose varieties; Weed competition; Photoperiodism; Stay-green; Agricultural transition

1. Introduction

Genetic improvement of annual grain crops in West Africa has not met the same success in terms of adoption and economic impact as compared to Asia or South America (IRRI, 1997). A frequently cited explanation for this is a difficult environment, such as highly variable climate (particularly, rainfall), pests and diseases, or infertile or toxic soils, but these or similar constraints affect cropping systems in other regions of the world as well, without having prevented the impact of genetic and technical innovation. For example, the Cerrados of Brazil were considered unsuited for cultivation only a generation ago and are now under highly intensive cultivation (Cirad, 2003), and semi-arid environments in Australia, although rather extensively cropped, are cultivated with modern genetic and cultural technologies (Turner, 2004). Why did the Green Revolution bypass much of West Africa?

Maredia et al. (1998) presented a broad analysis of the economic impact of food crop improvement research in sub-saharan Africa for 1971–1997. They observed that adoption of improved grain crop cultivars has been substantial in southern and eastern Africa, particularly for maize and wheat (>50% of planted area), mostly associated with a rapidly evolving, commercial seed sector. Hybrid seed has become economically important in southern and eastern Africa (maize in southern Africa, sorghum in Sudan) but not in West Africa where most improved maize cultivars are open pollinated varieties.

In West Africa, adoption of improved cultivars has been has been greatest in hydrologically favourable environments. This applies particularly to maize, although estimates are contradictory because information obtained from breeders and the seed sector differ markedly (Maredia et al., 1998). For irrigated rice, 97% of the planted area is under improved cvs. (but this is only 0.5 of 4.0 Mha of rice land), whereas only 39% of rainfed upland rice area is under improved cvs. (UNEP, 1998). In West Africa's semi-arid zones where sorghum, millet and cowpea are the most important grain crops, information on adoption is scanty but it seems that the overall impact of breeding has been very small. Adoption of new varieties tends to be temporary because in the wake of dry years such as 1985 and 1988, farmers revert to their traditional, low but stably yielding cultivars (Maredia et al., 1998). Consequently, return of investment (ROR) of national crop breeding programmes is low and frequently, negative (e.g., Rep. Niger). The Technical Advisory Committee (TAC) of the CGIAR concluded that sorghum and millet improvement research in West Africa has had no overall economic impact and is not likely to be more successful in the future (TAC/CGIAR, 1995). Whether this is the cause or the effect of the particularly low spending on agricultural research (both as % of GNP and annual growth rate) of francophone governments, constituting much of semi-arid West Africa, is unclear (Maredia et al., 1998).

These observations indicate that grain crop improvement has generally been less successful in West than in East and South Africa, and that within West Africa, breeding had a much greater impact in irrigated (rice) and moist (maize) environments than in dry areas (domain of sorghum, millet and cowpea). There are, however, local exceptions to this rule, in most cases attributable to concentrated development efforts, supported by favourable economic frame conditions and local experience with intensified cash crop systems (spill-over effects): the cases of improved millet and cowpea cvs. in the peanut basin of Senegal (Maredia et al., 1998), improved upland rice cvs. in the cotton areas of North Ivory Coast (Adesina, 1996), and improved cowpea and sorghum cvs. in the densely populated North of Nigeria with its evolved markets for agricultural products and inputs (Harris, 1995). Many other regions in West Africa are characterized by limited access of producers to markets and credit, and frequently by political insecurity discouraging investment, factors that generally hamper agricultural intensification (Just and Zilberman, 1988; Feder and Feeney, 1991; Dingkuhn and Randolph, 1997). The positive exceptions cited, however, demonstrate that even in drought prone environments in West Africa, crop improvement can be economically successful, contrary to the pessimistic outlook of TAC/CGIAR (1995).

This paper will not focus on the rare situations in West Africa where economic development has already prepared the ground for the adoption of agricultural intensification practices, but instead on the vast areas where crop improvement has yet to make an impact. For these areas, we will critically assess past breeding objectives and discuss some emerging plant type concepts that appear to be promising for the future. We will thereby not focus specifically on drought and drought resistance, but on crop characteristics that crop scientists and producers consider key to profitable cropping. In fact, the breeding programs highlighted in this paper generally do include screens for physiological drought tolerance, but also emphasise more indirect adaptations to water limitation, such as phenology-based escape mechanisms or competitiveness with a weed flora that is usually more drought resistant than the crop.

We will limit the analysis to three crops, namely cowpea, upland rice and sorghum, which occupy different climatic zones and are part of different cropping systems in West Africa.

2. A brief profile of cowpea, rainfed upland rice and grain sorghum in West Africa

Cowpea [*Vigna unguiculata* (L.) Walp.] is important, particularly as an intercrop in cereal systems, in the drier regions of West Africa where rainfall is low and erratic and soils are sandy and of low fertility. Of the world total of about 14 million ha, West Africa alone accounts for about 9 million ha (Singh et al., 2003a). With >25% protein in seeds as well as in young leaves (dry weight basis), cowpea is a major source of protein, minerals and vitamins in daily diets and is equally important as nutritious fodder for livestock (Singh et al., 2003b). The mature pods are harvested and the haulms are cut while still green and rolled into small bundles containing the leaves and vines. These bundles are stored on rooftops for use as feed supplement in the dry season, making cowpea a key factor for crop-livestock systems. Cowpea haulms fetch 50% or more of the grain price (dry weight basis) and therefore constitute an important source of income. Cowpea also improves soil fertility (Carsky et al., 2001) in various, low-rainfall cropping systems. Yields, however, are between 100 and 400 kg/ha despite a biological potential 5 times higher. This is partly attributed to shading by intercrops such as sorghum, a prostrate (weed-competitive, but low-yielding) architecture, and susceptibility to pests such as *Maruca* pod borers, root-parasitic weeds such as *Striga*, and nematodes (Henriet et al., 1997). Being primarily an African crop, few countries have cowpea improvement programs. IITA in Nigeria has a global mandate for cowpea research and development, and maintains a world collection of 16,000 lines.

