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Changes in the concept of genotype × environment interactions to fit agriculture diversification and decentralized participatory plant breeding: pluridisciplinary point of view

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Abstract The standardization of environments (E) encouraged by modern society and by the productivist model of agriculture has resulted in the standardization of genotypes (G) thereby reducing G × E interaction. New societal values call for the diversification of agriculture to fit contrasted environments. This process can be depicted by four models defined by two axes, one socio-economic (individual logics versus collective governance), and the other agro-ecological (reductionist versus systemic approaches). These models differ in (i) their objectives (from improvement in yield to the empowerment of farmers), (ii) their specific expectations with respect to genotypes (from inherited genetic resources to varieties that represent genetic, ethical and social progress), (iii) their specific representations of the environment (E) (from a simple interaction between the bio-physical environment (B) and the crop management (C), to a complex interaction including the competences of the actors (A), outlets (O), regulations (R), society (S)), (iv) their particular relations between G and E (from G × E to G × B × C × A under evolving constraints represented by R × O × S). Taking this diversity into account changes the way plant improvement is considered. Thus, depending on the model, the order, interest and status of the five classic stages of plant improvement (setting objectives, creating variability, selecting, evaluating and disseminating) may be called into question. Between the existing analytical model (Model I) and a holistic model (Model IV) which remains to be developed, lies the challenge of ensuring the sustainability, efficiency and acceptability of plant breeding and resulting innovations. From a simple "statistical parameter" that we, as plant breeders, attempt to reduce, the G × E interaction is becoming an "objective" that we try to predict and valorize. Structuring the different components of E, G and G × E, enables us to extend the basic concept of representivity to both the cultivation conditions and the relational socio-economic positions of the actors involved.

Keywords Plant breeding · Sociotechnical approach · Diversity of agricultural models · Heterogeneous environments · Representivity · On-farm selection · Ex-situ/in-situ

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Abbreviations

A	Main *a*ctors (competences & resources)
B	*B*io-physical environment
C	*C*rop management
O	*O*utlet, market
G	*G*enotype
E	*E*nvironment
G × E	*G*enotype × *e*nvironment interaction
R	*R*egulations, coordinating structures (public policies, public or private standards, etc.)

Introduction

The scientific term “Genotype × Environment Interaction” (G × E), is used in biometrics, quantitative genetics, and agronomy and recovers different meanings according to each domain. Respectively, G × E (i) represents a deviation from an additive model of G and E effects (Gauch 1992), (ii) signifies that “depending on the environment, all the genes belonging to one genotype will not be expressed in the same way” (Gallais 1990), (iii) indicates whether a variety is suited to a particular growing environment (Nolot 1994).

In industrialized countries and especially for arable species, which represent the context of this paper, a variety (G) is defined by legislation as being distinct, uniform and stable (DUS). The environment (E) is described by the biophysical components (soil, climate) of the field homogenized by an intensive cropping system. The evaluation of a variety principally focusses on the yield and the industrial quality.

But new demands are emerging, responding to and in turn demanding a diversification of agriculture. Consequently, G × E is today increasingly, and in different ways, becoming the concern of all the actors in a given agricultural sector. Although G × E classically has been considered by plant breeders to be a “major obstacle to progress in genetics” (Lefort et al. 1979), G × E interaction is perceived (i) by the consumer to be a source of a specific quality linked to a local territory; (ii) by the farmer to be a way of breaking away from the standardization of crop management and of markets; and, (iii) by the citizen as a biodiversity issue linked to questions of identity, policy and legislation.

These different ways of looking at the relation between a cultivated plant and its environment led us to broaden our vision and to consider the G × E relation not only in a biotechnical space but also in a social space. Today both are undergoing profound changes that result from the diversification of production systems and markets, and from contradictions and tensions related to the sharing of skills and power among the actors concerned. The aim of this paper is to explore the impact of those changes in the ways of thinking about G × E interactions. To achieve this aim and give a pluridisciplinary point of view, researchers, from genetics, agronomy, biometrics, sociology and anthropology domains, share here their perception of the terms G, E and G × E to question plant breeding for organic and low-input agriculture.

