Chapter 4
Rethinking Plant Breeding

Nourollah Ahmadi, Benoît Bertrand and Jean-Christophe Glaszmann

Plant breeding is the activity of developing diverse plant varieties that can contribute usefully to cropping and production systems. These breeding efforts are directed at plant improvement. But ‘improvement’ is a subjective and relative goal and it becomes necessary to regularly break up plant breeding objectives and procedures into clearly defined and manageable units.

The goal of ecological intensification is to add the aspect of sustainability to increases in production. Plant breeding must combine this objective with that of adaptation to overall societal and climatic changes. It must integrate diverse objectives and selection criteria. It must accommodate demands made by new stakeholders willing to help define objectives and evaluate breeding results. Indeed, it should come to terms with demands for a completely fresh look at the concept of ‘genetic gains’. Such a gain must not only consider the benefits reaped by a farmer using an improved variety at the level of his plot, but also its expected economic, social and environmental impacts on a larger scale in the event of a wider dissemination of this variety. Global change occurs at such scales and speeds that agricultural systems could respond by replacing species rather than by

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N. Ahmadi (✉) · J.-C. Glaszmann
Cirad, UMR AGAP (Joint Research Unit Genetic Improvement and Adaptation of Mediterranean and Tropical Plants), Montpellier, France
e-mail: nourollah.ahmadi@cirad.fr

J.-C. Glaszmann
e-mail: jean-christophe.glaszmann@cirad.fr

B. Bertrand
RPB Joint Research Unit (Plant Resistance to Bioagressors), Department Bios, Cirad, Montpellier, France
e-mail: benoit.bertrand@cirad.fr

J.-C. Glaszmann
Director of the AGAP Joint Research Unit, (Genetic Improvement and Adaptation of Mediterranean and Tropical Plants), Cirad, Montpellier, France

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seeking better adapted varieties of the usual species. Therefore, it is also necessary to foresee the evolution of a 'portfolio' of species used in target regions. The likely increase in diversity and turnover of ecological, agronomic and socio-economic situations for each species raises the question of which varietal deployment strategy to select. Should one select many local genotypes with short lifespans or fewer versatile varieties with longer lifespans?

The key challenge in biological sciences is of integrating knowledge at different scales—of molecules, tissues, organs and whole plants at different phenological stages. This is a prerequisite to understanding the patterns of regulation by genes and assessing their relevance to the spatio-temporal variability of constraints for which an improvement is required. In addition to this scientific challenge, we also need to address the question of which innovation model to implement. Plant breeding is also a business which must ensure a 'return on investment' and produce goods (new varieties) that ensure a convergence of interests of different economic stakeholders.

Before getting into the details of challenges that face plant breeding in the twenty-first century, it may be useful to recall some concepts as well as some lessons learnt from plant breeding practices in the last century. We do so below and also present the levers that are available to us to address these challenges.

1 Plant Breeding: The Past and the Present

1.1 Genetic Improvement: From Empiricism to Science

Plant breeding is the art and science of modifying the plant genotype to achieve a desired phenotype. Man has practiced plant breeding, in an increasingly intentional, organized and efficient manner, from the time he first settled down, more than 10,000 years ago. These activities have witnessed a sharp acceleration in the last century. Domestication was the first result of selection. It involved trying to prevent spontaneous seed shattering (especially in the case of cereals) and also to obtain bigger grains and fruits. Modifications in genomic regions that determine these traits remain the key distinctive signs (domestication syndrome) between cultivated varieties and their wild relatives. With this *directed breeding*, man also reduced the total or *neutral* diversity used, as breeding was carried out in one or more limited-size populations which did not represent the entire diversity of the wild species. This diversity, thus greatly reduced by the domestication bottleneck, underwent further transformation and specialization resulting from the selective pressure exerted by man and the new environments he colonized. Thus were born local varieties or populations, adapted to environmental conditions and to cropping requirements of small agricultural regions.

The need to intensify agriculture in the face of population growth occasionally resulted in a centralized selection of species and varieties to grow. Varieties of the same species, originating from domestication efforts undertaken elsewhere, were then introduced. As early as in 1012, faced with an influx of migrants from the north and a real shortage of arable land, Zhao Heng, the Emperor of China ordered two annual rice crops using a short-cycle rice variety imported from Annam.

Until the early nineteenth century and the discoveries of Darwin and Mendel of biological processes at the origin of genetic diversity (mutation and recombination), plant breeding consisted of identifying individual plants with the best phenotypes in nature or in local varieties to help propagate their progeny. This *massal* selection led to many positive developments. For instance, it was applied to sugar levels in beetroot in 1786, resulting in sugar beet and the setting up, in 1802, of the first sugar factory in Germany. In 1858, Louis de Vilmorin made a first methodological jump by selecting individuals based on the yield of their progeny rather than on their own phenotype.

Man truly started manipulating natural diversity in the late 19th century with the practice of controlled crosses between individual plants with complementary phenotypes. Genetics progressed rapidly in the 1920s with the emergence of quantitative genetics, in particular the model of Fisher (1918) that reflected both Mendelian laws and biometric relationships between related individuals. This model considered an observed phenotype as the sum of a genetic effect, an environmental effect and the effect of the genotype × environment interaction. This led to the development of a wide range of methods for optimizing breeding procedures based on the statistical estimation of genetic parameters obtained from dedicated experiments. The increase in maize yields in the United States, from 65 kg/ha/year between 1925 and 1955 to more than 110 kg/ha/year thereafter, is often attributed to the optimization of breeding procedures based on quantitative genetics. This was undoubtedly made possible by a greater availability of chemical fertilizers.

The accumulation of knowledge in plant genetics was accompanied by the formalization of a plant breeding industry. A seed production sector gradually came into being and necessary regulations were put in place to help the commercial distribution of plant varieties and seeds.

1.2 Agricultural Modernization and the ‘Green Revolution’

The term ‘Green Revolution’ was first coined in 1968 by the director of the U.S. Agency for International Development (USAID) to describe the introduction and rapid increase in wheat yields in Mexico since 1950, and wheat and rice in Asia, especially in the Indian subcontinent since 1970. The phenomenon has been analyzed from various angles ranging from scientific and technological innovation to American foreign policy in the context of the Cold War and containment of the ‘red revolution’. It was the result of a combination of several factors, including the implementation of a rural development strategy advocated by the American economist Schultz in his books *Food for the World* (1945) and *Transforming*

Traditional Agriculture (1964), as well as major advances in the genetic improvement of cereals.

The strategy of this revolution was to bring about all the conditions necessary for the adoption of technical innovations by small producers. These pertained to all aspects of agricultural production: not only a ‘technology package’ (high-yield varieties, chemical fertilizers, pesticides and herbicides, irrigation, etc.) but also subsidies for the purchase of inputs, supply facilities, credit for the purchase of agricultural equipment, support prices, protection against imports, strengthening of agricultural research and extension services, irrigation schemes, etc. This policy resulted in the establishment of international research centres specialized in enhancing the productivity of food crops and of the Consultative Group on International Agricultural Research (CGIAR). Support was also forthcoming from international financial institutions for the setting up and strengthening of national agricultural research systems (NARS) and agricultural extension systems.

The contributions of genetics consisted in developing varieties whose response curve to chemical fertilizers, especially nitrogen, levelled off only at doses that were three to four times higher than those for traditional varieties. This was achieved by identification of dwarfing genes within the existing diversity of each cereal and its wild relatives, and by transferring them to a small number of traditional varieties adapted to a tropical climate. In addition to reducing plant height and increasing the harvest index and the resulting lodging resistance, some of these genes also had a pleiotropic effect on various other yield components. The production potential of wheat and rice varieties rose from 3–4 T/ha to 10 T/ha. Since that first breakthrough, genetics has progressed mainly along two fronts. On the one hand, it has focused on the consolidation of this production potential through the accumulation of resistance genes to diseases and insects. On the other, it has increased productivity per unit of time by shortening the cropping cycle. The transformation of these genetic advances into innovations was achieved through the extensive dissemination of these varieties and cultivation techniques—mainly the use of fertilizers and pesticides required to ensure the expression of the varieties’ production potential—via widespread and active extension systems. It was thus that the IR8 rice variety, created by the International Rice Research Institute (IRRI) in 1966, came to be grown over several million hectares by the mid-1970s. By 1980, semi-dwarf varieties of rice were being cultivated in more than 30 % of the rice paddies of the eleven largest Asian rice producing countries (excluding China).

There is no doubt that Green Revolution varieties have contributed in many ways to increasing production and productivity. To this increase in yields was added the effects of allocating larger areas to rice and wheat crops which happened at the expense of other, less profitable, crops. Also notable were the effects of double and triple annual cropping, made possible by shortening plant cycle duration and eliminating photosensitivity, and those of the expansion of rice cultivation to marginal areas that resulted from shorter cycles and better adaptation to abiotic constraints.

Economic, social and environmental impacts of the Green Revolution in the Third World have been subject to the same intense debate as has ‘intensive agriculture' in industrialized countries (Evenson and Rosegrant 2003). On the whole, the Green Revolution in Asia ensured that production grew at a faster rate than the population. This led to self-sufficiency in cereals from the 1980s for the continent. This increase in agricultural productivity helped maintain grain prices at affordable levels for the urban poor and thus helped the fight against hunger. At the farm level, while large landowners were the initial beneficiaries—being immediately able to take advantage of new technologies and associated economic measures—the Green Revolution also gradually reached other groups of farmers. However, irrespective of the size of the farm, it was possible to take advantage of new varieties and the associated 'technology package' only under favourable biophysical conditions. Yet, on this front, despite irrigation development efforts, large regional and local disparities still exist. For example, while the average yields of 55 % of the rice paddies of Asia with good irrigation systems increased from 2 T/ha to more than 5 T/ha, the yield in the remaining 45 % exposed to water excess or deficiency, salinity, or other physical or chemical soil problem stagnated around 2 T/ha. The success of the Green Revolution bypassed sub-Saharan Africa where well-irrigated rice paddies represent only 20 % of the total. Thus, differences in biophysical conditions have resulted in increased disparities in farm incomes and wealth. Finally, the Green Revolution was also accompanied by widespread environmental degradation: soils sterilized by salinization in India, water pollution and related diseases linked to excessive insecticide use in Vietnam.

While the Green Revolution was a major phenomenon in Asia, its impact was highly variable across regions, plants and stakeholders. The same period saw Europe and North America undergoing similar changes in agricultural productivity due to agricultural modernization that began in the early twentieth century and accelerated from 1945. In Africa, the principles of the Green Revolution were the basis of the development of peanut cultivation starting in 1918 (Box 1) and cotton cultivation in 1945 (Box 2). The example of rainfed upland rice (Box 3) shows that when genetic innovation is driven by specific needs, it can be disseminated almost spontaneously. Massive efforts were also undertaken to create high-yielding varieties of other food crops, including maize, sorghum, cassava and beans, yet leading to significant dissemination only in the case of maize case only. The pattern of widespread dissemination of a small number of high-yielding varieties in optimal growing conditions was also seen in various non-food crops and perennial plants.

Box 1. Genetic improvement of peanuts in Senegal: adaptation to technical, climatic and societal developments

In his report titled, '*The current state and future of trade in peanuts in Senegal*', Roubaud (1918) states: 'After the abolition of the slave trade in 1815, the processing of peanuts became the primary resource of Senegal. Insurance schemes, cooperative seed stores, etc. were established in most areas directly by the government. Very often, the harvest is booked in advance by the peanut processor who provides loans to the farmers. The agriculture department has undertaken a process of improving cultivation methods through the use of animal traction and fertilizers. The Senegalese peanut trade has consequently flourished. However, there are areas of concern. The oil yield from seeds has decreased significantly. At the same time, evidence has grown of increasing parasite-induced damages. The damage is all the more marked when drought conditions prevail. One promising control method could be the use of short duration peanut varieties. There are local peanut varieties of shorter duration than the commercial varieties. The variety named Volète deserves a special mention. It can mature in two months. However, Volète's unattractive appearance and low productivity has resulted in its disappearance from the European market, and it now only serves the native diet. Perhaps a hybridization with commercial varieties would lead to more acceptable plants in all respects. Long-term experiments should be undertaken in the colony's experimental stations for selecting seeds and choosing local peanut breeds that are most adapted to different climatic and soil conditions. The recently established research station at Bambey has yet to orient its efforts in a scientific manner in this important direction.'