Upland rice is a main staple crop in the humid forest and moist savannah (Guinea savannah) and humid (forest) environments (>1200 mm annual rainfall) in the coastal countries of West Africa, particularly Guinea-Conacry, Sierra Leone, Liberia and Ivory Coast, yielding less than 1 t/ha on average (Mathieu, 2000) despite a potential near 4 t/ha (Dingkuhn et al., 1998). Planted area is about 1.8 Mha, out of at total of 4.0 Mha for all rice ecosystems (UNEP, 1998). Overall, production area growth of rice is the largest for all major staple crops in Africa (2.3 %/a in 1971–1997) due to growing demand in the cities (Maredia et al., 1998). Although *O. glaberrima* Steud. cultivars have been domesticated and cultivated in West Africa 3000 years ago, *O. sativa* L. cultivars, introduced by Portuguese traders 500 years ago, dominate today's systems. The crop's high susceptibility to drought, weed competition and fungal diseases (particularly under intensive cultivation) is offset by adaptation to the prevalent acid soils and growing domestic demand, particularly in the cities (Buddenhagen and Persley, 1997). Sustained varietal improvement for local upland conditions since the 1960s by French research institutions, the International Institute of Tropical Agriculture (IITA) and the West Africa Rice Development Association (WARDA) has met limited adoption (about 39% of cultivated area, Maredia et al., 1998). A recent breakthrough in crossing *O. glaberrima* and *O. sativa* (japonica) rices at the West Africa Rice Development Association (WARDA; ''Nerica'' rices) appears to have partially reversed that trend in some countries, such as Guinea Conacry (refer to WARDA Annual Reports: www.warda.cgiar.org). Nevertheless, Africa's most populous state Nigeria, a major rice producer, has become the world's greatest rice importer in 2004 (Boris, 2004). Rice breeding in West Africa benefits from the global germplasm collection at the International Rice Research Institute (IRRI) in the Philippines (long-term storage) and a subset collection for Africa kept by WARDA at the International Institute for tropical Agriculture (IITA) in Nigeria.

Sorghum [*Sorghum bicolor* (L.) Moench] has been cultivated for millennia in West Africa, mainly in the moist savannah zone during the rainy season, which is monomodal with 800–1100 mm/year. Further north in the drier Sudan savannah, at 600–800 mm/year, sorghum is also cultivated although the rainy season is frequently too short to produce satisfactory yields. With about 24 Mha under cultivation, sorghum is Africa's second most important crop after maize, but mean yields are only 0.8 t/ha (maize: 1.3 t/ha; Maredia et al., 1998). Often associated with other crops like cowpea, sorghum displays in the savannahs its greater drought resistance compared to maize and upland rice (which are found further south) and its higher yield potential compared to highly drought-resistant pearl millet (which is grown further north where rainfall is even lower). Apart from rainfed upland cultivation, sorghum is traditionally also grown as a flood recession crop in the floodplains of the Sahel after the rainy season, temporarily as an aquatic crop (Chantereau and Nicou, 1994). Sorghum is traditionally consumed as stiff porridge (Toh) and couscous (steam cooked product) or as fermented beverages (Dolo, Chapalo), although sorghum foods are increasingly substituted with rice and maize (Debrah, 1993). Stalks are also a vital resource as animal feed, fencing material and fuel (National Research Council, 1996). From 1979–1981 to 2001, sorghum production in West Africa increased from 5.1 to 13 millions tonnes but mean yields are stagnant (890 kg/ha in 1979–1981, 780 kg/ha in 1992–1994, 830 kg/ha in 2001) (FAO, 1997). Regional production continues to depend mainly on traditional cultivars characterised by hardiness, photoperiod sensitivity, long stalks, good grain quality and low harvest index.

3. Germplasm diversity and conservation for cowpea, upland rice and sorghum

Germplasm diversity and conservation are at the basis of any long-term crop improvement strategy. Reorientation of breeding objectives in more recent times towards combining traditional with modern crop characteristics, for example, in order to achieve better weed competitiveness (Jones et al., 1997; Dingkuhn et al., 1998, 1999; Johnson et al., 1998) or timely maturity at the end of the wet season through photoperiod-sensitivity (Clerget et al., 2004), has called for the increased use of native donor materials. Unfortunately, at the time when native sorghum and African (*O. glaberrima*) rice germplasm was prospected and field-screened in West Africa in the 1960s and 1970s for future breeding purposes (Sapin, 1971; Barrault et al., 1972; Dobos, 1986), emphasis on the current agronomic selection criteria led to the de-selection and non-inclusion in germplasm banks of much of the exotic germplasm. This is particularly the case for West African sorghum landraces known as flood recession materials, which were grown in the Senegal river delta and valley (Durra types), the Niger inland delta (Durras and Guineas) and the floodplains associated with the tributaries of Lake Tchad (Durra-Caudatums, known as Muskwari and Babouri groups) (Chantereau, 2002). These materials have tall, massive stems and large leaves with good fodder quality, and are photoperiod-sensitive, cold- and drought-tolerant, and adapted to heavy clay soil and waterlogged conditions (Chantereau, 2002). In fact, the most extreme types found in the Niger inland delta, are sown or transplanted on residual moisture in the cool season (December), survive the scorching dry season and complete their growth cycle in the subsequent wet season, sometimes harvested by boat (Harlan and Pasquereau, 1969). These materials probably possess remarkable phenotypic plasticity and a broad range of physiological adaptations. Fortunately, at least for the flood-recession sorghums, in situ conservation through continuing cultivation seems to be working fairly well (Chantereau, unpublished observations), provided that climate change or river regulation does not dramatically affect the West African floodplains.

O. glaberrima germplasm, also mainly prospected during the 1970s, which shows a similarly wide range of environmental adaptation and originates from the same region and ecosystem as the flood-recession sorghums, has fared slightly better in terms of formal germplasm conservation, but the existing 3000-entry germplasm collection safeguarded by IITA (Nigeria) for WARDA has never been used for within-species breeding, and only recently for trait introgression into *O. sativa* backgrounds (Jones et al., 1997). Here, potential loss of biodiversity would probably be brought about by the continuing displacement of *O. glaberrima* by *O. sativa*.

Least endangered among the three species discussed here is the biodiversity of cowpea, because long-standing breeding and conservation programs at IITA make broad use of it, and because cowpea, in contrast to *glaberrima* rices and flood-recession sorghums, plays an increasingly important economic role in diverse ecosystems and cropping systems in West Africa. The wide range of climatic conditions where cowpea is grown (from rain forest to semi-arid habitats) also contributes to the in situ conservation of this species' genetic diversity.

4. Past paradigms for crop improvement

Although it is in the nature of any genetic improvement to change crop behaviour, it is striking how modern varieties bred for West Africa differ from traditional germplasm, selected by farmers over centuries. The improved cultivars are generally early maturing, have stable crop duration due to reduced photoperiod sensitivity, and have morphological features that enable a higher harvest index, indicating that priority was given to grain production, as opposed to other harvestable products such as stems or green foliage that have multiple uses in traditional systems. These choices, when translated into selection criteria, have different morphological consequences depending on the species.