The first section of the paper reviews two changes in the concept of “Nature” and of the relation between a cultivated plant and its environment (G × E) in the context of the upheavals agriculture has undergone in the twentieth century. The first change, which appeared together with the industrialization of agriculture, corresponds to a change from natural diversity (i.e. uncontrolled Nature) to uniformity imposed by legislation, technical progress, etc. The second change corresponds to the recent recovery of interest in “desirable” diversity, envisaged as a strategy for sustainable agricultural development and social progress. In the second section, the diversity of current agricultural models is linked with different ways of thinking about G × E interactions. The complementarity of models and the tools and resources needed to control and valorize interactions are discussed. Finally, procedures to enable a move from imposed uniformity to desirable diversity are envisaged through renewed plant breeding schemes that integrate decentralized participatory plant breeding.

G × E: from natural diversity to desirable diversity

Step 1: uniformity is imposed and results in the standardization of E and G

In Europe, until the nineteenth century, cultivated plants were identified by their geographical origin (species from the New World, populations from a specific area, etc.), and their local uses. G and E are therefore closely linked and interdependent. Farmers ensured that the reproduction of a plant conformed to a "morphotype" by choosing the best seeds to sow the following season (mass selection). Biological dynamics (natural selection, migration, drift and mutation) created variability between plants. The selection of plants for seed thus took place in a continuum of individual variations, with reference to a system of classification and nomenclature that was tautologically confirmed at each stage of selection. "Genetic progress" was not an objective in itself: varieties progressed thanks to a desire for novelty or in response to accidents (parasites, diseases, famines), or through the circulation of seeds or plants. This "ancestral" model was characterized by progressive domestication and valorization of genetic resources that evolved slowly in non or partly controlled environments (Bourdeix et al. 2008).

After World War II, European agricultural sector increasingly was considered as an industrial sector and, inspired by the Fordist production model (Allaire 2002), the seed sector was broken down into segments and professionalized. "Breeding firms were made responsible for innovation; seeds cooperatives were made responsible for multiplying and disseminating seeds; farmers were made responsible for producing grains from selected varieties and increasing their yield; and the State was responsible for allocating the gains obtained from genetic progress: such were the terms of the Fordist production compromise" (Bonneuil and Thomas 2007).

Selection techniques were perfected by recourse to (i) systematic crossing to increase "genetic recombination" and biotechnology, (ii) experimental protocols based on formal mathematical principles (Fisher 1938) and implemented in the controlled conditions of research stations. Each technical task became the domain of specialists. Farmers were stripped of their right to reproduce plants and were confined to production activities. In France, in 1941 and 1942 the seed sector was organized around official authorities (GNIS[1], CTPS[2]), joint committees of breeders, users, and public authorities which (i) control the creation and application of DUS[3] (Distinctness, Uniformity and Stability) standards, and VCU[4] (Value for Cultivation and Use) trials, both of which are required for registration in the national catalogue of seeds and seedlings, and (ii) regulate the sale of seeds. For instance, seeds from varieties that are not registered in the catalogue and not inspected by the Official Inspection and Certification service (SOC[5]) cannot be sold.

So in this compartmentalized and industrialized context, what did the plant become? A "pool of genes" for the biologist, a "phenotype" (G expressed in a biophysical E) for the agronomist, a "technical reality" (that genetic progress has achieved) for the national authorities which evaluate varieties, an "intellectual property" (to be protected and sold) for the plant breeder, a "production factor" (at x cost for y yield) for the farmer and for his supply cooperative, a "data base" (specifying choice of a variety and the appropriate cultivation system) for technical institutes, and a "quality" (adapted for industrial processing) for food manufacturers. Despite this diversity of view, reaching a consensus among all these actors was facilitated by three factors, (i) the continuous increase in genetic progress (yield: +0.1 t/ha/year), (ii) the prosperity of the seed sector, and (iii) the standardization of both G and E, which considerably reduced the expression of G × E interactions.

Step 2: imposed uniformity leads to desirable diversity

Beyond the agricultural sector, the standardization of practices and of points of view increasingly was contested finally leading to a profound rupture in western industrialized societies. This rupture corresponds to the switch from modern to "post-modern" societies. Illustrated by the social movements in the 60s–70s (as "May 1968" in France), post-modern societies can be characterized both by a claim for the

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[1] GNIS: *Groupement National Interprofessionnel des Semences et plants.*

[2] CTPS: *Comité Technique Permanent de la Sélection.*

[3] DUS trials eliminate a variety that is (i) not distinct from another variety that is already registered, (ii) not uniform (conformity of all individuals), (iii) unstable (appearance of off types in the 2nd generation).