The work of selection and breeding began at the Bambey research station in 1924. The selection from local material, introductions, especially from the United States, the biparental hybrids and improved populations obtained by recurrent selection, first by the colonial administration and then by the Oil and Oilseeds Research Institute (IRHO), and finally by the Senegalese Institute for Agricultural Research (ISRA) and by CIRAD, have resulted in continuous acquisition and dissemination of new varieties to meet changing needs. These have included an upright shape to facilitate mechanization, a grain size and shape suitable for use (oil mill or confectionery), disease resistance, shortening of the cycle and drought tolerance due to climatic deterioration since the 1970s, and resistance to aflatoxin-producing fungi in line with European standards (Ba et al. 2005). Until the 1980s, most of the production (700,500 T) was destined for industrial oil production for export, as part of a monopolistic model. The government, and subsequently a State-run corporation, fixed prices and oversaw the production and distribution of seeds, while meticulously sticking to the 'varietal map' that was regularly updated by research (Clavel and N'doye 1997). Subsequently, the withdrawal of the State from this process led to a disruption in seed supply and marketing. Production plummeted.

New and more promising perspectives have emerged since 2004. The Senegalese Association for Grassroots Development, with technical support from ISRA and CIRAD, organizes the production of basic seeds by farmer organizations and trains farmers to produce 'farm' seeds (Mayeux and Da Sylva 2008). The drought tolerant varieties used are a result of the breeding program carried out in Bambey (Khalfaoui 1991; Clavel and Annerose 1995; Clavel et al. 2005).

Box 2. Genetic improvement of cotton: the Green Revolution in an agro-industrial sector

Agricultural research was the weak link in the first attempts to develop the cultivation of cotton in sub-Saharan Africa, which began in the 19th century. The establishment of the Research Institute of Cotton and Exotic Textiles (IRCT) in 1946 and of the French Company for the Development of Textiles (CFDT) in 1949 was a turning point. Production increased from 0.1 MT in 1950 to 2.6 MT at its peak in 2004. More than 16 million small farmers made their living from it (Levrat 2009). CFDT and national cotton companies took 'control' of production and enjoyed a monopoly over purchase, collection, ginning and marketing. This 'control' involved providing inputs on credit and dispensing agricultural advice. The choice of inputs, including varieties, and agricultural advice were based on research conducted by the IRCT and subsequently by its national successors associated with CIRAD. This research was conducted in close collaboration with cotton companies, which also provided its funding. It was an integrated system typical of the Green Revolution, with industry ensuring that the farmers met all the conditions necessary for appropriating the results of research. In the case of varieties, this entailed, on the one hand, ensuring production and distribution of the seeds of new varieties, since the variety was selected through research and by the cotton company and not by farmers. And, on the other, the distribution of everything else that was necessary to achieve the full expression of the genetic potential of these varieties to each farmer: fertilizers, a phytosanitary 'umbrella' programme, a guaranteed purchase price and input subsidies. On their part, plant breeders had to pay particular heed to improving the yield of ginned cotton and the quality of fibre, the main determinants of profitability for cotton companies (Collectif 1991).

A network of regional research entities was set up which brought together multidisciplinary teams from each country. Agronomists, entomologists, pathologists and fibre and grain technology specialists contributed to the definition of the plant ideotype and the evaluation of plant material created by geneticists. In the mid-1950s, the focus shifted to improving the species *Gossypium hirsutum*, which currently covers more than 90 % of the world's cultivated area under cotton, without abandoning the use of interspecific crosses. The most tangible genetic advances have focused on plant architecture and the ratio of dry cotton grain to total dry matter; on resistance to diseases and insects; and on fibre characteristics and ginning out-turn, which increased from 35.5 % in 1962 to 41.9 % in 1992. Its potential and yield stability were also boosted, taking the average seed cotton yield in Francophone Africa from 198 to 975 kg/ha between 1962 and 1992. However, it is difficult to pinpoint the exact contribution made by the variety and other production factors in this increase. The deliberate implementation of breeding schemes and seed production that help maintain a residual genetic variability is probably not unrelated to the combination of productivity and hardiness of varieties such as ISA205 and STAM-F. These varieties were cultivated on over 300,000 ha/year in the 1980s. Another significant genetic advance was the creation of *glandless* varieties for Africa. The grain protein of these varieties can be used in human food and animal feed as their gossypol toxins have been removed (Hau et al. 1997). In 2008, varieties that were developed or co-developed by CIRAD covered 83 % of the 1.2 million hectares of cotton grown in eight Francophone African countries.

Box 3. Varietal innovation for a constrained environment: rainfed rice cultivation in the highlands of Madagascar

The highlands of Madagascar (1,200–2,000 m in altitude) have long been confronted by a mismatch between population growth and agricultural productivity. Despite rice being a staple food here, its yields are stagnating and there is an acute shortage of land suitable for irrigated rice cultivation. Initial attempts were made to introduce another form of rice cultivation, called ‘rainfed upland’ rice, where rice is grown, like other cereals, on non-flooded aerobic soil. These failed because of the region’s cold climate. Low night temperatures greatly stretched the sowing-heading cycle, leading to sterility in upland rice varieties usually grown in low-elevation, hot and humid areas.

Madagascar’s National Centre for Applied Research on Rural Development (FOFIFA) and CIRAD took up the breeding of rainfed rice varieties tolerant to high-altitude cold temperatures in the mid-1980s. A crossing programme was launched as no suitable varieties could be identified through the introduction and evaluation of numerous traditional and modern varieties from other cold regions of the world. Cold-tolerant irrigated varieties were crossed with recently developed upland rice varieties for the low and medium altitude areas of Madagascar. Pedigree selection based on evaluation of progenies of these crosses at an altitude of 1,500 m and a multi-local evaluation of the best progenies over four years led to the registration of five cold-tolerant rainfed rice varieties in the official catalogue (Dechanet et al. 1997). These varieties have a yield of 5 T/ha for a cycle time of 145–165 days at 1,500 m in experimental conditions. The only downside to this pioneering achievement was the narrow genetic base of the new varieties: the five varieties had the same cold-tolerant parent, a traditional Malagasy variety grown in irrigated rice paddies at altitudes greater than 1,750 m.

The participatory, multi-local and multi-year evaluation of these varieties, conducted in conjunction with seed-producing farmer organizations, quickly led to the adoption of upland rice cultivation by more than 10 % of the farmers (Dzido et al. 2004). A more recent survey of 843 farms in 26 villages in the Vakinankaratra region located above 1,250 m showed that 62 % of these villages and 36 % of the farms cultivated upland rice using one of the varieties created by FOFIFA and CIRAD. The 'new technology' of upland rice cultivation was adopted mainly through informal exchanges of information and seeds between villages and between farmers (Radanielina 2010).

However, since the early 2000s, the large-scale dissemination of upland rice has led to increasingly frequent outbreaks of blast, a disease caused by the fungus *Magnaporthe oryzae*. The resistance of the first released varieties of relatively narrow genetic base, was quickly overcome (Sester et al. 2008). The breeding programme is now focused on building up blast resistance, diversification of the grain quality of upland rice varieties and efficiency in the use of resources (nitrogen, phosphorus). All this without forgetting the necessary cold tolerance. The programme is also paying attention to upland rice adaptation to cover-crop based cropping systems developed and disseminated by agronomists to improve the sustainability of upland cropping systems in the region (Naudin et al. 2010). The effectiveness of the strategy of mixed varieties using diverse sources and types of blast resistance is also being tested (Raboin et al. 2012).

Agricultural modernization in the North and the Green Revolution in the South led to a decrease in the genetic diversity of crops. This was largely due to the substitution of a large number of local varieties by a small number of 'improved' varieties. Subsequently, commodity-based process integration led to additional technological specifications and selection criteria that further narrowed down the range of varietal diversity that could be deployed.

2 Recent Changes and Developments

2.1 Development of Participatory Approaches

One of the key features of agricultural modernization in industrial nations and of the Green Revolution in developing countries has been the separation of the functions of agricultural production, varietal innovation, seed production and germplasm conservation. The latter three functions moved from farmers to public and private professionals.

Plant breeding programmes were carried out in research stations and targeted plant ideotypes maximizing production per unit of area and time under optimal cropping conditions, giving little consideration to specific end-user perspectives. They ignored the spatial variability of biophysical conditions as well as local knowledge and practices for the use of genetic variability. A homogenizing agronomy thus became associated with a unidirectional varietal improvement.

In developed countries, varietal innovation became subjected to a global organizational framework. This started with approval procedures (registration in the official catalogue) based on performance criteria, predictable 'agronomic and technological value' and 'distinctiveness, uniformity and stability'. These criteria were evaluated in highly artificialized conditions (fertilizers, pesticides, etc.) of experimental stations under standard technical processes, eliminating all forms of diversity of the environment. Varieties thus approved were assumed to have wide adaptability, and were recommended by technical-administrative committees for large geographic areas. They were multiplied by public or private seed companies under conditions that ensured the preservation of their conformity, and were distributed to all farmers in the target area. Thus, a small number of inbred lines and hybrid varieties replaced the large number of local and often heterogeneous varieties, each linked to specific biophysical conditions and uses. These varieties, grouped and categorized according to criteria defined by the plant breeder, have become 'genetic resources' conserved ex situ, under conditions that do not leverage their adaptive and evolutionary potential.

This pattern of varietal innovation, that minimizes the impact of genotype × environment (G × E) interaction, soon proved, like the whole Green Revolution model, unsuitable for areas with high soil and climatic variability, high diversity of production systems and high inter-annual climatic variability. In his book '*Rural Development: Putting the Last First*', Chambers (1983) highlights the need to mobilize complex knowledge to manage risks. He recommends taking advantage of diversity and combining scientific knowledge with local knowledge in order to optimize research and rural development. These precepts were subsequently gradually integrated into plant breeding programmes. 'Participatory selection' approaches were developed to take local socio-agroecological specificities into account by encouraging farmers to participate in developing new varieties. Formalized as *Participatory Plant Breeding* in the mid-1990s (Hardon 1995) and advocated widely internationally, this new line of research reinstated the farmer at the heart of varietal improvement efforts. While defining the selection criteria, priority is accorded to leveraging of G × E interactions with limited recourse to expensive inputs and to managing risks that small farmers are subjected to. Emphasis is also placed on the diversity of stakeholders, in particular women, given their important role in production and processing activities. The experiences of participatory breeding, carried out at a small-scale have broadly resulted in an increased adoption of varieties developed by the target communities (Eyzaguirre and Iwanaga 1996). Questions have then arisen on the generalization and sustainability of these actions. Several complementary approaches have attempted to address these issues. Plant breeding activities were somewhat decentralized at the global level by dividing tasks related to *pre-breeding* and actual varietal development between the CGIAR centres and NARS (Box 4). The effectiveness of multi-actor platforms for dialogue and action was tested at the national and regional levels (Box 5). The most ambitious experiments are seeking to transfer the skills and responsibilities of significant parts of the process of varietal creation and dissemination to farmer organizations (Box 6).

Box 4. The decentralization of plant breeding: a new division of tasks between stakeholders of plant breeding

Under the auspices of the FAO, Mahsuri, a semi-dwarf rice variety was widely disseminated in India in the mid-1950s while IR8, arguably the star variety of the Green Revolution, was disseminated throughout Asia (excluding China) and Latin America in the late 1960s. These two varieties boosted the average yield from 2 T/ha to 4.5 T/ha for over 33 million ha of irrigated rice fields. Subsequently, genetic progress focused on stabilizing yields by increasing resistance to diseases and insects, as well as on the 'yield/growth duration' ratio. The lack of progress in genetics with regard to the yield potential was reflected, from the mid-1990s onwards, by stagnating yields and farm production levels.

New breeding patterns and new ways of sharing responsibilities then emerged in response to this stagnation in genetic progress, a result of the shrinking genetic base of disseminated varieties and the inadaptability of Green Revolution varieties in large areas subject to abiotic constraints. This change was also driven by the desire of the NARS, whose capabilities had increased dramatically, to strike out on their own and by the growing interest of private companies in the rice market of developing countries. In Asia, this trend led IRRI to focus on understanding the genetic bases and improvement of specific traits, while leaving to the national systems the responsibility of incorporating them into varieties adapted to the specific conditions of each country and each agricultural region. In Latin America, the division of tasks led to the establishment of a plant improvement programme consisting of decentralized recurrent selection. Synthetic populations with a broad genetic base were thus created, derived from intercrossing dozens of parents. This intercrossing was facilitated by introducing a recessive gene for male sterility into the population. These populations were improved for some major traits by the International Centre for Tropical Agriculture (CIAT) in association with CIRAD. They were then distributed to national research systems to help extract new varieties adapted to each country's specificities as well as to enrich them with local parents. Information from national programmes was, and continues to be, used to orient recurrent breeding at the central level.