In rice, for example, reduced height of semidwarf materials is generally associated with increased tillering, which multiplies the number of organs but reduces their size (e.g., leaf dimensions, stem diameter, grains per panicle) (Yoshida, 1981). In sorghum, however, dwarfing has mainly reduced internode length and increased stem diameter, while tillering was reduced and leaf size remained unchanged (Morgan and Finlayson, 2000). The leaves therefore are more densely stacked on a thicker axis. This remarkable difference between the two cereals is probably related to different genetic dwarfing mechanisms but we know of no comparative genetic study that would explain it. In cowpea, the objective of increasing grain production has mainly reduced the creeping habit in favour of a more erect morphology, enabling improved radiation use efficiency.

Breeding objectives for the three species were not limited to substituting traditional with modern architecture, but have also included quality traits and whatever resistances to biophysical stresses were required, mostly selected for by exposing the materials to the stresses experimentally or at hotspots. Particularly cowpea, despite being of African origin, is highly susceptible to indigenous pests and diseases, which remain the main priority in breeding. Since the desired plant type and stress resistances rarely coincide naturally, stress resistances are introgressed from selected donors into materials that have the desired phenotype, phenology and general adaptation to the environment. We will, in the following, not further discuss such characters unless they interact with plant type.

What is the reason for the generic phenological objectives (shorter and stable duration) in crops as diverse as cowpea, sorghum and rice, and for environments as diverse as the

Sahel and the humid forest? And, why are traditional crops comparatively late maturing? A comparative phenological study on introduced and traditional rices in West Africa gave a partial answer that may be of general significance (Dingkuhn and Asch, 1999). Traditional, *O. sativa* rices grown in rainfed environments (uplands and lowland swamps) have relatively long duration, whereas *O. glaberrima* rices domesticated in the same environments have shorter duration. The latter are highly weed competitive due to vigorous early growth whereas most *O. sativa* materials are not (Dingkuhn et al., 1999), and thus require a longer vegetative period to produce a satisfactory biomass. Short duration materials, to be productive in weed prone environments, must therefore have rapid early growth and leaf area expansion. Conversely, improved, short-duration, japonica-type upland rices having high yield potential, such as WAB56-104 (Johnson et al., 1998), are poor competitors and thus require a level of protection that is mostly unaffordable to producers. It is likely that farmers selected their traditional germplasm on the basis of two alternative agro-ecological strategies, probably depending on the materials available to them: either weedy, opportunistic types having strong vigour, expansive architecture and a short or variable cycle depending on photoperiod, but low potential yield; or longer-duration types deriving yield stability from greater final biomass and resources extracted from the soil.

Breeding for modern cultivars has generally deselected weed competitive architecture (prostrate habit for weed suppression or tallness to outgrow weeds; high specific leaf area (SLA) for rapid canopy development; Dingkuhn et al., 1999), shortened the basic vegetative phase (BVP) and reduced photoperiod sensitivity, which serves to synchronize flowering with the end of the cropping season. This is equally true for cowpea, rice and sorghum, and probably explains in part why improved crops had a greater impact in hydrologically more favourable and more intensively managed systems. This is not to conclude, however, that improved cultivars of the pattern described have no place in West African production systems. They do have a place wherever traditional systems can be converted to market-oriented production using external inputs, for example in association with already existing cash crop systems (Adesina, 1996; Dingkuhn and Randolph, 1997).

The previous analysis is a simplification that does not do justice to reality in all cases. For example, a short crop duration insensitive to photoperiod (and therefore, planting date) is advantageous where the rainy season is predictably short. Improved germplasm of this type has probably allowed sorghum, upland rice and maize cultivation to shift further north beyond their traditional zones of cultivation, although this is difficult to evaluate because decreasing rainfall totals in the past 40 years in the Sahel (Nicholson, 1986) have at the same time contributed to the opposite trend. Because of their adaptation to very short wet seasons, some modern sorghum cultivars have met greater adoption in areas traditionally cropped with millet, but were less successful in the species' traditional climatic environments (Kouressy et al., 1998). Furthermore, crops having a short and photoperiod independent crop duration also have an important place in inter- and relay cropping systems and in flood recession farming. Both sorghum and cowpea are commonly intercropped, frequently with each other. Lastly, very early maturing crops may serve as gap-filling food source before the main crop attains maturity (case of cowpea in Senegal: Maredia et al., 1998).

It is difficult to argue whether or not ''improved'' grain crops failed in water limited environments of West Africa because of poor adaptation to local climate and climate variability. They were selected by breeders in and for the biophysical target environments and are therefore adapted to them, but were not necessarily always selected for the prevailing cropping systems. In sorghum, for example, breeders opted for drought tolerance in exchange for the traditional drought escape strategy based on opportunistic sowing dates and the use of photoperiod sensitive crops. A ''modern'' crop, even if highly drought tolerant, would thus not necessarily display this advantage where traditional cropping systems still function. To have generate impact, breeding must therefore target cropping systems that are changing, usually driven by demographic and economic change and the collateral agro-ecological disturbance associated with the transition (Dingkuhn and Randolph, 1997). Such systems, although ready for change, neither have good use for traditional production technologies (because they are not competitive) nor are they ready for improved germplasm requiring intensive management (because during the transition, impoverished producers are not able to invest in land and resource quality, a major condition for intensified production; Just and Zilberman, 1988; Dingkuhn and Randolph, 1997). In South-East Asia, the green revolution, fuelled by an input-responsive rice plant type (Peng et al., 1994), could build on an existing culture of agricultural intensification, necessitated by high population density and high land value. Similar situations are the exception in West Africa but can be found, for example, in peri-urban and irrigated agriculture or in parts of Nigeria that are densely populated (Harris, 1995).

During the past decade, responding to growing awareness among scientists and donors of inefficiency of many long standing crop improvement programs, breeders have invested in farmer participatory breeding. This approach does not only serve to know better the adoption criteria used by farmers, but also to provide materials for specific, local needs by letting farmers select appropriate germplasm from demonstration plots or locally managed field trials. This approach is not always easy to reconcile with strict (and arguably useless) national rules for varietal certification, but has clearly re-dynamized crop breeding in West Africa, particularly at the international research centres WARDA, ICRISAT and IITA, as well as their national counterpart institutions. Rattunde (2004) reports that sorghum farmers in Mali generally have precise, knowledge-based criteria for varietal adoption that are not always in agreement with established breeders' views. For example, farmers rejected materials that would flower at a fixed crop age (as opposed to a fixed calendar date, brought about by photoperiodism) because untimely crop maturity would bring about losses in grain quality; on the other hand, they were in favour of some morphological traits of the improved materials and were open to intensification technologies.