[4] VCU trials eliminate any variety that shows no improvement in cultivation value (yield and factors influencing the regularity of yield) or technological value (quality with respect to the manufacturer's specifications).

[5] SOC: *Service Officiel de Contrôle et Certification.*

right to be different and by a fundamental questioning of standards and of institutions (Giddens 1991; Beck 1992). The ban on exchanging "farm" seeds of varieties that were not registered in the official catalogue, the dependence on multinational seeds firms and the threat of the widespread diffusion of genetically modified organisms strengthened the resistance among farmers and citizens (Bonneuil et al. 2006) and encouraged the emergence of networks such as Réseau Semences Paysannes in Europe, or GRAIN, an international non-governmental organization.

The quest for diversity and the call for less centralized systems of knowledge production (Aggeri and Hatchuel 2003) contribute to the "greening" of part of the agricultural sector. The resulting diversity of production systems such as organic or low-input agriculture and of ways of thinking is considerable (Cochet and Devienne 2006; Gibson et al. 2007). We propose to analyze the diversity through four models, based on the work of Sylvander et al. (2006) (Fig. 1). These models are built around two main axes: one socio-economic (individual logics versus collective governance) and the other agro-ecological (strict respect of specifications versus design of a new system). The latter axis distinguishes respectively a reductionist or factorial approach from a holistic approach (Hubert 2002; Lammerts van Bueren et al. 2003).

This representation associates the notion of spatial and temporal scale (from local to worldwide, short or long food supply chains), with status (public, associative, private), and with the sharing of tasks and competences (specializing versus delegating) (Table 1). The challenge is to analyze if the diversity of the objectives carrying by these models may renew the concept of E, G and G × E and results in diversification of processes used in plant breeding.

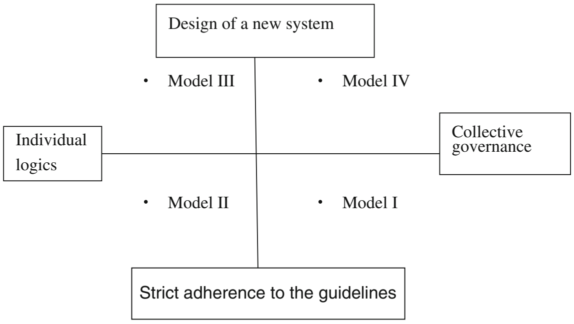

Fig. 1 Differentiation of agriculture and environments (after Sylvander et al. 2006)

Model I includes conventional agriculture and some segments of reasoned, organic or sustainable agriculture systems that were developed in response to new concerns about the environment and embodied in national or European public policies (environmental cross-compliance, reinforcement of the second pillar of the CAP,[6] etc.). These were in most cases federated by producers associations or supervised by farm trade-unions who want to keep the collective governance of such political issues. Farmers who adhere to this model strictly respect specifications, using a analytical approach, factor by factor. Their innovations consist in removing or adding certain inputs in accordance with the official guidelines.

Other farmers may be under contract to produce grain with a target outlet for specific cooperatives or food manufacturers. The logic of integrated value chains focusing on individual profit led us to consider *Model II*. This model corresponds to niche markets that may interest industrial enterprises that control both the seed sector and the agri-food sector (for example, a company creating wheat varieties that are intended for a particular type of bread produced by one of its subsidiaries).

All projects concerned with "militant" initiatives of producers and/or consumer groups who claim individual rights and autonomy are included in *Model III*. In this system, individual logics are promoted and collective governance of markets is controversial: each farmer aims to control the whole chain from the production of seed to the valorization of the final product through direct selling. Some examples that fit this framework are (i) farmer-bakers who belong to the "*Semences Paysannes*" network currently emerging in Europe, (ii) target actions undertaken by international consumer associations, such as the "Slow Food" movement whose members wish to maintain local varieties, sometimes more for the personal pleasure of eating than for large public interest goals such as the conservation of biodiversity.