Similarly, public–private partnerships were set up in which public research undertakes the pre-breeding phase and passes on the plant material to private firms that are fee-paying members of a consortium. These firms then finalize the breeding for their own geographical areas and target market segments. This is how the Hybrid Rice Development Consortium (established by IRRI) and Fondo Latinoamericano Para Arroz de Riego (established by CIAT) function*.

It is expected that these changes will promote the expansion of the genetic diversity that is deployed, take advantage of genotype × environment interactions, contributing thus to an increased resilience and productivity of rice systems. However, we currently have few means of quantifying their impact.

*Hybrid Rice Development Consortium, http://hrdc.irri.org/; Fondo Latinoamericano Para Arroz de Riego, http://www.flar.org/ (retrieved: 2 May 2013).

Box 5. A platform for varietal innovations of the plantain: a linking of scientific and local knowledge

More than 8 million tonnes of plantain is produced each year in West and Central Africa by small farmers for their own consumption as well as for local and regional markets. In Cameroon, an estimated 600,000 farmers grow plantain as a monoculture or through intercropping.

Several plant breeding programmes based on distinct but complementary genetic concepts have helped breed new varieties since 1987. Their main objective is to improve resistance to diseases and pests such as cercosporiosis, nematodes, and weevils (Tomekpe et al. 2004). Once the improved varieties were obtained, questions arose as to how amenable they were to farmers' choosing criteria, which go beyond mere disease resistance.

To address this issue, the Cameroon-based African Research Centre for Bananas and Plantains (CARBAP) introduced, in 2006 with support from CIRAD, a mechanism called the 'varietal innovation platform'. The objective of this platform is, on the one hand, to get target users to evaluate the varieties developed by research and, on the other, to establish a framework for dialogue between researchers and other stakeholders of the sector.

'Clubs' of users and local experts were set up at the level of small agricultural regions. Members consist of producers, nursery growers, merchants, restaurateurs and consumers. Each club was asked to define a set of constraints concerning their cropping systems and marketing modalities. It then became incumbent upon the CARBAP plant breeders to address these constraints through the development of plant 'ideotype(s)' in terms of on-field performance (robustness, drought resistance, resistance to cold temperatures and leaf diseases, plant height, early cultivation, resprouting ability, etc.), fruit characteristics (size of the plant and stem, fruit size and shape, pulp colour, etc.), leaf characteristics (usability for packaging) and processability (ease of peeling, suitability for different cooking methods, appearance, texture, taste, storability, ability to satiate, etc.). The plant material chosen by the plant breeder was grown and evaluated by the clubs on their plots and under their own real-world conditions. In addition, these clubs have together set up a common steering committee to interface with the research team and public authorities.

This arrangement helps establish links between local knowledge and scientific knowledge, strengthens public–private partnerships in the sector and stimulates the organization of civil society. The closer integration of post-harvest usage criteria in the breeding programme has led researchers to study the relationship between qualitative user preferences and the physicochemical and functional properties of fruits in greater detail (Gibert et al. 2009).

There currently exist three sub-regional platforms for promoting the participatory propagation and evaluation of a dozen hybrid varieties and exotic cultivars in Cameroon, Gabon, Equatorial Guinea, Central African Republic and the Congo. Similar platforms are being set up in Ghana, Togo, Benin and the Democratic Republic of Congo.

While the Green Revolution model was being called into question, other issues on biodiversity and sustainability of production systems arose. This led to the integration of the participatory approach and the in situ management of diversity (Box 6). In addition, the focus of varietal improvement shifted to adapting plants for more sustainable farming systems (Box 7). It is well known and recognized that the reflections on and practical experiences of participatory breeding in Europe originated mainly from proponents of *organic farming* (Wolfe et al. 2008; Ostergard et al. 2009; Dawson and Goldringer 2012).

Box 6. Improvement of sorghum for West Africa: from breeding ideotypes in a research station to the sharing of responsibilities with farmers

Sorghum is a traditional cereal from the African savannah, where it is the staple food of the rural population. It is normally consumed as a thick gruel called *Tô*. The last 50 years have seen a growth in the production of sorghum, due largely to an increase in the acreage devoted to it. In West Africa, while the cultivated area almost doubled, increasing from 5.4 million to 10.5 million hectares between 1961 and 2010, the yields (840 kg/ha) increased by a mere 12 %.

Breeding programmes for sorghum varieties, inspired by Green Revolution ideotypes of other cereals, have focused since the 1960s on modifying plant architecture (short size and single stem) and the panicle (compact).

They have also worked towards eliminating photoperiod sensitivity, something that is considered inconsistent with intensive agriculture. A large number of improved fixed line or F1 hybrid varieties were developed based largely on exotic genetic resources. It was thus that the IRAT204 variety, for example, was released in 1980. It was a *caudatum*-type variety of short height (1.4 m against 2.5 m for local *guinea* ecotypes), with a rather compact panicle and very short cycle, not photosensitive, and with a production potential of 5 T/ha, against 3 T/ha for local varieties (Chantereau et al. 1997). These varieties were only marginally adopted by farmers (Ouedraogo 2005) for at least two reasons: the economic conditions for intensifying sorghum production were not met and most of this material did not possess the qualities required for traditional grain and straw uses.

Recently, CIRAD plant breeders and their partners showed the importance of photosensitivity in the adaption of sorghum to climatic and disease constraints (Vaksmann et al. 1996) and analyzed the biological bases of the grain's technological and organoleptic qualities (Fliedel 1995). They thus reoriented their work towards valorising local genetic diversity, based on methods that balanced productivity, quality in a multi-use context (human food and animal feed) and in situ conservation of agricultural biodiversity. In Mali where intensive cereal cultivation practices are being progressively adopted in cotton-growing areas, recurrent selection scheme using populations consisting of a broad local genetic pool was associated with decentralized participatory breeding. This was done in an attempt to develop photoperiodic varieties with a reduced size and a better yield index, while maintaining grain quality (Vaksmann et al. 2008). In Burkina Faso, ancient local varieties which were conserved ex situ and improved varieties released by research, were evaluated in a participatory process. This participatory evaluation and the participatory development of new varieties led to an improved inclusion of farmers' highly specific selection criteria (Vom Brocke et al. 2008, 2010). This work helped in identifying several varieties with a reasonably wide geographic adaptation and in confirming the capacity of farmers and their organizations to implement important components of a plant breeding programme (Vom Brocke et al. 2011). Supported by the French Global Environment Facility, this programme is currently seeking to build the organizational capacity of the farmers as a prerequisite to a formal transfer of the management of activities of sorghum breeding and evaluation, registration and protection of the new varieties developed, and production and marketing of seeds.

Box 7. Development and dissemination of Arabica varieties for agroforestry production systems

Two species of coffee are grown worldwide: *Coffea arabica* (about 65 % of global production) and *Coffea canephora* (known commercially as 'robusta') representing the remaining 35 %.

Coffea arabica was introduced in Latin America using a very small number of plants (Anthony et al. 2002), a fact that led to a marked founder effect. Nevertheless, this initial low genetic diversity was used judiciously by breeding programmes launched in the 1930s. They gave birth to a dwarf variety that allowed the adoption of full-sun intensive cropping systems similar to the Green Revolution described above, mainly in Brazil, Colombia and Costa Rica. However, the combination of dwarf varieties, high-density cropping and expensive pest control methods never took hold in the rest of Latin America and Africa. Coffee continued to be grown under shade without any major technological innovations, resulting in a stagnation of yields. And yet, it became clear in the 1990s that despite their low productivity, agroforestry systems had positive effects on the maintenance of biodiversity, soil fertility, etc. and the quality of the coffees grown.

CIRAD proposed creating hybrid varieties that were suitable for agroforestry systems. The selection method used was based on intercrossing two pools of genetic material: the American lines and the 'wild' coffee varieties from Ethiopia or Sudan. Following 20 years of experiments in controlled environments and on the producers' farms, it appears that the F1 hybrids produce 30–60 % more in agroforestry systems without the use of added fertilizers (Bertrand et al. 2011). It was possible to select individuals from the hybrid families which demonstrated strong resistance to leaf rust and nematodes. Finally, the overall quality of the hybrids is comparable to that of standard varieties (Bertrand et al. 2006). In some specific environments, we even observe a much higher aromatic quality, for example, floral notes in hybrids grown above an altitude of 1,200 m.

The somatic embryogenesis technique was used to reproduce these hybrids (Etienne et al. 2012). This technology was developed by CIRAD over 20 years and was transferred to the private sector which built two tissue culture laboratories. More than 4 million plants have now been sold in Central America and Mexico. The Nicaraguan experience (pilot laboratory and technology transfer) appears to be a model that can be replicated in other countries around the world. It is estimated that 500 million new plants will be needed to renew all the planet's agroforestry plantations. The enthusiasm for the new hybrids is genuine and the impact of these new varieties is only limited by the method of reproduction used. Using genetic male sterility may help overcome this bottleneck. Preliminary hybrids obtained by this technology are currently being evaluated by farmers and it is hoped that they can be widely distributed to agroforestry systems as early as in 2016.

2.2 The Advent of Molecular Tools and Breeding on Genotype

Most traits of agronomic interest are quantitative and are determined by a large number of genes as well as by their interactions with each other and with environmental factors. Breeding based on the phenotype is inefficient for these traits because of the confusion between the effects of genes and those of the environment. Quantitative genetics improves breeding accuracy by segregating these effects and their interactions. However, it is a statistical approach based on genetic parameters (genetic variance, genetic correlations) of the population subject to breeding. Any increase in the average population performance from one generation to another depends on the accuracy of phenotypic data and trait heritability. Moreover, even setting aside the precision necessary and the associated cost, some traits of some species can be observed only at maturity or in an adult individual. The breeding cycle can then extend over several years and the breeding efficiency per unit time is reduced. Finally, the effect of genes and their interactions is treated arbitrarily as a single block, without taking their distribution on chromosomes into account.

These limitations quickly led to the development of methods for labelling genes with particular agronomically useful traits with the help of markers with a low dependency on the environment and the age of the plant (Sax 1923). However, it was not until the late 1980s that the first genetic map was created using polymorphism found directly in DNA. This map broke down a quantitative trait into discrete Mendelian factors, *quantitative trait loci*, or QTL (Paterson et al. 1988). Genes can be labelled at two levels of precision: with the causal mutation of the phenotypic variation or through nearby markers presumed to be non-functional. The former are currently thought to be almost exclusively related to qualitative traits while the latter to both qualitative and quantitative ones. In recent years, there has been a flood of information for labelling agronomically useful genes. Methods of genetic mapping of progeny derived from model crosses (such as ‘good × poor’) are being enriched by methods using phenotypic and genotypic diversity of representative populations of the species or of the material from a breeding programme (Jannink and Walsh 2002), as well as by information from the annotation of genomic sequences and different methods of analyzing gene functions in model organisms. This information, combining genetic segregation and functional assumptions, helps define the ideal genotype, i.e., the mosaic of chromosomal segments of the parent population that needs to be combined in a single individual to get the best possible expression of the target trait(s). The integration itself is achieved through a succession of crossing cycles and selection on genotype or marker assisted selection (MAS). One must note, however, the instability of QTL effects in different genetic backgrounds and biophysical environments as well as the erosion of QTL-marker linkage over breeding generations. For these and other reasons, labelling with non-functional markers must be redone for each population, and must be regularly renewed over breeding generations (Dekkers and Hospital 2002).

These methods, already commonly used by private firms, are gradually being adopted in breeding practices by CGIAR centres and NARS in developing countries, both for simple and complex traits (Box 8).

Box 8. Creating the ideal genotype: case of marker assisted recurrent selection in sorghum

Marker assisted recurrent selection (MARS) is part of a set of new approaches that use molecular markers to create varieties. In this approach, molecular markers are used to break down the variation of different quantitative traits which breeders are interested in into single traits (QTL). The originality of the approach lies not only in incorporating the use of markers in the breeding method, but also in working simultaneously with all useful traits and in diverse environments. One or more ideal genotypes can thus be defined as the mosaic of chromosomal segments that carry favourable alleles from the parents for all traits considered. It is theoretically impossible to obtain this ideal genotype using a classical pedigree method and with realistic population sizes when a large number of QTLs are involved. The MARS method—which involves several generations of successive crosses between progenies on the basis of their genotype to molecular markers associated to target QTLs—and the definition of multi-trait breeding indices is used to create material that is close to this ideal genotype. The value of the material evaluated by the breeder is thus optimized. In addition, the multi-trait and multi-environment aspect of this approach helps explore different breeding assumptions and objectives using the same material.