5. Three examples of new breeding objectives—will they make a difference?

We will now briefly describe some more recent breeding strategies for cowpea, upland rice and sorghum that aim at morphological and phenological plant types developed for specific cropping systems and biophysical environments. These plant types generally combine traditional characters (required by the cropping system) with modern characters (required for improved yield potential) in combinations that can neither be found in local nor in introduced germplasm. In all three cases, the breeding strategy was driven by the realization that the West African agricultural transition from extensive to intensive systems requires crops that respond positively to intensification measures while taking into account that farmers have limited means to control the crop environment (Dingkuhn and Randolph, 1997).

5.1. Dual purpose crops

Cowpea is a source of both food and fodder in the dry savannas of West and Central Africa. Traditional farmers who keep livestock frequently intercrop two cowpea cultivars in alternate rows with millet and/or sorghum in the same field, one for grain and the other for fodder. Both have prostrate architecture, the grain type being early maturing (80–85 days) and the fodder type late maturing (100–120 days). Grain cowpea and millet are harvested late in the wet season (late August to early September) whereas the late maturing cowpea varieties are left in the field into the dry season while using residual soil moisture (October–November). Farmers wait until the cowpea leaves show signs of wilting before they cut the cowpea plants at the base and roll the plants into bundles with leaves attached. The bundles are air dried and sold in the peak dry season when prices are high. If rains occur in October/November, the fodder-type cowpeas produce some grain as well (Mortimore et al., 1997; Singh and Tarawali, 1997).

Although this intricate system utilizes rainfall from May to November, overall productivity is low because the grain-type varieties flower and pod under the shade of millet and the fodder-type varieties are often affected by terminal drought. Therefore, an ideal cowpea cultivar for this system would be a dual-purpose type with semi-determinate growth habit and intermediate maturity (85–95 days) that would flower in September when millet has been harvested, and would be ready for first picking at the onset of the dry season. Several such varieties have been developed at IITA that yield 1.5–2.5 t/ha grain and 3–5 t/ha fodder (Fig. 1). They continue producing leaves after grain maturity, enabling harvesting the green plant tops 2–3 weeks after grain harvest.

The dual-purpose cultivars derive their high productivity from an erect growth habit (Singh and Sharma, 1996), which distinguishes them from the flat and creeping traditional types, possibly to the detriment of competitiveness with weeds. On the other hand, this plant architecture makes the dual-purpose cultivars responsive to plant population density, and therefore suitable for intensification (Fig. 1). Across genotypes, there were no tradeoffs between grain yields at high and low population and the dual-purpose lines out-yielded the traditional cultivars at both high and low plant population (Fig. 1 left). Fodder yield was similar in traditional and dual-purpose materials (Fig. 1 centre). However, unsurprisingly, there appeared to be (in this case statistically insignificant) tradeoffs between grain and fodder yield. The dual-purpose materials have undergone screening for drought resistance, but their tolerance to shading (by taller intercrops) and weed competition remains to be studied further.

As indicated by preliminary, unpublished observations made at the Regional Centre for Studies on the Improvement of the Adaptation of Plants to Drought (CERAAS) in Senegal,

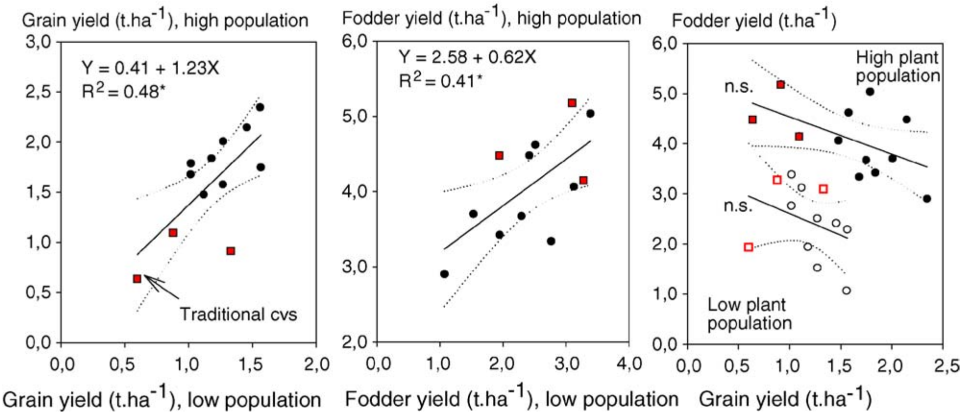

Fig. 1. Grain and fodder yield relationships (dry wt) for 3 traditional, check cultivars (squares) and 9 improved, dual-purpose lines (circles) of cowpea at the IITA research station at Kano, Nigeria, in 2002. Left: Effect of plant population on grain yield (recommended intensified vs. traditional levels). Centre: Effect of plant population on fodder yield. Right: Fodder vs. grain yield.

it may be possible to transfer the dual-purpose concept to other leguminous crops in West Africa, such as groundnut. It might even be extended to cereals such as sorghum. Although sorghum is not an indeterminate plant such as cowpea, which is able to produce new leaves even after flowering, the stay-green phenomenon that has recently received much attention by breeders may be used. Stay-green is a trait originating from Ethiopian *Durra* and Nigerian *Kaura* sorghums (Mahalakshmi and Bidinger, 2002), enabling the crop to maintain a green canopy during grain filling and to provide better forage quality. Surprisingly, this trait is compatible with high harvest index, indicating that the plant has an alternative (internal or external) source of nitrogen that can satisfy grain demand while protecting the leaf nitrogen from remobilization (Borrel and Hammer, 2000). Stay-green is associated with post-flowering drought resistance for unknown reasons. It also reduces the probability of lodging or stem collapse and stalk rot (*Macrophomina phaseolina*), which frequently occurs if the plant senesces early.

Stay-green is only in its early stages of characterization by sorghum breeders and physiologists in West Africa, for example at ICRISAT at Bamako, Mali, and CERAAS at Thiès, Senegal. Its contribution to terminal drought resistance alone might improve attainable yields and yield stability considerably, but the prospect of developing dual-purpose, fodder/grain sorghum for crop-livestock systems, possibly by combining stay-green with the sweet-sorghum trait, is intriguing.