Model IV is concerned with the dynamics of collective action aimed at coordinating the development of systems of plant breeding, production and diffusion in ways that ensure the complementarity of roles, responsibility and actions in the public interest. Participatory plant breeding projects linked with the

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[6] The Common Agricultural Policy.

Table 1 Specificity of the concepts of genotype, environment of their interactions (G × E) in the four models represented in Fig. 1

Model	Examples	*G* desired	Agro-ecological *E*	Socioeconomic *E*	*G* × *E*/*evaluation criteria*	Scale of adaptation desired
I	Conventional or organic agriculture strictly respecting tender specifications or guidelines	Uniform (imposed by legislation) Commercial, productive, standard quality variety	*Standardization* *B* homogenized by *C*	*R* public policies, premiums, industrial or associative guidelines, collective labels and brands *O* long food supply chains *A* conventional producers, opportunist organic producers	Limited a priori, observed ex-post. *DUS-VCU*	Mega-environment, country, large regions
II	Integrated sectors (segmented market),	Uniform (imposed by specifications) Variety fixed by specifications	*Prescription* *C* imposed in a chosen *B*	*R* industrial specifications (club), private brands *O* sales under contract, long food supply chains *A* industry, market actors	Framed strictly controlled *Criteria specific to brand*	Production basins
III	Farmer-bakers	Heterogeneous due to a desire to be different. Flag variety, evolving population	*Adaptation* *B* chosen or undergone, relatively unmodified by *C*	*R* amateur catalogue of plant varieties, contracts with farmers for experimental production of seeds *O* direct marketing *A* militants, minority trade union organizations	Promoted, source of singularity *Consumer satisfaction*	Farm
IV	Participatory plant breeding	Heterogeneous due to a desire to adapt to *E* Multiple and multi-functional varieties	*Optimization* *C* reasoned, organic, or low input, systems that cannot correct all the limiting factors of *B*	*R* partnerships, public domain, European bio catalogue *O* long and short food supply chains *A* producers, consumers, industrials, artisans	Optimized (joint choice of *G* and *C* according to *B* and *E* (socio-eco) *Specificity and multifunctionality*	Sector and territory

A, main actors (competences & means); *b*, bio-physical environment; *C*, crop management; *O*, outlet, market; *G*, genotype; *E*, environment; *G* × *E*, genotype × environment interaction; *R*, regulations structures (public policies, public or private standards, etc.)

diversification of markets have such aims. Since considerable negotiation is required, this model is difficult to bring into being and to optimize but it is an integral part of technical and political transitions towards sustainable development (Stengers 1999).

The models are situated between representation and reality: tension and even conflict can arise between them. Whereas the aim of Model IV is to achieve a new social contract, Model I progresses step by step towards improving a definition of sustainability that does not disturb the existing contract; Model II exemplifies individual pathways to satisfy confidential market niches, while Model III has difficulty in mobilizing sufficient actors and resources to generalize its individual approach. Our aim here is to show the latent complementarity of the four models and the contribution of each in the context of agricultural diversification.

Whatever the agricultural model, we propose that in today's world a wider range of components of E have to be taken into account. In addition to the components classically considered as 'production factors' i.e. (B) Bio-physical environment and (C) Crop management, we propose to take into account the roles, skills, responsibilities and resources of the main stakeholders and Actors (A). Market and target Outlets (O), structures of Regulations linked with seed sector (R) (specifications, contracts, environmental measures, etc.), and more general Societal dynamics (S) also form part of the environment in the widest sense of the term, and all interact strongly with Genotype.

Status of G, E and G × E in each of the four models

The challenge we face is to understand and structure the diversity that is called for in terms of G, E and G × E. For each model (Fig. 1), it is possible to define the main objectives, the main components of E, a targeted G, and to conceive specific breeding programmes to achieve these objectives.

Model I: the classic plant improvement system

The classic plant improvement system, described as a centralized, sequential, linear process (Sperling et al. 2001), may be useful for Model I. Five main stages (setting of objectives, creation of variability, selection, evaluation, and diffusion) compose the breeding program (Sperling et al. 2001). At each of these stages, the understanding of G, E and G × E interactions may vary considerably (Table 2). Thus, from G as an ideotype (in the first stage), to G as a commercial variety (in the last stage), these are successive statuses of G, as a genetic resource, a main effect, a nursery line, and as a micro-plot in DUS and VCU trials. In the same way, depending on the breeding stage, E can be considered either as the genome into which the desired genes will be introduced (second stage) or as the combination B × C of the environment targeted for diffusion (last stage).