Since 2008, CIRAD and the Institute of Rural Economy (IER) in Mali have successfully implemented the MARS approach for sorghum to obtain photoperiodic varieties which combine productivity with grain quality. In this endeavour, they have received financial support from the Generation Challenge Program and the Syngenta Foundation, and methodological support from Syngenta Seeds.

2.3 Complex Crop Stands

The past decade has seen a spurt in efforts to develop improved varieties for better efficiency in using resources (fertilizers, water and even pesticides) and for resilience and robustness. This was the result of the environmental impacts of the

Green Revolution observed in the South and the development of organic farming and low-input agriculture in the North, which were more exposed to biotic and abiotic constraints than conventional agriculture. Various experiments were conducted, including some on the use of intravarietal diversity of crop stands. Breeders and pathologists started using varietal mixtures as far back as the 1920s to counter a rapid reduction of varietal resistance to diseases (Finckh et al. 2000). This approach is also used to dampen variations in environmental constraints, improve resources (water, fertilizers, etc.), increase usage efficiency, or improve lodging resistance or grain quality (Ostergard and Fontaine 2006). In some ways it is akin to restoring erstwhile uses of intraspecific diversity as it existed within local varieties, and interspecific diversity of crop associations. After all, it still remains the basis of traditional agriculture on hundreds of millions of hectares.

Numerous studies have focused on multi-line stands, particularly for cereals in organic agriculture (Newton et al. 2009; Wolfe et al. 2008; Kiaer et al. 2009; 2012). They are seen as a promising option for general agriculture in developing countries (Faraji 2011). While the modalities of the functional advantage of complex populations still need to be spelt out, techniques of analysis have advanced using molecular procedures. For example, the dynamics of the diversity of a variety of multi-line bean, composed of contrasting root behaviour lines, was studied in the field for different fertilization levels (Henry et al. 2010). Molecular markers were used to quantify the contribution of each line to root stand and grain yield. The test's level of accuracy was, however, not high enough to arrive at any conclusion regarding a potential advantage of the composite population. New methods under development, based on a quantitative DNA analysis, should help quantify the root development of different components of multi-varietal and multi-specific heterogeneous crop stands (Haling et al. 2011). Similarly, the concept of *evolutionary plant breeding* has emerged recently. It envisages the deployment of varietal stands that are capable of adapting to changes in environmental conditions (Döring et al. 2011). A more detailed understanding of ecophysiologic interactions involved in improving the performance (primary production and its stability) of monospecific stands endowed with a functional diversity is necessary to help select the best possible complementary components. Which traits are to be diversified, and how to go about it without adversely impacting the homogeneity desirable for other traits?

3 The Challenges of Ecologically Intensive Agriculture

While it is well known that conventional intensification, as part of the Green Revolution, helped boost yields substantially in some countries, it also had serious negative effects on the environment. This has led to a search for new ways of increasing production. Ecological intensification represents a comprehensive transformation of agriculture through the adoption of production models to ‘obtain desired *output yields* from a cultivated ecosystem that are intrinsically high per biosphere unit, while maintaining the functionality and viability of various ecosystem functions and without forcing with artificial inputs' (Griffon 2007).

This new model can only be adopted through the use of a new generation of plant material. In addition to producing biomass, this material will have to optimize biological interactions to ensure adaptation under various environmental constraints, protection against pathogens, symbiotic fixation of atmospheric nitrogen, greater mobilization and recycling of soil minerals, protection against erosion, and a maintenance of agricultural biodiversity, including intraspecific genetic diversity. The example of rice (Box 9) shows that research in genetics and plant breeding has started down this path. It has endeavoured to create plant material suitable for constrained environments and which uses resources with greater efficiency. Yet, much remains to be done in terms of acquiring knowledge as well as of practices.

Box 9. Adapting rice to ecologically intensive agriculture

One of the central pillars of the Green Revolution has been the combination of semi-dwarf varieties and a high level of mineral fertilizer. But not only is the production and distribution of these fertilizers very energy intensive, existing phosphorus resources are limited and may well run out before the end of the twenty-first century. Furthermore, nitrogen use often leads to water pollution.

Two lines of research are being explored to reduce the use of nitrogen fertilizers: biological nitrogen fixation or BNF (Choudhury and Kennedy 2004), and nitrogen use efficiency or NUE, i.e., the efficiency of nitrogen use by the plant (Peng and Bouman 2007). The genetic programme for the endosymbiotic association between rice roots and nitrogen-fixing bacteria is currently being dissected. It has already been shown that rice possesses the essence of the genetic programme involved in the nodulation process in legumes. Combined with work on the ability of bacteria to associate themselves to cereal roots, this research should lead to operational results with regards to BNF in the next decade. As far as NUE is concerned, such operational results seem to be available already. Transgenic rice varieties that halve the requirement for nitrogen fertilizer while maintaining production levels are being evaluated on a large scale in China*. Patents related to the biological processes involved here have been filed. The possibilities of monetizing the reduction of CO_2 emissions resulting from the use of NUE rice is an additional motivating factor.

As far as reducing phosphate fertilizer requirements is concerned, the most promising line of research is to attempt to improve the plant's ability to use the insoluble fraction of soil phosphorus. The genetic diversity for such ability exists in most major field crops. Efforts to clone the gene (*Pup1*) responsible for this capability in rice are very advanced (Gamuyao et al. 2012). The transgenic approach of transferring microbial genes to increase root excretions that can utilize non-soluble forms of soil phosphorus also shows promise.

In another vein, while the first Green Revolution was based on the combination of the semi-dwarf varieties and mineral fertilization, it is generally accepted that, for rice, any further significant increase in production potential can only come from changing its photosynthetic mechanism from type C3 to type C4. This transformation would enhance the efficiency of rice to convert solar energy into biomass by 50 %, without additional consumption of water or fertilizer. The C4 Rice Consortium is exploring two complementary lines of research: research into wild relatives of rice that have already changed partially to the C4 type, and into transgenic transfer of genes from maize and/or other C4 plants to rice (Sheehy et al. 2007).

[*] See http://www.arcadiabio.com/nitrogen (retrieved: 4 May 2013).

3.1 Understanding Complexity

3.1.1 Biological Interactions

Biological interactions, defined at the level of the plant breeder, reveal unprecedented dimensions of complexity. To select genotypes that are adapted to a particular use in a given type of environment (one among the target population of environments, or TPE, of agronomists/ecophysiologists) is in itself an important task. The selection power will increase with the number of genotypes sorted, the number and diversity of selection sites, the accuracy of description of sites, and the accuracy of measurement of the target plant traits. It entails manipulating large numbers, optimizing flows and making the best possible use of available capabilities. Taking into account biological interactions with other living entities and variable components of the system leads to an exponential expansion of the conditions that require testing. Using the individual genotype as a factor in these interactions seems impractical.

For example, an extensive experimental effort was needed to determine the effect of maize genotypes on the composition of the associated rhizobacterial community. It was possible to show the influence of the varietal type, but not of the interaction with the genotype within a varietal group (Bouffaud et al. 2012). This kind of result emphasizes the existence of a potentially significant effect of soil biology but does little to indicate how the breeder could use it. Rather, it is an invitation to cultivate an intraspecific and interspecific diversity to promote biological diversity.

The valorisation of biodiversity's ecosystem functions via the use of varieties/populations with large internal diversity raises a whole new set of questions.

Expanding the scope to multispecies populations widens the issue to encompass new traits which correspond to the mutually beneficial functions sought. To what extent should the role of a cereal be promoted as a guide to facilitate the development of the associated legume? What are the implications for harvesting methods and the use of the products?

The challenge of integrating knowledge becomes even greater if we transpose the issue of the valorisation of biodiversity's ecosystem functions from a cultivated plot to a wider canvas: the *terroir* or a landscape. We would then have to consider intraspecies and interspecies diversities, their interactions and their spatio-temporal arrangement. Faced with this complexity, we must identify local and contextualized solutions, while allowing more room for empiricism, local knowledge and its interactions with the knowledge related to mechanisms involved.

3.1.2 Interactions with the Abiotic Environment

A large amount of data has been gathered on different plant species over the past two decades. It pertains to the functioning of genes studied individually or in small groups in contexts of responses to specific stimuli (salinity, drought, cold, etc.). The major scientific challenge is the integration of this data at different scales (of molecules, tissues, organs, entire plants at different phenological stages). This is a prerequisite for understanding the principles of regulation by genes and assessing their relevance in terms of spatio-temporal constraints for which the adaptation is sought. Ongoing research on adaptation to climate change illustrates the scope of the challenge. Genes and gene networks involved in basic biological processes that underpin the growth and development of plants as they interact with different environmental factors (water, minerals, light, temperature, CO_2) are described quite extensively. Significant efforts are underway at the level of the plant to assess the genetic diversity available for traits necessary for adaptation: tolerance to non-optimal temperatures at different development stages, valorisation of higher atmospheric CO_2 concentrations, regulation of nocturnal respiration, etc. The uncertainty of climate change and its variability adds further complexity to the process of defining plant ideotypes (relative weightage of adaptation traits) and their construction (hierarchy of genes and gene networks to be considered). Given the logistical and temporal difficulties that would arise from the evaluation of all new trait combinations in in situ experimental conditions, it becomes essential to make use of *ex ante* methods based on modelling and simulation to evaluate new ideotypes. The example of variation of the effect of drought tolerance QTL in maize, according to target environments (Box 10) shows the importance of such an assessment. There is still a long way to go before we can integrate multidisciplinary knowledge and understand complex biological reality in order to develop innovative production systems which combine varietal innovation and innovative cropping practices (Hammer et al. 2010; Passioura 2012; Tardieu 2012; Parent and Tardieu 2012). This complexity is further multiplied when perennial plants are considered.

Another area where modelling and simulation can guide plant breeding is the characterization of the target population of environments (TPE). Environments can be characterized, not in terms of the variation of classical physical descriptors (temperature, rainfall, solar radiation, soil water retention capacity, etc.), but also in terms of their impact on plant performance (target yields, stress indicators during the cycle, efficiency of resource use, etc.). The characterization of upland rice and maize growth environments in central Brazil using the Sarra-H model (Dingkuhn et al. 2003) is a good example of TPE definition (Heinemann et al. 2008).

Box 10. Modelling gene-phenotype at the stand level

A major challenge in predicting the performance of a genotype (G) in a range of environments (E) is the taking into account, at the level of the entire plant, of a multitude of G × E interactions at more basic levels: of the gene, molecule, cell and organs, throughout the entire growth cycle (Cooper et al. 2009). This is especially significant considering that the analysis of the contributions of 10 genes with two alleles in 10 environments would lead to an examination of $3^{10} \times 10$ combinations! Another approach based on biophysical simulation models has been developed over the last 20 years in order to meet this challenge. Integrating physiological processes and their genetic control, these predictive models can integrate G × E interactions at different levels of the organism (Messina et al. 2009). They also allow us to explore in silico a large number of genotype combinations (alleles at many loci) and environments. However, the simulation of the effect of genes/QTL for complex traits such as the response of the plant's growth and architecture to the environment requires modelling physiological processes that remain stable irrespective of the environment (Tardieu 2003; Hammer et al. 2006).

This approach was recently tested to predict the behaviour of maize vis-à-vis drought (Chenu et al. 2009). The leaf elongation rate (LER) is a major factor in maize's response to water stress. It is the same for anthesis-silking interval (ASI). Several QTL that control LER and ASI were mapped, and Reymond et al. (2003) were able to simulate and validate the effect of these QTL in different environments for new lines defined by their genotypes for these QTL. Welcker et al. (2007) have shown that several LER and ASI QTL co-exist. Chenu et al. (2008a) subsequently incorporated the leaf elongation model (which functions at the organ level with time steps ranging from a minute to an hour) in another model (APSIM-Maize) that works at the level of the stand and incorporates more complex population × environment interactions (Fig. 1). The APSIM model thus complemented was used to simulate the effect of LER on soil water reserves throughout the plant cycle. It was validated by comparing experimental and simulated results of a hybrid maize variety in different environments, for leaf surface area, biomass and grain yield. Finally, Chenu et al. (2009) used this model to simulate the impact of LER QTL on maize yield under different drought conditions. This simulation showed that the two major QTL, having similar effects on LER, affect yield differently under water stress. The authors thus demonstrated that robust gene-phenotype models can be used as decision-making tools to select traits (and associated QTL) based on target environments.