5.2. *Weed competitive crops*

A semi-quantitative ‘‘Delphi’’, ex-ante analysis of the potential impact of crop research on regional rice production in 1996 at WARDA (Fig. 2) indicated that weed competition is the most important, biophysical, yield reducing factor, particularly in the rainfed upland ecosystem. Across ecosystems, it is probably more important than drought and soil

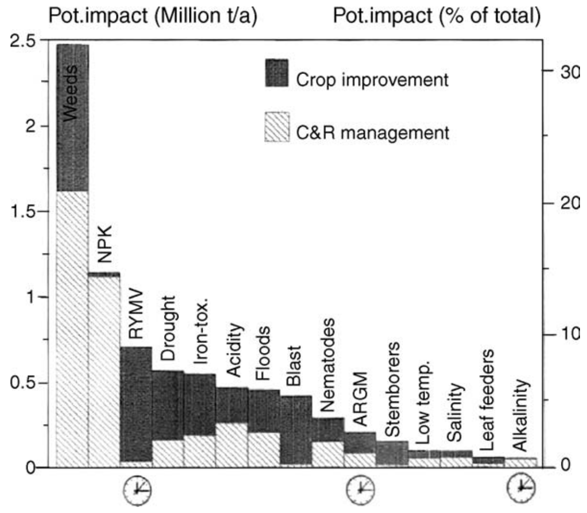

Fig. 2. Summary result of a Delphi-type, ex-ante impact analysis conducted at WARDA in 1997 for research on rice and rice systems in West Africa, specified by the bio-physical constraints addressed by research and by type of research [crop improvement or crop and resource (C&R) management]. All ecosystems confounded. Weeds appear as the most important constraint.

infertility combined, although these stress factors are not independent. Weed pressure and soil infertility problems are aggravated by inappropriate intensification measures, such increased land cropping coefficients in the absence of soil conservation measures (Becker et al., 2003). Particularly in degraded systems, hand weeding is the largest variable cost factor in upland rice production (WARDA, 1999). An innovative plant-type concept and breeding program were therefore initiated in the mid 1990s that aimed at (1) combining the superior weed competitiveness of *O. glaberrima* rices with the better yield potential of improved *O. sativa* tropical-japonica types, and (2) expressing the weed competitive morphology of *O. glaberrima* during vegetative growth (when the outcome of competition with weeds is decided) and the traits contributing to yield potential in subsequent phases of development (Jones et al., 1997). Methods to overcome the sterility barrier between the two species, aided by the use of naturally compatible parent combinations, had been developed a few years earlier.

The plant type concept calls for thin (high specific leaf area, SLA), droopy leaves enabling rapid ground cover and light interception early on, and the opposite features (wide, thick, erect leaves) during reproductive growth in order to maximise radiation use efficiency (RUE) (Dingkuhn et al., 1998; Johnson et al., 1998). This concept has been metamorphic because it calls for architectural change in the course of development. Although civil unrest in Ivory Coast led to the suspension of breeding activities at WARDA's headquarters at Bouaké in recent years, the inter-specific "Nerica" rices became synonymous with upland rice improvement for Africa and are reported to be successful in Guinea and other humid, weed-prone production environments (refer to WARDA Annual Reports: www.warda.cgiar.org). The schematic diagram in Fig. 3 illustrates the metamorphic concept that is behind the Nericas, expressing the droopy and

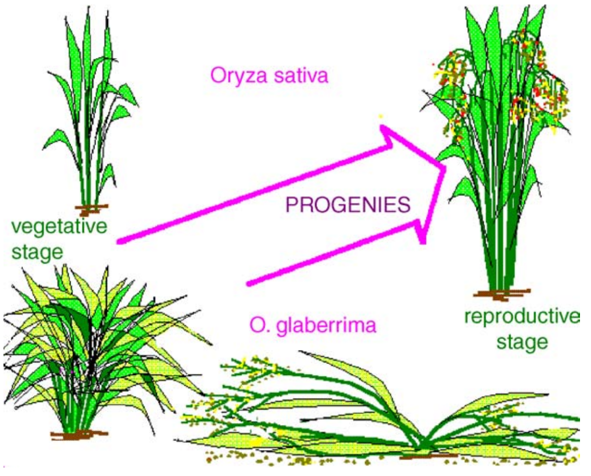

Fig. 3. Schematic diagram illustrating the juvile (left) and mature (right) habits of *O. sativa* (top) and *O. glaberrima* (bottom) upland rices. The arrow indicates the inter-specific breeding strategy, which aims at realising a weed-competitive architecture initially and a more erect, high-yielding architecture during reproductive stages. Adapted from WARDA Annual Reports.

leafy architecture of *O. glaberrima* during vegetative growth and the erect and dark green appearance of the plant towards flowering, inherited from *O. sativa*.

Field selection for the growth stage dependent expression of morphological traits is not simple and at present not fully implemented, although a good theoretical basis exists. Mass selection for specific leaf area (SLA), in this case required for at least two growth stages, would be impractical if based on destructive sampling and laboratory analyses. Measurements of associated crop parameters such as high leaf area at early stages (frequently a result of high SLA and desirable anyway), followed by selection during reproductive development for high leaf nitrogen or chlorophyll content on a leaf area basis (e.g., measured non-destructively by SPAD; Chapman and Barreto, 1997) to select for low SLA, is one possible example of how the dynamic plant type concept might be inexpensively screened for. Currently available Nericas, selected with less sophisticated screens, have excellent yield potential and overall adaptation but are not as weed competitive as *O. glaberrima* (Dingkuhn et al., 1999). At present, it is not certain that the metamorphic concept will work in practice, and it is conceivable that the much-publicised Nerica success story reflects mainly the successful selection of high-yielding, short-duration upland rices having good adaptation to local conditions.

The metamorphic concept for weed competitiveness might also be applied to aquatic rice ecosystems where weeds are a major constraint if seed is broadcast (instead of transplanting) to save labour (Becker et al., 2003). Much progress has been made recently towards developing genetically stable, vigorous and high-yielding *O. glaberrima* × *O. sativa* indica materials at WARDA's research station in Senegal (Miezan, unpublished observations) but their ability to compete with weeds requires further study. In general, weed competitiveness deserves more attention in crop improvement for West African ecosystems.