For economic reasons, the main objective of breeding programs is usually to develop varieties that can be widely distributed and are thus suitable for a broad range of E (macro-contexts). The need for wide adaptation inevitably leads to a minimization of G × E interactions. The main pathway to minimization within industrial agriculture has been standardization of production conditions so as to render each E as uniform as possible. Indeed, as genetic progress is here defined as proportional to the heritability of the desired trait, breeders have aimed to maximize heritability by reducing environmental variance. They have done so chiefly by clustering environments on the basis of agro-ecology data and by observations of genotypes in these environments.

Clustering E on the basis of agro-ecology

Plant breeders cluster environments into "macro-contexts" (or mega-environments) within which the interaction is expected to be negligible (Yan and Hunt 2001). In the absence of other relevant descriptors, clustering often is based on geographical criteria (location × year) (B) (Nolot 1994). This corresponds to the practice of registering varieties in a national territory segmented into zones assumed to be "uniform". Trials are conducted at different locations within each zone and the results are grouped. This approach does not allow the environment to be taken into account in detail. To achieve a given degree of precision, further experimentation would be required at a fixed cost for each new environment that is defined. As organic or low-input farming make the diversity of environment more effective in relation to crop behavior, the resulting

Table 2 The five stages of a formal breeding program (after Sperling et al. 2001) showing the concepts of genotype and environment *with their related questions*

Stages	*G*	Agro-ecological *E*	Socio-ecological *E*
Setting selection objectives	Ideotype *Combination of useful characters*	*B* × *C*: Targeted cultivation conditions *Uniformity or diversity*	*O*: A priori target: utilization, quality target market *R*: Regulations: fixed
Creation of variability	Genetic resources *Relation between characters and genes of interest*	*G* × *G*: Genomic context *Interactions among genes*	*R*: Context of access to genetic resources (public, private)
Breeding	Main effect $(G = A^{*} + D^{*} + I)^{a}$ *Identification of favorable recombinations*	Research station *Discrimination and representivity (inference zone)*	*A*: Roles, responsibilities, and resources *Efficiency requirement*
Evaluation and registration	Fixed lines *Rating of phenotype*	Experimental network *Representivity and discrimination*	*R*: Regulations for registration Experimental quality assurance *Certification of result*
Diffusion	Commercial variety distinct, homogeneous and stable, genetic progress	Demonstration zone, recommendation zone *"Inference zone"*	*R*: Protection of breeders and users *O*: Outlet, market (contract, cost of seeds and advice)

A, actors; *B*, bio-physical context; *C*, crop management; *O*, outlets, markets; *G*, genotypes; *E*, environment; *R*, regulations structures (public policies, public or private standards, etc.)

[a] A, additivity; D, dominance; I, epistasie value

potential explosion in cost calls for a different G × E interaction model.

The interaction between the biophysical environment (B) and crop management (C) is always strong. In Model I, C is viewed simply as a way of modifying or controlling B by minimizing or exacerbating its limiting factors (depending on whether one wishes to express the potential or the defects of G). G also contributes to shaping B by the dynamics of its interaction with E, such as nitrogen absorption, balance between yield and quality, vigor of growth, dynamics of the water budget, weeds competitiveness, presence of a microclimate within the vegetation that favors disease to a greater or lesser extent, phenology, and sensitivity to climate events and parasites, etc. These G × (B × C) interactions nevertheless often are neglected, leading to a risk of carelessly extending the validity of the variety ranking beyond the empirical evidence.

Clustering E on the basis of a given set of Gs

Joint regression and stability analysis (Yates and Cochran 1938; Finlay and Wilkinson 1963) use the average performance of the varieties in a given environment to characterize the environment. In this case, E is described with the help of a specified set of Gs. However, this does not enable us to predict what will happen in another context without first measuring the average yield of the same set of genotypes as that used in the initial field tests. In addition, the commonly used environmental index reduces the differences between environments to a single dimension referred to as "fertility" or "potential", which may not appropriately reflect the diversity of situations. More dimensions are allowed with the AMMI method (Additive Main Effects and Multiplicative Interactions) (Gauch 1992), but this method also does not enable reliable predictions to be made for a new E.