This example outlines a two-step selection process for adaptation to environmental conditions: first, the genetic analysis of traits that boost resilience to environmental conditions, resulting in an agronomic value for alleles, and second, the creation of ideotypes adapted to a given region, based on the combination of these alleles. The first step is based on phenotyping platforms that help the genetic analysis of a large collection of plants under varying conditions. These platforms, whether in greenhouses or fields, involve semi-controlled conditions and continuous measurement of environmental conditions and responses of plant materials. The second step comprises an in silico search of alleles favourable to a given situation (taking the results of the previous step into account), followed by the testing of a limited number of promising combinations in field trials. These trials are accompanied by a frequency study resulting from the simulation of the productivity of genotypes with different allele combinations. This simulation helps predict the frequency at which a combination of alleles is favourable in a given region and cultivation system (Tardieu 2012).

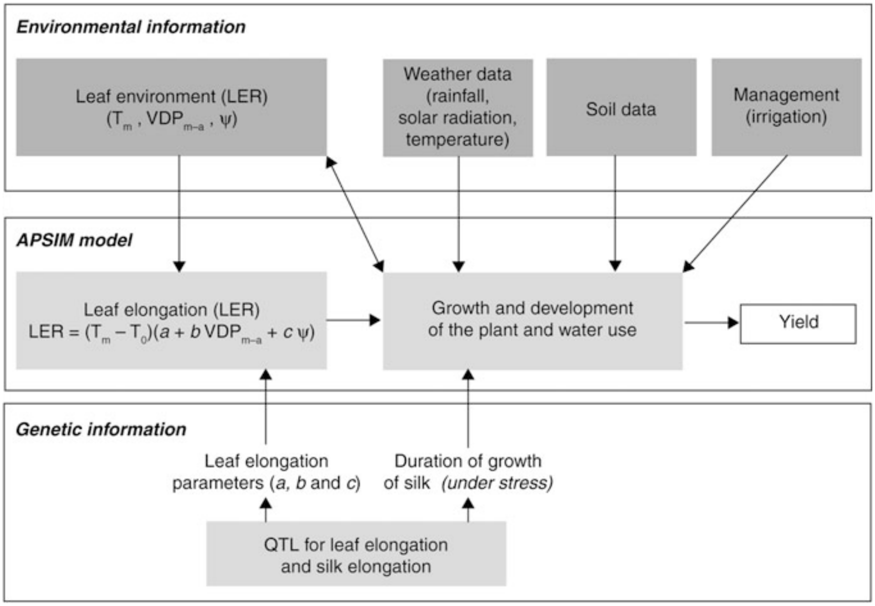

Fig. 1 Schematic view of the 'gene-phenotype' model showing how the leaf elongation module interacts with other components of the APSIM model (adapted from Chenu et al. (2009))

Environmental and genetic information is used as input to simulate leaf growth, plant growth and development, and grain yield of the crop. Leaf elongation (LER) is a function of environmental factors of the leaf: temperature of the meristem (T_m), base temperature (T_0), water vapour pressure deficit between meristem and surface area (VPD_{m-a}), the leaf water potential at dawn (ψ), and leaf elongation parameters (*a:* rate of LER potential; *b:* response of LER rate at VPD_{m-a}; *c:* response of LER rate at ψ).

3.2 Rethinking the Varietal Innovation System

Plant breeding in the twenty-first century has to contend with a context of rapid global changes (climatic, technological, etc.) and a multitude of often divergent requirements of decision makers and users (civil society, governments, farmers, processors, distributors, consumers, etc.). It also has to take into account the increase in the number of actors involved in the production and distribution of varieties and associated knowledge (national and international research institutions, private seed companies, NGOs, farmer organizations, etc.) and the increase in the number of stakeholders who fund the production and dissemination of plant varieties (national governments, international organizations, charitable foundations, producer organizations, etc.). In such a context, the dissemination of genetic progress in the form of new varieties is no longer a linear and unidirectional process, moving from the geneticist-breeder to the farmer via agricultural extension services or seed companies. This dissemination takes place rather within a complex innovation system that requires the convergence of views and interests of a large number of stakeholders. The proper functioning of this system depends on freedom from technological bottlenecks (e.g., incapability/difficulty of adapting processing equipment to traits of the new variety), regulatory impediments (e.g., standards to distinguish homogeneity and stability of varieties which prevents the marketing of varietal mixtures), commercial restrictions (e.g., use of hybrid varieties requiring the purchase of seeds for each cropping cycle) or ideological resistance (e.g., out-of-hand rejection of genetically modified organisms). The transformation of a varietal prototype developed by the breeder into a varietal innovation that is disseminated widely and quickly among farmers thus requires several back-and-forth cycles between stakeholders. Such exchanges allow each stakeholder to evaluate the constraints and the opportunities associated with the adoption of the new variety. Constraints in terms of altering practices (e.g., in order to adopt an F1 hybrid rice whose seed price is much higher than that of line varieties, a farmer must reduce planting density and thus change the seeder) and opportunities in terms of income and organization of work (e.g., the adoption of the F1 hybrid rice variety results in increased productivity and shorter cycle time, facilitating the establishment of the next crop).

If the objectives of ecological intensification are taken into account, the varietal innovation system becomes even more complex. Indeed, the optimization of biological interactions involved in the adoption of this new production model requires a clear contextualization of varietal solutions (taking into account not only soil and climatic conditions, but also production systems, succession and intercropping, processing, etc.). We thus have to proceed in stages and/or decentralize the process of creating and evaluating varieties. However, this complexity is also an opportunity to incorporate local knowledge, something that is particularly difficult to formalize in the context of family farming in the South.

The process of breeding and dissemination of varieties has to change from the breeder-extension officer-farmer triptych to a more complex innovation system. This constitutes a challenge for the breeder who must manage and coordinate the mobilization of a wide range of knowledge and skills to design future varieties (ideotype/prototype) and who must then create and evaluate prototypes and promote the resulting innovation. To this end, we would have to study action models proposed by the sciences of analysis and creation of innovation systems in other economic sectors in order to adapt them to varietal innovation (Klerkx et al. 2009; Berthet 2010).

4 Mechanisms to Help Meet the Challenges of Ecological Intensification

Faced with these challenges, we must find more nimble ways to undertake plant breeding for the benefit of farmers and for leveraging agrobiological interactions in different environments and for different plant species.

Plant breeding can be made flexible, quick and responsive, on the one hand, by using the knowledge and ability to manage important genetic factors and, on the other, by producing populations with a large genetic base and at a high enough analytical resolution. This would allow the creation of material that is adapted to a broad range of farming systems.

To be really beneficial to farmers, plant breeding must progress with them through a better understanding of their limitations, aspirations and practices. It must draw on strengthened interactions and partnerships for joint design and joint validation of new material. The material produced by the breeding programme should incorporate characteristics of their preferred material and offer incremental improvements over varieties in use.

In order to valorise agrobiological interactions, plant breeding must be considered in terms of traits that are known/expected/proven to be favourable, and must include regular tests and implementations in interactive situations. In particular, it must strengthen breeding methods for complex crop stands that are composite mono-specific populations or have multispecies associations.

In order to be efficient in different environments, plant breeding will have to incorporate analyses of the diversity of environments and rely on the modelling of methods of local adaptation in the broadest possible overall environmental diversity.

In order to be implemented for large array of plants, plant breeding will have to adapt itself to work in stages and with numerous partners. It will have to include amongst its outcomes a provision of access to genetic resources described in the most relevant way possible, or provide rapid characterization to guide the efforts of stakeholders.

The principal elements of the process include a systematic mobilization of the diversity of genetic resources; appropriate partnerships and innovative ways of collaboration; and shared research objectives and questions to bring different disciplines closer together.

4.1 A Systematic Mobilization of Genetic Diversity

4.1.1 Structured Access to Genetic Diversity

Genetic diversity forms the basis of all genetic progress. Viewed as such, it has become a strategic issue, and sometimes even the source of political tensions. Some international initiatives aim to maximize access to global genetic diversity for a large number of species by offering representative samples of large collections created both on an ecogeographical and a molecular basis (Glaszmann et al. 2010; Billot et al. 2013). These ‘core’ or ‘mini-core’ samples are offered as references to different research stakeholders. This allows bringing together various traits in order to better understand the relationships between observed traits and to explore the link between behaviour and molecular polymorphisms. This concentrated diversity is also a gateway to global diversity, which can then be explored on the basis of trends observed in the reference sample (e.g., towards a geographical region rich in diversity or in sources of resistance, etc.). It can also be used to identify an even smaller sample (core sample) which can be used to represent the species in comparative studies or as a starting point for the intermixing of diversity.

It is the understanding of diversity, more than the describing of it, that will guarantee its best use. In the course of domestication, it was—and continues to be—influenced by natural selection and human selection in all their complexities. Also influencing it is the demographic history of cultivated populations, basically linked to the histories of the environment and of mankind. Understanding history helps identify situations which may have led to the emergence of unique genetic factors, and which can be utilized in new contexts through recombination. Sometimes the evolution of cultivated forms is achieved through successive jumps, related, for example, to the emergence of new hybrid forms or even new genomic configurations. This knowledge helps identify successful breeding directions, accompany or accelerate them, or even re-explore them on new bases. Histories of cocoa, coconut or banana all reveal episodes of genetic intermixing slowed down by an extended cycle or the pre-eminence of vegetative propagation (Loor Solorzano et al. 2012; Gunn et al. 2011; Perrier et al. 2011). These structuring episodes help inspire hybridization strategies for crop breeding. The analysis of contemporary situations helps clarify another level of evolution by throwing light on the current processes governing seed management and their diversity in societies (Leclerc and Coppens d'Eeckenbrugge 2011; Pautasso et al. 2013). Such an analysis helps us in the overall understanding of the dynamics of diversity.

4.1.2 Intensive Intermixing in Exploratory Populations

Why practice an intensive intermixing? Because retrospective analysis shows that intermixing has been the source of major advances. Recent studies on the domestication of rice in Asia show that it was carried out in eastern Asia on a local wild species and led to the selection of specific allelic forms for several genes distributed in the genome. It was the recycling of these alleles by spontaneous hybridization that allowed the replication of this domestication from wild rice species from South and South-East Asia (Huang et al. 2012). We can similarly say that cultivated wheat, cotton, bananas and peanuts originate from early crosses that combined different species. Moreover, conventional breeding produces new crosses between distant species, a fact made possible by the technology of in vitro culture to not only get, for example, disease-resistant genes (rice, barley, etc.), but also productivity-boosting genes, as was done in tomato (Gur and Zamir 2004) and in rice (Thalapati et al. 2012).

A detailed knowledge of the structure of diversity helps us create populations that will be able to host new variability traits through intensive intermixing, e.g., as *Multi-parent Advanced Generation Inter-Cross* (MAGIC) populations (Cavanagh et al. 2008), which consists of intercrossing a limited number (usually 4, 8 or 16) of representative genotypes. Another example is NAM-type focused populations, where NAM stands for *Nested Association Mapping* (Yu et al. 2008), made from recombinant lines derived from crosses between a central genotype and a series of diverse genotypes.

4.1.3 Detailed Information on the Genome, its Structure, Diversity and Expression

Genomics is a recent and growing discipline. It involves studying the functioning of organisms at the level of the complete genome. Genes and their arrangement in genomes are decoded and their role is explored by studying the genome's expression at the transcriptomic level, derived directly from this expression and its regulation, and at the proteome or metabolome level which are an indirect result of expression and regulation and are more related to the physiology of organisms.

Technological advances allow the rapid analysis of genomes on an increasing number of plants, even on those considered orphans until recently (Varshney et al. 2010).

The sequences of basic genomes are being decoded more and more rapidly, the latest being tomato and banana (D'Hont et al. 2012). This allows us to reconstruct the evolution of genomes and analyze the dynamics of gene families involved in the most important functions and metabolic pathways.

The extent of advances on the plants most commonly worked on is impressive. Thus, data on the re-sequencing of over 1,500 varieties of rice (446 wild rice species and 1083 cultivars) have recently been made public (Huang et al. 2012). Nearly 8 million polymorphisms are available for analysis, allowing a detailed description of the domestication of rice and a listing of the parts of the genome most responsible. Huang et al. (2010) were able to identify genetic factors that explained about 36 % of the phenotypic variation observed for 14 agronomically useful traits with this type of data.