5.3. Combining photoperiod sensitivity with improved yield potential

As pointed out earlier, past breeding criteria for improved sorghum has had limited impact in the core climatic zones of sorghum cultivation of West Africa (800–1100 mm/a, about 14-9°N). Photoperiod-insensitive materials, when planted after the first major rains of the season as practised by most farmers, would frequently flower too early and sometimes too late, resulting in plant health or drought problems, respectively. The duration of the Sahelian wet season is variable but closely linked to the date of its onset, whereas the rains terminate during a fairly constant period (Fig. 4). If one accepts that sorghum should be sown upon the first major rains of the season, and not at a particular calendar date, photoperiod-sensitivity is essential to ensure flowering near the end of the rains. The same rule applies to millet, a cereal that occupies the same climatic environment as sorghum but extends further north due to its greater drought resistance.

Why is it important that sorghum be sown at the earliest possible date? From a climatic and hydrological point of view, it does not make sense. Recent studies indicated that the ‘‘true’’ rainy season in terms of the summer monsoon, which is associated with a sudden northwards jump of the inter-tropical conversion zone (ITCZ), begins at a very constant date (23 June). The irregular rainstorms occurring prior to the onset of the monsoon can be called a pre-rainy season, constituting only 10% of total seasonal rainfall on average (site of Niamey) (Sultan et al., 2003; Sultan and Janicot, 2003). According to climate and soil hydrology-driven crop simulations for a 90-day, photoperiod-insensitive crop, the highest and most stable yields can be expected for sowing dates around the onset of the summer monsoon, whereas erratic results are obtained with earlier sowing dates during the ‘pre-rainy’ season (Sultan et al., 2005) (Fig. 5).

Cereal farmers in the Sahel and Sudan savannahs apparently accept a high risk of failure of crop establishment, thus requiring re-sowing, in order to avoid other problems associated with the later, hydrologically safer sowing date. These problems are related to

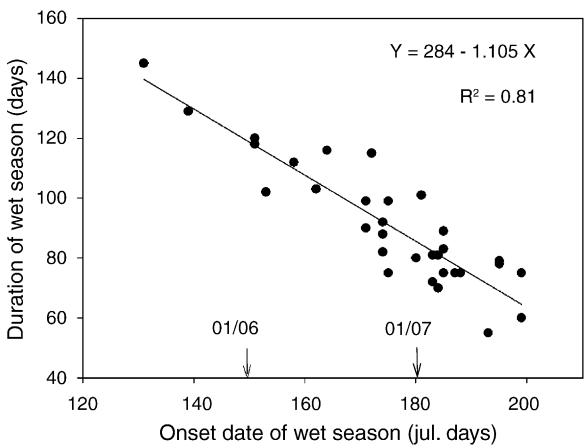

Fig. 4. Relationship between the duration of the wet season and its onset date for 1960–1990 at Ségou, Mali. The monsoon rains in the strict sense, which are associated with much greater reliability of rains than the ‘‘pre-season’’, begin roughly on 170 julian days (day of year).

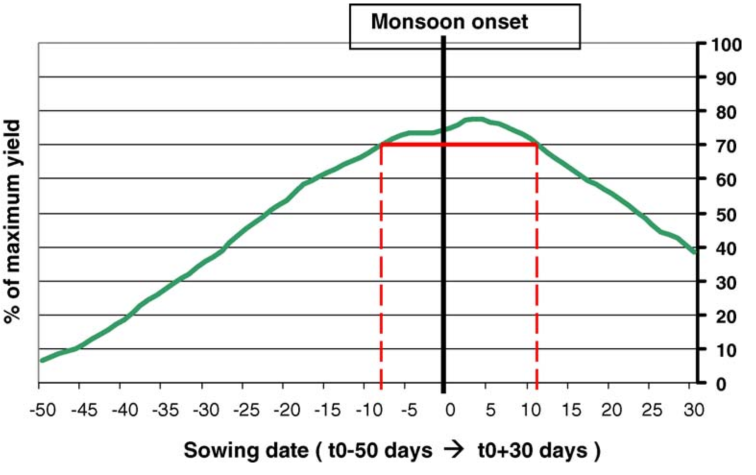

Fig. 5. Relationship between relative, attainable yield simulated for 19 years with the crop model SARRAH for a 90-day millet crop at Niamey, Republic of Niger, and the sowing date (expressed relative to the onset data of monsoon rains, typically around 23 June). 100% = mean of simulated, attainable yield for optimal sowing dates calculated individually for each year.

soil fertility and weed pressure: the early rains cause nitrate leaching and trigger a flush of gaseous nitrogen losses caused by de-nitrification of nitrate stored in the soil during the dry season (Blondel, 1971a,b,c), and at the same time initiate weed growth (Stoop et al., 1981; Vaksmann et al., 1996). A crop sown late in the wet season therefore misses some of the potentially available nitrogen resources (which are relevant because fertilizers are rarely applied), and the farmer also has to use scarce labour to remove an established weed flora. Consequently, the hydrologically and climatically ideal sowing date may be of relevance to future, intensified systems that use fertilizer inputs and herbicides, but as long as systems are extensively managed, farmers are forced to sow at variable dates and use photoperiod-sensitive cultivars.

In view of these findings, Vaksmann et al. (1996) proposed developing sorghum cultivars that combine a ‘‘modern’’ architecture (reduced height and tillering rate, thicker stems, higher harvest index) with photoperiod sensitivity. This concept has stimulated a large number of ongoing ecophysiological and genetic studies because it is far from simple. The main difficulties reside in (1) strong effects of photoperiod on plant architecture in photoperiod-sensitive materials, (2) the complexity of photoperiodic responses, particularly in sorghum, and (3), apparently, limited sink capacity in panicles of photoperiod sensitive cultivars, resulting in suboptimal use of assimilate reserves in internodes. We will provide some detail on these issues because they are not well documented:

(1) The problem of photoperiod-dependent architecture is mainly related to variable leaf number per culm and the phenological timing of internode elongation (Singh and Rana, 1997). Depending on sowing date, photoperiod-sensitive cultivars produce canopies between 1.5 and 5 m tall, with between 12 and 41 leaves on the main stems at flowering stage (Fig. 6). Internode elongation is triggered by panicle initiation when