In Model I, the aim in fact is not to predict G × E interactions but rather to reduce their effects and to adapt E to G by standardizing E. This standardization consists to eliminate all limiting factors present in B (biophysical environment) by reliance on C (supply of inputs). This approach contributes to a standardized G, under R that is, regulations for registration that imposes uniformity, and under O, the dominant market conditions that impose specific yield and technological quality.

Models II, III and IV as responses to the limits of Model I

In low-input environments a different breeding logic is required. A limited margin of maneuver does not allow C to compensate for the factors that limit B; and the wide range of uses prevents the emergence of a uniform, universal logic for G. The aim is no longer to adapt E to G but just the reverse, to try to adapt G to a wide range of Es.

This change is potentially disruptive to established plant breeding. The effort required partially explains the difficulty in rethinking breeding systems for new environments.

As Model II (Fig. 1) comprises market niches that respond to integrated value chains; here the objective is no longer to ensure the wide diffusion of a varietal innovation but to control and target the diffusion (stage 5, Sperling et al. 2001) of a specific final product by imposing a variety (G), its guidelines (C × B) and the exclusive delivery of the harvest. The evaluation stage of the breeding scheme (stage 4) thus may be narrow or even circumvented; the variety might not have to be registered in the official catalogue because seeds are diffused only within specified limits, such as an integrated value chain or a club. The purchase of the harvest at a guaranteed price is a main reason the G × C × B kit is accepted by farmers. The selection stage (stage 3) is either conducted generically by choosing from the genetic diversity reviewed in Model I, or is considerably simplified, by introducing the gene of technological interest into a variety resulting from Model I to obtain for instance a waxy maize or oleic sunflower. The logic of Model II can be extended to include the privatization of genetic resources and their economic valorization via the integration of an entire sector (by firms involved both in plant breeding and agro-industrial sectors). The stage of setting objectives (stage 1) creates opportunities for the combination or the emergence of value chains and specific market niches. It is as if the stages proposed by Sperling et al. (2001) (Table 2) were inverted (from stage 5 to stage 1) by the desire to first control the diffusion stage.

Another form of logic is offered by Model III, characterized by a strong demand for individual rights to control the whole chain, from seed production to marketing of the final product. All the stages of the plant breeding system, even the system itself, are called into question by farmers who claim autonomy in the seed sector. In this case, the farmers typically are looking for a genetic resource with patrimonial and identity characters, capable of becoming a "flag" variety at reduced cost, (a symbol of a social movement) or a "sentry variety" (considered by the Slow Food movement as a shield against uniform industrialized products). The G of interest here is a designated phenotype, labeled "local population" or "old variety". E is the farm environment and the G × E interaction exemplifies the extreme case of "one variety—one farmer". The objective here is an extremely localized individual adaptation—at the scale of one farm, or even of one field. "Farmers must have at their disposal an enormous range of varieties which are as adaptable as possible: in other words, are accessible to different types of evolution, and thus neither very uniform nor very stable" (Kastler 2006). Irrespective of the biology of the species (self or open pollinated), the means range from the cultivation of populations under natural selection to mild pressure of mass selection by dynamic management (Goldringer et al. 2007). Evaluation and diffusion are no longer based on the classical criteria defining genetic progress (e.g. yield or technological quality) but rather on consumer satisfaction. In this model, G × E includes interactions among designated actors (A) in a relatively circumscribed farmer-consumers relationship.

This interaction could be considerably expanded if a more holistic approach is taken, as proposed in Model IV. Here, the aim is to reconcile the design of a new system for plant breeding and collective action. This model gives more equal weight to agro-ecological interactions (environmental aspects of sustainability) and socio-economic interactions (between actors). The target is thus G × C × B × A interrelated with R × O × S. In consequence the latter needs to be redefined. The organization of the emergent system of complex interactions may be facilitated by a participatory approach.