Knowing the repertory of genes (30,000–50,000 per basic genome) one can analyze their expressions throughout development stages in different environmental conditions in order to identify genes that meet specific conditions and specific breeding objectives.

The analysis of the genome's structure and functioning opens up access to new features such as transposable elements (Kidwell 2005) and small RNAs, whose activity induces changes in the genome's expression, some of which are carried over to the next generation (He and Hannon 2004). This pertains to epigenetics, a field concerned with environment-induced changes that are usually reversible, but can sometimes be inherited. Epigenetics bears a troubled history, its reputation marred by the excesses of Lyssenko, but whose biological basis can shed new light on epistasis, heterosis and reproductive isolation, and thus encourage new paths in plant breeding (Tsaftaris et al. 2008; Durand et al. 2012; Paszkovski and Grossniklaus 2011).

The sheer stream of data generated by genomics poses a massive challenge to existing data processing capabilities and even those of data storage. Phenomics, a technological domain for describing organisms (phenotypes) in various conditions and at different levels (of the cell, tissue, organ, organism, stand, etc.) is also developing. It is also churning up data, albeit not as much as genomics, that is biologically and mathematically very complex. Just as technological changes have resulted in the creation of high-density, high-tech platforms, so too bioinformatics is being influenced by a realignment of strengths beyond the boundaries of traditional disciplines. It often brings together specialists in human health, evolution, animal, plant or microbial biology, much like the Computational Biology Institute in Montpellier, France, is doing (Box 11).

Box 11. Computational Biology Institute in Montpellier, France

Plant genomics projects are increasingly using new and very high-throughput sequencing technologies (*next generation sequencing*, or NGS) and high-throughput phenotyping methods. The application of NGS is not limited to the sequencing of new genomes; it can be used for genome re-sequencing and detection of genomic variations such as *single nucleotide polymorphism* (SNP) or transcriptomics. These projects generate a large quantity of information. Its integration, for association studies at the genome level for example, requires the deployment of innovative approaches for data analysis. The lack of software tools capable of dealing with ever-increasing volumes of data constitutes a major bottleneck.

In this context, the Computational Biology Institute (IBC) in Montpellier, France, is developing methods and software applications to analyze, integrate and contextualize biological data on a large scale in the fields of human health, agronomy and the environment. Several domains are involved: algorithms (combinatorial, numeric, highly parallel, stochastic), modelling (discrete, quantitative, probabilistic) and data and knowledge management (integration, workflow, cloud). The challenges are thrown up by the exponential growth of data, the complexity of the models as well as the heterogeneity and distribution of data and biological knowledge. In order to address these factors and make a concerted approach to solve this well-defined set of problems, the project is divided into five work packages. Each of them pertains to one key aspect of existing biological-data processing techniques: methods for high-throughput sequencing; advancing to the level of evolutionary analysis; structural and functional annotation of proteomes; integration of cell and tissue imaging with omics data; and integration of biological data and knowledge. Concepts (computational methods, mathematical models, etc.) and tools (software applications, platforms and databases, etc.) will be validated mainly with the help of agronomic applications (plant genomics, agriculture of the South) and environmental ones (population dynamics, biodiversity).

This work involves 57 permanent scientists, encompassing a broad spectrum of disciplines drawn from one private company and 13 public institutions in Montpellier, including CIRAD, the National Centre for Scientific Research (CNRS), the National Institute for Agronomic Research (INRA), the National Institute for Research into Computer Science and Automation (INRIA), the Institute of Research for Development (IRD), and the Universities of Montpellier 1 and 2.

4.2 An Integrative Approach to Biology

The phenotypic response of a plant, observed macroscopically (growth, development, transition from vegetative to reproductive phase, etc.), to stimuli or environmental stresses (light, drought, salinity, high or low temperatures, fertilization, disease, etc.) clearly results from the integration of diversity and the expression of a large number of genes. While the plant breeder seeks to identify and recombine the modules segregated in the progeny as best as possible, the major challenge in biology is to understand how metabolic pathways, cell signalling pathways and different developmental processes are linked to the expression of the genome, on the one hand, and to phenotypic expression, on the other. It is a matter of describing relationships that are intrinsic to the system under study by characterizing relationships that connect the system in its entirety to the systems that surround it.

A study group set up by INRA's scientific council concluded in 2004 (Charrier et al. 2005) that integrative biology is the new paradigm that must 'make sense' of the analytical and quantitative approaches of genomics. It must also help integrate the information acquired at different approach levels to elucidate and accord a significance to the processes studied. While the approach is still in the conceptual phase, it is expected to lead to new lines of thinking and to discover original epistemological directions. New methods and concepts are emerging. Investments in bioinformatics, stimulated by the 'mass' of data produced by genomics, together with new methodologies based on artificial intelligence and statistics have resulted in new hypotheses on genomics data and efforts to validate them. Various technological developments help improve the in vivo monitoring of metabolism and the detailed observation of functional ultrastructures of the living cell.

By equating plant communities to mass and energy exchange surfaces, the field of ecophysiology has been able to model the primary production of plant communities without delving into the underlying biological processes and their genetic regulation. By working at the level of the individual plant, this approach takes processes into account which control the distribution of assimilates and thus of the biomass between different parts of the plant that result from morphogenesis. They can only be understood through an architectural approach to plant growth. This has led to the development of the approach that considers communities or stands to be a collection of individual plants that interact among themselves, with their emergent properties reflecting the collective functioning of the population.

In integrative biology, genetics plays a pivotal role in determining the functions of genes in the expression of the phenotype by analyzing natural variation.

Large-scale studies in molecular biology highlight the dynamics of expression and co-expression that characterize interactions between genes as regulatory networks. At the same time, genome-wide association studies (GWAS) present statistical connections between genotypes (in terms of allele combinations) and phenotypes. These two types of studies provide aggregated information that could be put together with the help of mathematical modelling (Nuzhdin et al. 2012).

Plant models are simplified mathematical representations of biological and environmental interactions of the dynamics of growth and development of a plant or community. They represent the preferred tool to understand and predict genotype-phenotype relationships for complex traits such as phenotypic yield or plasticity (adaptability) (Dingkuhn et al. 2003; Hammer et al. 2006). However, most existing models do not contain the required level of detail of biological functioning. It is therefore necessary to emphasize explanatory approaches through an understanding of the dynamics of the processes that underlie the plant's growth and development. To this end, the modelling of morphogenetic processes of the whole plant, based on a source-sink relationship for carbon assimilates (Box 12), is a promising approach. It provides the bases for breaking down physiological functions that underlie changes in the main adaptative traits and for identifying genomic regions involved in the control of these functions.

Box 12. EcoMeristem: model simulating plant growth within the crop stand to support phenotyping and ideotype exploration

The EcoMeristem model (Luquet et al. 2006) formalizes the morphogenesis of the plant (rice, sorghum and other tropical grasses) and its phenotypic plasticity as a response to the abiotic environment in the stand or community. This formalization is done on the basis of equations whose genotypic parameters define a morphogenetic potential (phytomere height, tillering ability, phyllochron, etc.), physiological potential (radiation interception, carbon assimilation, leaf transpiration) and its regulation by the nutritional status (carbon, water) of the plant (threshold parameters and rates of regulation of potentials) according to its photothermal and hydrological conditions. The model thus formalizes hidden morphophysiological parameters that control the functioning of source and sink organs in response to the environment and the potential competition between sink organs for the same pool of resources within the plant. In this way, it formalizes the compensation and regulation of these processes which could result from their physiological and/or genetic connections.

Once calibrated on a panel of varieties representative of the species diversity, the model helps estimate the genotypic parameters mentioned in the model for any new variety studied by using a set of relatively simple experimental data. These genotypic parameters are supposed to be less influenced by the environment than the directly measured variables (Luquet et al. 2012a, b). EcoMeristem has thus been extensively used to analyze the phenotypes for growth and vegetative vigour of rice and sugar cane. In particular, its ability to represent the genetic diversity of behaviours related to vegetative vigour and susceptibility to water stress (stomatal opening) in a diversity panel composed of 200 *japonica* rice accessions has been demonstrated (Luquet et al. 2012a, b).

The parameters of the model are optimized for each of the 200 accessions of *japonica* rice and will now be used to identify the genetic bases of these parameters by genome-wide association analysis. Similarly, the range of values for the parameters representing the diversity of *japonica* rice will be used to define, in silico, varietal ideotypes for tolerance to water stress. The EcoMeristem model will be used in the ANR Grand Emprunt Biomass Crop for the Future project (2012–2019). It will be applied to phenotyping and ideotypaging sorghum—biomass for the production of bioproducts. These future applications involve linking it to 3D representation models of plants (Soulié et al. 2010). There are also plans to deploy a more elaborate photosynthesis model in order to access, depending on the application, additional architectural or physiological traits.

Recently, the fundamental concepts of the EcoMeristem model were simplified and integrated with the Sarra-H model (Dingkuhn et al. 2003) to create a new generation of agricultural models. The Samara model thus developed provides a simplified representation of source-sink relationships for carbon assimilates. It can simulate the plasticity and multiple yields (grain, sugar, and biomass) of tropical grass stands in a very elaborate representation of the cropping systems specific to its flagship species: rice and sorghum.

In the immediate term, the proposed models are assessed by genetic improvement practitioners in terms of their ability to simplify the representation of the inheritance of phenotypic behaviour by identifying hereditary modules with significant effects on the target phenotype.

These approaches should help effectively address not only conventional plant breeding objectives such as ‘adaptation to abiotic constraints’, but also new and very complex objectives. These can include the competition-mediation process, which underlies the improved performance of heterogeneous stands, or the plant’s interaction with elements of its surrounding environment, such as pathogens, pollinator insects, neighbouring plants, seed-dispersing animals, etc.

4.3 *Shared Purpose and Research Questions for a Bringing Together of Disciplines*

4.3.1 Ideotype

The ideotype is a concept originally proposed by ecophysiologists. It represents an ideal plant endowed with a set of traits that give it the best adaptation to a given agricultural system (of cultivation, of production). It originates from an initial understanding of associations between traits that form the basis of agronomic behaviour and is an intellectual construct similar to a model. Progress in this area helps improve simulations, place ideotypes in perspective based on environmental conditions, incorporate genetic factors identified through logical reasoning, and guides recombination programmes across breeding generations. In a wider sense, beyond that of biologists alone, the ideotype is a virtual object which combines the vision of researchers from different disciplines and of different stakeholders of agriculture, processing and distribution, or even of framers of public policy. It becomes an issue of sharing, participation, co-adaptation, or negotiation between stakeholders, which leads to shared representation and a phase conducive to innovation. This process starts with each stakeholder's objectives and relies on the analytical capabilities of researchers to assess feasibility and scientific opportunity, and on the ability of co-adaptation of different stakeholders. When considered fixed, the ideotype induces a planning process that has little to do with innovation. When considered as a result of iterations, it creates an opportunity for multidisciplinary synthesis and cyclic and programmatic communication and interactions capable of fostering innovation. It is through these interactive processes that the objectives of ecological intensification, their diversity and specificity can best be incorporated into varietal improvement programmes.

4.3.2 Populations Which are Vectors of Genetic Progress and Biological Resolution

The ability to produce new segregating populations based on an understanding of genomic diversity and recombination encourages research to produce populations which will be most likely to lead to genetic progress as well as fulfil the desire to better understand the genetic factors that can be best used by the breeding programme.

This approach leads to different options depending on the biological traits of the species under consideration. Vegetatively propagated species often represent an extreme situation. These species can benefit greatly from the dissemination of allelic diversity because of a strong heterozygosity, of complex and relatively unknown genetics, of a fragmentation of habitats or due to a limitation of exchanges for prophylactic reasons. Such dissemination can be organised by using reference samples that are cleared of their pathogens, or progenies of crosses between germplasms selected for their ability to replicate a broad and new diversity. Thus, DAD (*distribution of allelic diversity*, Lebot et al. 2005) opens up excellent prospects for crops such as cassava, yam, taro, or plantain banana.

Creating nested association mapping (NAM) populations, i.e., focused on a selected genotype, helps mobilize a broad-based genetic pool while maintaining a controlled analytical framework and a genomic interlace with high genetic resolution. The recombinant lines derived from crossing of the same key variety with a group of varieties having different and complementary traits give more control to genetic analyses and help better assess incremental genetic progress. Thus, the NAM populations have helped launch a new generation of highly informative analyses (Cook et al. 2012; Hung et al. 2012). The generalization of this kind of approach holds great promise.