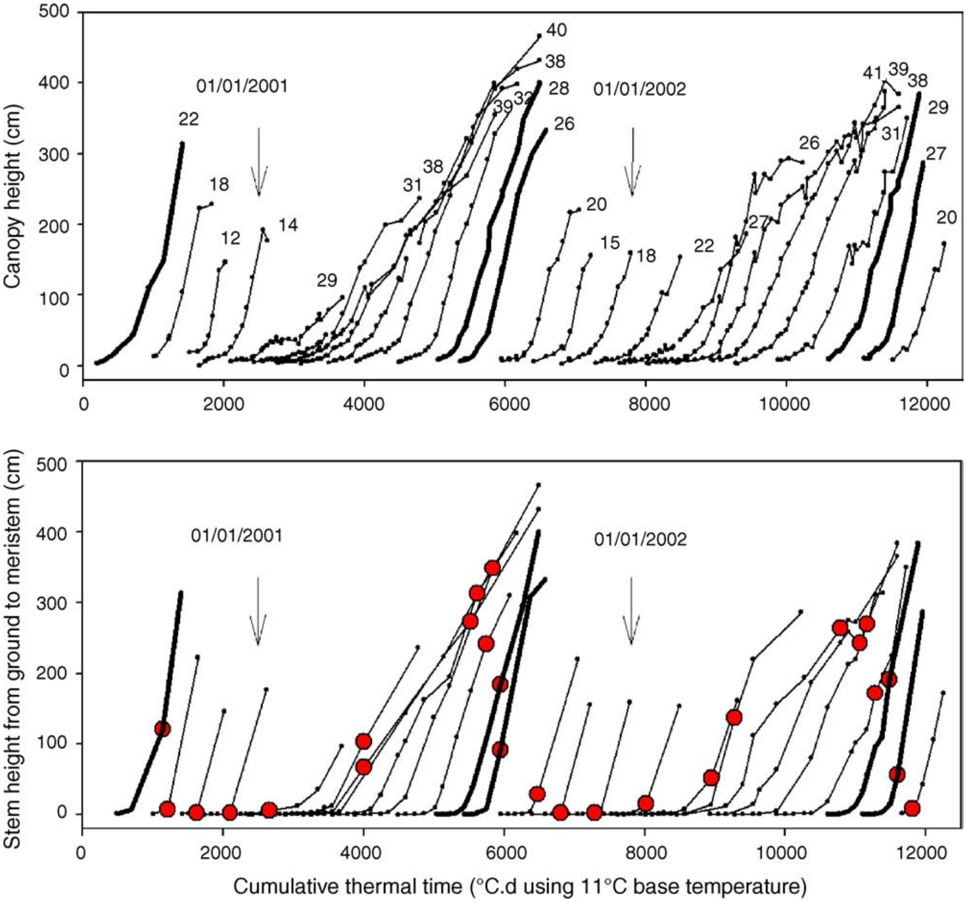

Fig. 6. Development of canopy height (top) and stem length from ground to the apical meristem (bottom) for the photoperiod-sensitive sorghum cultivar CSM 335, sown at Bamako, Mali, on 26 consecutive months in 2000–2002. Crops were irrigated during dry periods. Bold lines indicate crops sown according to farmers' practice in mid June and mid July. Inserted numbers (top graph) indicate total leaf number produced on main stems. Circular symbols indicate panicle initiation observed by dissection.

floral induction happens early, or occurs spontaneously after the initiation of about 23 leaves. Stem elongation is a very costly process in terms of assimilates and competes with panicle development when leaf number and area are too small to provide sufficient assimilates for both (Clerget, 2004).

(2) In sorghum, photoperiod not only influences the time of panicle initiation but also leaf initiation and appearance rate, resulting in poor leaf area development and low yields when plants are sown late in the season (August or September, period of decreasing day length; Clerget, 2004). The simple model of thermal and genetic determination of plastochron (Rickman and Klepper, 1995) is therefore inaccurate in this case. Moreover, the photoperiodic signal(s) sensed by the plant seem not only to include absolute daylength at a given time, but also its rate of day-to-day change, and depend

strongly on light quality (Clerget et al., 2004). As a combined result, the effects of sowing date on the duration of phenological phases are complex and differ even among photoperiod-sensitive genotypes (Fig. 7).

(3) In contrast to other cereals such as rice (Kropff et al., 1994), panicle size and spikelet number per panicle in African sorghum cultivars are not strongly linked with crop