As we move the 'focus' further towards a target genotype, producing introgression lines becomes possible by successive backcrossing assisted and accelerated by the use of molecular markers. Similar to what has been achieved at the level of the entire genome with the development of populations of chromosome segment substitution lines (CSSL) using interspecific hybrids in peanuts (Fonceka et al. 2009; 2012a, b) (Box 13) and in rice (Bocco et al. 2012), the rapid and systematic production of introgression lines on a gene pool with proven agronomic interest allows us to test the effect of the introgressed chromosome segment in the very genetic pool to which it will be transferred. Geneticists are thus able to get rid of epistatic relationships that usually render genetic analysis more complex, and to accurately measure the phenotypic impact of the introgressed factor. Similarly, biologists are able to understand pleiotropy from which a lot can be learnt and farmers are able to assess the usefulness of the applied change. These approaches have the benefit of simultaneously producing information that is directly useful and easily applicable in breeding, and material that could very likely be of use to the actors.

Box 13. Valorisation of wild species related to chromosome segment substitution lines: the case of peanuts

The cultivated peanut, *Arachis hypogaea,* is an allotetraploid derived from a recent hybridization between two wild diploid species, *A. duranensis* and *A. ipaensis*. This tetraploidy isolated it from a reproductive point of view from about 80 known species of the genus *Arachis*. Since the diversity available within the crop is limited, its expansion by crossing with wild relatives constituted an important aspect of the peanut's varietal improvement. The first step was to create synthetic tetraploids by crossing two wild species and by doubling the hybrid's chromosomes. A synthetic amphidiploid was thus developed by Empresa Brasileira de Pesquisa Agropecuária (Embrapa) in Brazil by crossing the two wild parent species, *A. duranensis* and *A. ipaensis*, of the cultivated peanut.

Based on this amphidiploid, CIRAD has embarked on an ambitious programme to create chromosome segment substitution lines (CSSL) with the dual objective of increasing the diversity of the cultivated peanut and of producing a material that allows the identification of genomic regions (QTL) involved in traits of agronomic interest. To this end, the Fleur11 variety that is grown widely in Senegal was selected as recipient parent. A genetic map (Fonceka et al. 2009) was constructed for the BC_1F_1 generation to monitor and control, using markers, the distribution of the introgression of wild genome in that of Fleur11 in subsequent backcross generations. A population of 122 CSSL lines was obtained (Fig. 2) at the end of the BC_4F_3 generation. It represented the entire genome of the wild species in the form of overlapping segments introgressed in a cultivated genetic background (Fonceka et al. 2012b). Most of the lines of this population (62 %) have a unique segment, thus making it possible to directly link observed effects to it through comparison with the cultivated parent.

In the course of development of the CSSL population, an advanced backcross population was used for an early detection of QTL for plant architecture, morphology of seeds and pods as well as yield components (Fonceka et al. 2012a). This revealed the existence of wild alleles having a positive effect on agronomic traits such as the number and size of grains and pods and pod maturity. In addition, some of the QTL identified were unlike any QTL with adverse effects and could, thus, be directly used for breeding purpose.

An initial study of CSSL has confirmed the usefulness of this type of population to dissect the genetic control of useful traits such as plant bearing and height (Fonceka et al. 2012b). In light of this study, plant bearing which hitherto was described as a relatively simple trait controlled by one to four genes, appears to be the result of a greater number of QTL. This leads to ‘crawling’ or ‘erect’ phenotypes and to their intermediates as seen in cultivated groundnut.

Developed in the framework of international collaboration and exchange of genetic material and through a major effort to integrate molecular markers in the breeding process, this CSSL population is an important resource for the discovery of favourable wild alleles and the study of the genetic control of agronomically useful traits.

4.3.3 Diversifying the Species Worked On

European history is studded with examples of power plant breeding (Stamp and Visser 2012). It only took a century following the blockade imposed by the British navy on Napoleon 1’s French empire to transform fodder beet to sugar beet, a temperate-zone sugar crop to rival tropical sugar cane. In less than 50 years, the quality of rapeseed was radically improved, mainly by reducing its erucic acid content, in response to a directive from the European Union. In less than 40 years, soy has been adapted to the European climate to become an economically viable crop north of the Alps. With the help of tools like molecular markers, reproductive biology and physiology, plant breeders are now able to adapt an annual crop to completely new conditions or requirements in less than 25 years if the necessary research is undertaken, genetic resources are available and the context of the agricultural system is conducive.

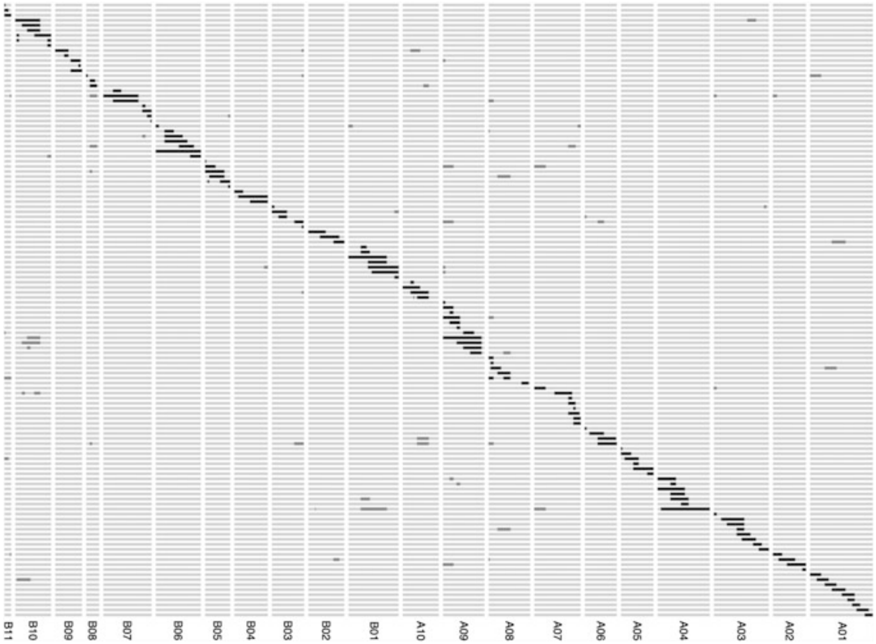

Fig. 2 Graphical genotype of 122 chromosome segment substitution lines (CSSL) in peanut. The 21 chromosomes A01–A10 and B01–B11 are represented on the abscissa. The *122 lines* are represented on the ordinate. The *white* chromosomal areas represent the cultivated gene pool; the *black* areas represent the segments substituted by the wild genome; the *grey* areas represent wild additional chromosomal segments (unintended)

Without seeking to expand the area of distribution or changing uses, an attempt can be made to maximize the value of species that are identified as largely underutilized. These can be revisited with new analysis methods. Public research institutions should probably undertake a new generation of research on a number of chosen plants, such as fonio (*Digitaria exilis* Stapf, *D. iburua* Stapf), considered to be the oldest cereal in West Africa. Currently grown from Senegal to Lake Chad, it is adapted to dry and low-fertility environments, is not labour-intensive, and can bridge the hunger gap before the harvest of a major cereal with its high nutritional value (Vodouhè and Achigan-Dako 2006). Its rehabilitation raises issues linked not only to genetics, but also of integration into cropping, processing and distribution systems, as also of perception of rural and urban consumers.

Similar tools and approaches can be adapted to numerous plants that are currently neglected, such as service plants that make decisive contributions to the sustainability of cropping systems. Public agricultural research cannot probably handle all the genetic improvement programmes that appear useful. It can, however, share its tools and sign up partners for work that is simple but with very high added value. It can provide these partners with some molecular markers (cytoplasmic and nuclear), facilities for in vitro culture and cytology, seeds conservation capacities, etc. We could soon witness the sequencing of genomes of representative samples of genetic resources being offered as a service.

Agricultural research could also arrange for training by drawing on its experiences—including on work currently under way within ARCAD[1] projects supported by the Agropolis Foundation. This is particularly relevant with regard to strategies for exploring genetic diversity, the associated survey methodologies and modalities for accessing and sharing this diversity, all of which are components that promote processes likely to lead to a real leveraging of local knowledge.

4.3.4 Experiments in Genetic Improvement of Complex Crop Stands

The challenge of breeding for complex crop stands, i.e., mixtures of several genotypes of the same species or of associated crops, also needs addressing. But, as we pointed out, if we take biological interactions into account, we literally flood the matrix of conditions that need to be compared in order to make a choice similar to those in conventional breeding.

Developing near-isogenic material in the context of incremental breeding provides the opportunity to use very similar genotypes. These genotypes differ only in some behavioural aspects that are easy to characterize as the isogenic lines have few genes that differ.

An approach of a progressive and iterative exploration from an initial existing system becomes easier to adopt with the use of such material with discontinuous genetic variation (e.g., inbred lines) and which is limited in scope (e.g., near-isogenic). This facilitates experiments in a space where complexity is reduced to situations that can be identified by the experimenter, thus accelerating a global empirical approach.

Complementation tests can be carried out in mono-species populations for plant shape, root establishment, early vigour or other traits that differentiate the genotypes used. Maintaining a finite number of variable components helps draw conclusions based on genetics and ecophysiology, and reuse them in a simple way in succeeding generations and in models used to explore what is achievable.

The same reasoning applies to multispecies stands. The evaluated parameters have to characterize the quality of co-adaptation between genotypes of associated species. The Fabatropimed[2] project, supported by the Agropolis Foundation, provides an interesting framework to encourage breeding measures for cereal-legume association. It provides a multidisciplinary framework for the functional characterization of the benefits of the system's fertility.

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[1] Agropolis Resource Centre for Crop Conservation, Adaptation and Diversity, http://www.arcad-project.org/about_arcad (retrieved: 6 May 2013).

[2] http://www.agropolis-fondation.fr/ (retrieved: 6 May 2013).

4.4 Tools and Methods to Accelerate the Creation of Prototype Plants

4.4.1 Fine Control Over Recombination

Methods for controlling the recombination of genomes within populations continue to progress with advances in high-throughput genotyping and statistical methods. Marker-assisted recurrent selection (MARS) has already been discussed (Box 8). An extreme version of the application of genome marking is ‘genomic selection’, where the value of candidates available for selection is no longer determined on the basis of the genotype with a small number of QTL, but by estimating the effect of thousands, or even hundreds of thousands, of markers on a phenotype. The absence of a priori assumptions about causal relationships between markers and target traits allows the breeding of complex traits whose genetic basis is not completely known (Heffner et al. 2009).

At the same time, marker assisted selection allows massive and rapid transfer of targeted alleles or chromosomal segments from one gene pool to another and to test the transfer’s phenotypic impact. It thus provides new insights on the effects of pleiotropy and epistasis and consequently leads to a better understanding of agronomic behaviour and biological processes that underlie them, while producing material of great agronomic utility.

4.4.2 A Parsimonious Use of Genetic Transformation

Altering the genetic makeup of plants by inserting one or more new genes in their genome (transgenics) is a new form of hybridization. It allows the exchange of genetic information between organisms that cannot do so by conventional reproductive means. This brings us emphatically into the realm of GMOs. Few topics in recent times have engendered such fierce debates as GMOs. However, these debates remain inconclusive and unproductive since the concept is as yet vague and the context includes rapidly evolving technologies, high economic stakes, conflicting and changing laws, and public controversy between very active stakeholders.

The first GMOs resulted from using rather primitive technologies, leaving large traces in the genome and integrating copies of the transferred gene in indeterminate numbers and sites. Recent methodological advances have made it possible to envisage gene ‘surgery’, i.e., to make the desired changes with perfect accuracy. Examples include adjusting the expression of a pre-existing gene or replacing a gene by an allelic version from elsewhere by changing some targeted nucleotides—or even just a single one amongst hundreds of millions or billions (depending on the species) that the genome contains. This is the goal of Genius project, funded in the framework of the “Investment d’avenir” initiative, dedicated to develop new technologies to 'breed varieties that are more resistant, less polluting and better adapted to consumer needs.'[3]

Research in biocellular and biomolecular technology therefore promises a future with far more efficient genetic engineering and opens an almost limitless range of possibilities. Considering this, it is important to translate aims into precise objectives of genetic progress before selecting the technique to achieve these aims. A finer and more comprehensive analysis of the diversity of genetic resources will often lead to sources of high-value diversity that can be mobilized by conventional breeding. Only occasionally will it be found necessary to rely on genetic engineering to help incorporate some new traits into the plant material. Analyzing the issue, the partnership framework, expected benefits and their recipients, risks and their origins—such as biotechnical challenges—will help gauge the ethical relevance of such a path.