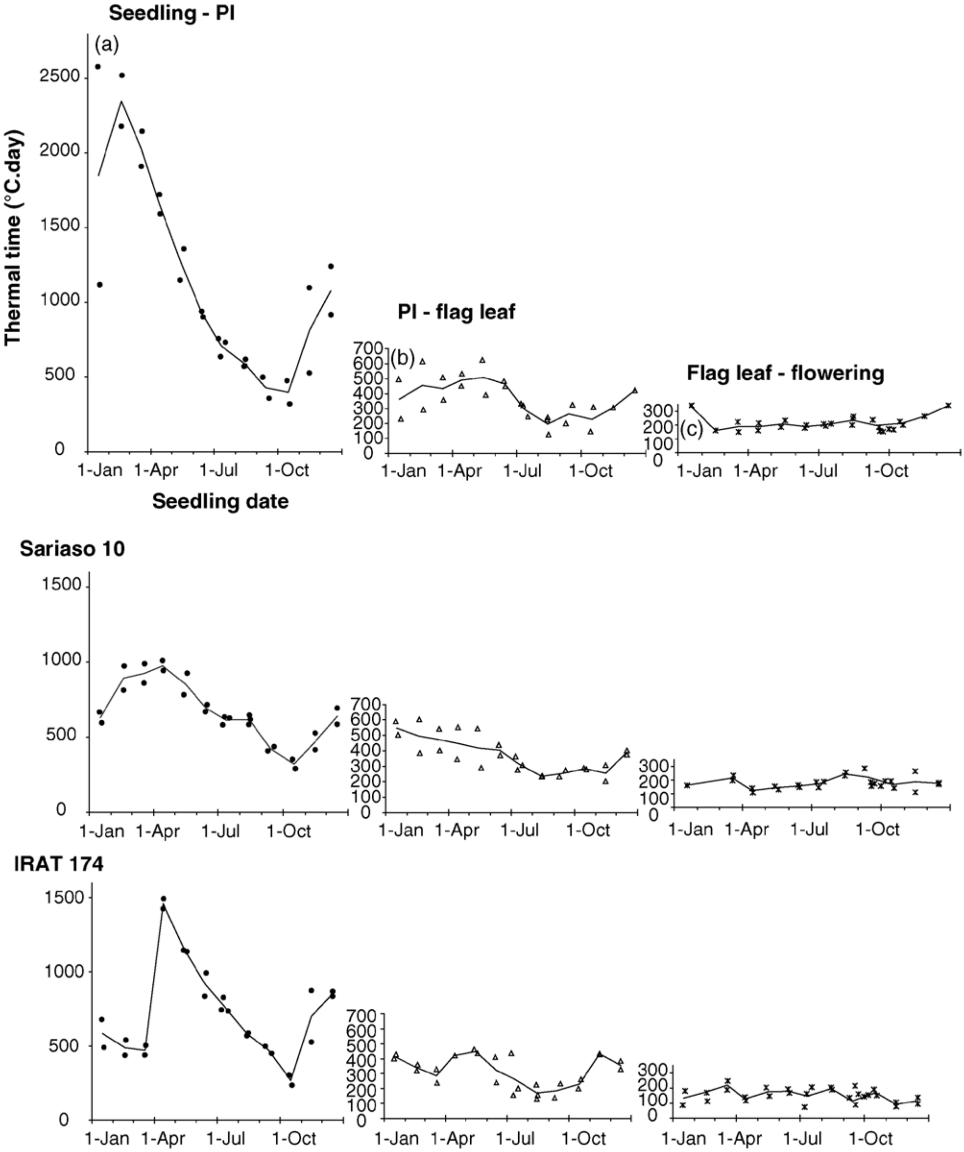

Fig. 7. Thermal duration of three consecutive phenological phases (from emergence to panicle initiation (PI) (left), from PI to flag leaf exertion (centre), and from flag leaf exertion to flowering (right); as a function of sowing date, observed in three sorghum cultivars at Bamako, Mali. Lines join the monthly averages of the 2 years' records.

growth rate before heading. Consequently, yield potential is comparatively insensitive to resources (Clerget, 2004).

These observations suggest that photoperiod-sensitive sorghums have extreme phenotypic plasticity, which may convey excellent biological adaptation to variable environments, but make it difficult to develop plant types combining photoperiod sensitivity with desirable agronomic traits such as short stature and high harvest index. More research needs to be conducted on trait interactions before a breeding strategy for high yielding, photoperiod sensitive sorghums can be implemented efficiently. Promising, intermediate breeding products have recently been developed in Mali (Vaksmann and Kouressy, Bamako, pers. comm., 2004), but they have not yet been studied thoroughly.

6. Outlook

In this paper we described past breeding objectives and their underlying plant type concepts, and noted that the results were frequently disappointing, particularly in semi-arid environments, because breeding criteria tended to address intensive production systems that are not yet reality in much of West Africa. On the other hand, trying to improve genetic materials for extensive, traditional systems would probably be futile because traditional germplasm is already well adapted to them, and because traditional systems are bound to change anyway due to demographic growth. Lastly, some recent breeding concepts were presented that address more specifically West Africa's current agricultural transition towards intensification, associated with high risks of soil degradation and weed proliferation because farmers intensify production without providing the necessary external inputs. Crops are therefore needed that (1) reward the use of inputs by being responsive to them, (2) tolerate or constraints brought about or aggravated by low-management intensification (essentially, increasing cropping coefficients by eliminating fallow periods), such as weed competition, (3) suit the farmers' current objectives, such as combined grain and fodder production, and (4) provide flexibility in sowing and crop management calendars according to climatic variability and labour availability.

These are ambitious objectives, but the example of dual-purpose cowpea cultivars at IITA demonstrates that innovative and viable solutions can be achieved. In the cases of dual-purpose (grain/fodder) sorghum, high-yielding but photoperiod sensitive sorghum, or weed-competitive upland rice, breeders have yet to provide material proof of these promising concepts. Ongoing genetic, physiological and agro-ecological research is designed to provide the theoretical basis and tools needed for their realization. Success will depend on the resources made available for this research, which is multi-disciplinary and thus expensive. Designing a new plant type and adapting it to a broad range of environmental and socio-economic constraints, and adapting its phenology to climate and local cropping systems, requires a broad-based breeding program backstopped by disciplines ranging from economics and agronomy to physiology and molecular genetics. Expensive, long-term projects are increasingly difficult to fund, and in Africa, they are even subject to risks associated with political stability, as demonstrated by the history of WARDA that has successively been disrupted by civil wars in Liberia and Ivory Coast.

Both the Nerica (WARDA) and photoperiod-sensitive sorghum (CIRAD, ICRISAT and the Institut d'Economie Rurale (IER) in Mali) breeding programs are undersized, and require more multi-disciplinary input to meet their respective challenges. Innovative breeding approaches should also be able to make greater use of molecular tools and advances in functional and structural genomics. Rice, being a model crop, happens to be on the frontline of genomics research and sorghum is likely to become a model crop for studying the genomics of C_4-type cereals, principally because of its comparatively small genome. If the Consultative Group for International Agricultural Research (CGIAR) and other research entities would rigorously invest in Africa's agriculture, we might in the near future see real progress in areas where breeding can potentially make a big difference: drought-resistant, high yielding, stay-green sorghums, flowering at the right time; dual-purpose, grain/fodder cowpeas, peanuts and sorghums; and high-yielding, weed-competitive rices (and possibly sorghum, cowpea and other African staple crops).

This analysis emphasised the need to breed crops specifically for the current agricultural transition from extensive, subsistence-oriented systems to intensified, market-oriented systems driven by demography. The transition situation, frequently described as socially and ecologically degraded, requires seed based technologies that differ from both the existing traditional and improved germplasm. Given the experience that the development of new cultivars takes about 10 years (or more if new genetic backgrounds are used), will the agricultural transition in Africa take long enough to justify specific breeding programs for it ? And, beyond the transition, will systems have similar technical and varietal needs as intensified agricultural systems in comparable climatic situations elsewhere in the world?

There are no sure answers, but if it is true that the Green Revolution failed in Africa because of lack of political stability and favourable agricultural policies (discouraging investment) and the predominance of subsistence agriculture (in sparsely populated areas, lacking market stimuli), as suggested in the introduction, it should not be difficult to identify regions where intensification strategies will likely take hold and thus enable a strong impact of crop breeding—wherever water resources allow intensification to be economical. With regards to the agricultural transition in semi-arid areas of West Africa, the Australian model combining extensive land use with mechanization will probably not be applicable because of small farm size, land tenure issues and persistent poverty. Specific breeding objectives for such areas and their current agricultural transition, such as photoperiod sensitive sorghum, will therefore probably remain relevant for a long time. Such breeding programs will strongly benefit from farmer participatory approaches providing solutions for specific situations.

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