4.5 A Decentralized Distribution of Plant Material

Once a new 'improved' variety is created, it has to be maintained and propagated, and disseminated to potential users. The modalities for such maintenance and propagation depend, on the one hand, on the reproductive pattern of the species (sexual self-pollinated, sexual cross-pollinated, asexual) and, on the other, on the variety's genetic structure (homozygous and stable over generations of sexual propagation or heterozygous and unstable). Dissemination modalities also have to include an economic angle, as it is usually through the sale of seeds that the investment made in the plant breeding activity can be recovered.

Self-pollinated crops (wheat, rice, soyabeans, etc.) disseminated as homozygous varieties (pure lines) are the easiest to distribute. Because of their stability over generations, these varieties can be reproduced from year to year on the farm. This is clearly beneficial for the farmer but poses a threat to the breeder of the variety if equitable compensation mechanisms are not put in place. The situation is similar for species with asexual or vegetative reproduction (banana, yam, cassava, etc.). Moreover, vegetative propagation allows the maintenance of the same heterozygous genetic structures.

Cross-pollinated species, on the other hand, often with heterozygous genetic structures, are difficult to maintain and disseminate. Farmers must procure their seeds every year, a fact that translates to an economic opportunity for the breeder but creates a dependency for the farmer. Maintenance and dissemination difficulties increase when varietal improvement of a species (cocoa, teak, mahogany, coffee, rubber, etc.) relies on unique heterozygous genetic entities and on their

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[3] http://media.enseignementsup-recherche.gouv.fr/file/Fiches_biotech_bioressources_2/93/4/GENIUS_208934.pdf (retrieved: 6 May 2013).

dissemination by vegetative propagation—which is not their normal way of reproduction.

The choice of the procedure through which new varieties are developed is therefore not inconsequential. Public research must, on the one hand, analyze its impact in terms of access to genetic progress for various farmer categories. On the other, it should strive to reduce seed production costs and prevent monopolistic situations that arise from exclusive control of the production and dissemination of seeds.

Heterozygous genetic structures often present genetic and agronomic advantages: higher and more stable yields, homogeneity, speed of combination of favourable dominant genes in the same genotype, etc. They encourage breeders to increasingly use hybrid varietal formulas, even for self-pollinated species (Gallais 2009). Mastery of apomictic reproduction would help propagate these hybrids at the farm without a risk of altering their genetic structure (Box 14). The use of techniques to produce hybrid seeds in perennial plants that are based on the use of male sterility, already widely used for annual plants, would allow the production of hybrid seeds on a large scale in these species (Box 15). The development of somatic embryogenesis techniques would lead to the massive propagation of exceptional heterozygous genetic entities and the diversification of actors in this propagation, a factor of self-sufficiency conducive to a more intensive and diverse agriculture (Box 16).

Box 14. Apomixis: decentralizing the exploitation of hybrid vigour

Apomixis is the ability to produce seeds that contain only maternal genetic heritage. It can thus be compared to vegetative reproduction, but with a difference—it is disseminated by seeds. This possibility of identical reproduction is especially helpful for the use of hybrid varieties in self-pollinating as well as cross-pollinated species. It avoids the need to continuously renew seeds from parental lines, which would push up seed prices and require the existence of a well-organized seed industry. Apomixis also helps seed producers maintain elite genotypes from cross-pollinated species without pollen isolation. The introduction of the apomixis trait in major food crops (maize, wheat, millet, rice, etc.) would therefore be an effective way for expanding the use of hybrid vigour over a larger cropping area (Hoisington et al. 1999).

The phenomenon has been observed in many botanical families. There are several types of apomixis (apospory, diplospory and adventive embryony), ranging from an embryo formed immediately after the interruption of meiosis in megaspore mother cells to an embryo formed from cells of the nucellus or the ovule.

A good amount of research is needed to understand the molecular mechanisms of apomixis for its use to become more widespread in breeding programmes and seed reproduction (Grimanelli et al. 2001). Currently, such research is mainly the preserve of the private sector, leading to patents, especially for methods aimed at increasing the percentage of apomictic seeds from plants that reproduce sexually or from facultative apomixis. It is important for public research programmes to invest in this field of reproductive biology which promises a ‘democratization’ of the use of hybrid formulas.

Box 15. Seed production based on self-incompatibility or genetic male sterility

In the reproduction of many cultivated cross-pollinated species, it is almost impossible for male and female gametes produced by the same plant or plants with identical genotypes to produce viable zygotes (Gallais 2009). This is self-incompatibility. This feature is used by breeders of perennial crops, such as coffee and cocoa, to obtain hybrids between complementary clones (Charrier and Eskes 1997). The two clones are planted together in ‘seed fields’ in order to obtain these ‘hybrid clones’. This was how hybrid clones derived from research on cocoa by CIRAD and its partners were disseminated in Côte d’Ivoire, Togo and Cameroon at subsidized rates. More recently, the rootstock variety Nemaya (species *Coffea canephora*) which is multi-resistant to nematodes was reproduced and disseminated as seeds by the Asociación Nacional del Café of Guatemala (Guatemalan National Coffee Association or ANACAFE) (Bertrand et al. 2000).

Another reproductive technique which can be readily popularized is based on the use of male sterility. The plants undergo mutations in the genes involved in the development of reproductive organs, leading to male sterility (no stamen, no viable pollen grain, etc.). Although rare, sterile male mutants have been found in all cultivated species which were subject to such research (Gallais 2009). In perennial plants where vegetative reproduction is also possible, the sterile male mutants can enter the hybrid composition of clones and be used through the system of seed fields described above. CIRAD did just this with a sterile male of the arabica coffee to produce a hybrid variety.

The genetic determinism of male sterility is generally simple, making it possible to rapidly locate and clone the gene responsible, and to ensure the transfer of a variety (or clone) to another with the help of marker-assisted selection or genetic transformation.

Both these techniques of seed production and valorisation of heterosis are relatively simple to use and can be easily implemented in other species and transferred to producer groups.

Box 16. Somatic embryogenesis

Somatic embryogenesis is a technique of in vitro culture based on the ability of some species to develop embryos from one or more somatic cells. These embryos, when placed in suitable culture conditions, grow to plants in a morphogenesis similar to that of the zygotic embryo, which is itself derived from sexual fertilization. Somatic embryogenesis allows the multiplication of clones whose unit production cost by conventional methods is otherwise high, and of genetically transformed individuals which, in some cases, cannot be propagated sexually.

It is possible to carry out in vitro culture in large containers, or bioreactors, and produce over a thousand seedlings per bioreactor. CIRAD has developed such devices for the production of coffee plants. Its plastic bioreactor (Matis) is inexpensive and easy to use, and ensures competitive costs for producing germinated somatic embryos (<0.50 Euro) (Etienne et al. 2012). Once developed in a bioreactor, the seedlings are planted on a horticultural substrate.

The major challenge now is to transfer the tools to producer organizations or to private companies. For this to be possible, the culture media and procedures will have to be simplified further, phases of autotrophic conditions increased and horticultural phases also simplified. In addition, stakeholders will have to be involved in these simplification processes through participatory approaches. For example, to make the technology more accessible, it is envisaged to build laboratories using natural light to provide heating and lighting. This would reduce the time required to obtain autotrophic embryos that germinate directly in the bioreactor.

4.6 A Renewed Varietal Innovation System

Industrial innovation systems are based on two main innovation models: through dissemination or through incentives (Akrich et al. 1988). The dissemination model assumes that the new object can disseminate by itself, by contagion, due to its intrinsic properties. It further assumes that its use presents the same benefits to everyone and in all places. In contrast, the incentive-based model assumes that the fate of the new object depends on the possibilities of simultaneous evolution of the innovation and the social environment that adapts and adopts it. The fate of a project thus depends on the alliances it forms and the interest it evokes, leading to the conclusion that no criteria or algorithm ensures, a priori, its success. Rather than discuss the rationale of decisions, we must speak of the convergence of interests that they can, or cannot, produce. Innovation is the art of evoking interest in a growing number of allies who, in turn, make you stronger (Tidd and Bessant 2011).

This attention to innovation process clearly explains the successes and setbacks of the creation and dissemination of new varieties over the past 50 years. And it is even more necessary today since ecological intensification entails a greater valorisation of G × E × cropping-system interactions. When a wider range of situations is taken into account, the probability that any one variety would present the same advantages and ease of use to everyone and at every place is reduced. Similarly, an adaptation to ecological intensification would also probably lead to disruptions of varietal traits. This would require major changes and/or disruptions in user practices and thus the adoption of innovative models that open doors to numerous fruitful exchanges between developers and users, as well as to adjustments and initiatives that mobilize local knowledge. These issues are explored more extensively in Chap. 7.

It is therefore necessary, more than ever, to establish platforms for dialogue and participatory action with all stakeholders to formalize their expectations and motivations. This will also help define with them the specifications of new varieties and evaluation and feedback methods, including their environmental and social externalities. Given the increasing diversity of scientific disciplines to be mobilized, it is also necessary to formalize, within research teams, the nature and sequence of knowledge to be developed as well as the methods, tools and actions necessary for developing prototypes for varietal innovation.

In such a context, the plant breeder is expected to play the important roles of initiator-coordinator of dialogue and of integrator of knowledge for varietal innovation. By observing and tracking the impact, he will help in the proper recognition of the roles of the various stakeholders in the innovation process and help share the resulting benefits equitably.

The establishment of such renewed varietal innovation systems depends on supportive and incentive-based policies from sponsors as well as from research institutions involved in varietal innovation. Beyond these incentives, it is necessary to ensure the implementation of *ex post* monitoring-evaluation procedures for assessing the impact of new varieties, especially in the context of family farming.

5 Conclusion

For a long time, plant breeding activities have been undertaken in an agricultural context of artificialization and standardization of the crop environment. Up to now, only a limited number of target environments were even considered. Plant breeders optimized the use of resources and practices—population size, selective pressure, etc.—in this configuration. This approach was very effective in applying quantitative genetics and in according limited importance to the biological fundamentals of variation in traits and adaptation. Recent technological and methodological developments in the field of genomics now offer plant breeders new capabilities in analyzing the traits' genetic architecture and biological adaptation mechanisms. They also have a better understanding of the dynamics of diversity and adaptation during domestication. New partnerships are also being explored, incorporating more participatory methods, in order to diversify the environmental frameworks of intervention and fine-tune the adaptation of the final products. Some methods of decentralized dissemination are already available or will be soon.

In the context of ecologically intensive agriculture, plant breeding must also address more diverse needs and take into account more complex biological functions which are in interaction with other organisms of the cropping systems. In some cases, these functions can be explained by specialized research and can be translated into absolute selection criteria (e.g., an intrinsic ability to use mineral resources). In a majority of cases, however, new and multifaceted phenotyping methods of unprecedented complexity will have to be implemented, ones that use biological interactions.

Plant breeding must also expand its scope to include a greater number of species in order to encourage a general expansion of the biological bases that agronomists and farmers rely upon.

The search for continued technological and methodological improvements and their use in sustaining existing dynamics will help address some of these challenges. We must, however, affirm and strengthen plant breeding in some of its reorientations and initiate newer ones.

Genetic diversity should be actively and systematically mobilized, based on a better description and understanding of this diversity and with the help of a rapid and accurate management of genomics. The modelling of biological systems must help translate a greater number of complex biological objectives into traits that can be inherited and selected for breeding.

The systematic creation of populations centred around established varietal types (known as 'quasi-ideotypes') will help provide opportunities for incremental breeding that will not lead to agroecological destabilization. These 'progressive' populations will be accessible to all actors for analysis and qualification.

We will have to expand the range of species we work with to include new ones, especially service species and/or those that have not been—or are as yet little—domesticated. Our range of breeding objectives and conditions under which we undertake breeding should also be expanded. Plant breeders should focus on developing new skills in multigenotypic breeding for using internal complementarities in order to create complex crop stands which are conducive to ecological intensification.

Associations with farmers—in their roles as intermediaries or full partners—must be strengthened and simplified. This will require an analysis of roles of all actors, a translation of methods and a structuring of partnerships in order to optimize the process of innovation as a whole, including the fine-tuning of the innovation to the local context. Dissemination methodologies and approaches will remain important issues and a source of determinant technological options.

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