"Participatory plant breeding" (PPB) was originally developed in countries in the South. In Europe today, PPB concerns local projects for the creation of varieties adapted to environments in which organic and low-input agriculture is practised (Desclaux and Hedont 2006). PPB is described as an approach involving all the actors of a given sector not only in setting of breeding objectives, but also in managing the breeding process and the creation of varieties (Gallais 2006). It aims to respond to systemic issues and demands for which classic breeding (Model I) appears to be unsuited (Cecarelli et al. 2001; Witcombe et al. 2003; Almekinders and Hardon 2006).

In contrast to Models II and III, Model IV does not attempt to eliminate any of the stages of the classic system (Table 2). The reason this model is of considerable heuristic interest is that it modifies the stages profoundly: each stage becomes a function that will tend to exacerbate and reveal G × E interactions in both the agro-ecological and socio-economic dimension of the environment.

Transitions among models

The diversity of agricultural conditions, when linked with sustainable development goals, require that selection and evaluation result in a range of varieties adapted to the range of environments and production objectives. The G × E interaction thus assumes new importance; it can call into question the choice of a particular G when there is a change in E. Because the range of E is too varied to be explored in any one type of experiment in a reasonable time and at reasonable cost, it becomes important to be able to predict interactions in situations that have not yet been the subject of experimentation. We discuss in the remainder of this paper a decentralized participatory plant breeding and the transition toward prediction and valorization of G × E in changing conditions.

Tools to implement a participatory approach

The need for sharing objectives

The objectives and the scheme of plant improvement require discussion and negotiation among diverse stakeholders. Stakeholders might include: farmers with their empirical observations and expertise concerning G × B × C relations, geneticists with their knowledge of G × G interactions and how these evolve during genetic mixing, upstream operators who can objectively quantify the usefulness of technological criteria in G × O, and legislators who can change the G × R conditions. The confrontations among these different representations leads to a reasoned and transparent weighting of each interaction and to identification of one or more pertinent ideotypes In this way, the notion of "ideotype" itself is renewed. The aim is no longer to produce or reproduce a "photo-fit picture" of the "ideal" plant, but to envisage an "archetype". Pragmatically, the objective is to fulfill a "minimum requirement" to overcome a certain number of deficiencies rather than to satisfy the desires of all the different actors. In all cases, the desired G appears as a social fact defined within a social and technical innovation network (Callon et al. 2001). Targeted diffusion environments are characterized by both agro-technical and socio-economic features. Evaluation thus not only concerns the objective, but also the process for achieving it and recognition of the social or ethical progress achieved.

Socio-economic environment to be structured

The creation of a participatory network raises the question of the choice of partners and their representivity and, more generally, the type of institutional arrangements that might enable the construction of consensus on the traits of interest.

Network sociology offers a way of clustering actors and the environment into categories, or according to (fixed) functions, or in terms of control (by macro-structures). It involves modeling socio-economic environments in terms of relational "positions", understood as specific sets of people linked with others or with objects in a similar manner (White 1981) irrespective of their social status or class. These "positions" form social units that are likely to behave in a similar way in a given context (i.e. they have both explanatory and predictive value). The approach has been applied to breeding programs (Chiffoleau 2006): in this case the challenge is to take into account different positions of actors in four appropriate types of networks: (i) a socio-technical network (relations with Gs via technical breeding and cultivation practices), (ii) a network for advisory and technical dialogue, (iii) a marketing network, (iv) an institutional and policy network for seeds, varieties and products. If the policy goal is sustainable development, these different positions have to be connected. Partial and contingent forms of agreement about "what is relevant to be done" (to breed) can then be designed among actors with similar positions. The participation of the end-users of any plant breeding process is important in so far as participation enables different positions to be revealed and incorporated for the benefit of the joint activity. Ongoing experiments are confirming that the involvement of users in the breeding process enables the practices and values of the networks associated with the varieties to be expressed freely and in-situ (Chiffoleau and Desclaux 2006).

The question of participation has been raised also in connection with the decentralization of plant breeding activities in contexts where genetic progress is not the sole objective. The question of the decentralization of breeding activities (in addition to the management of trial plots) also has been raised in the new context of an almost infinite diversity of diffusion areas.

Tools to implement a decentralized approach

The formal plant breeding activities described in Model I are particularly efficient in cultivation systems similar to those in experimental stations but are unsuitable when there are strong G × E interactions (Cecarelli et al. 2000). In Model IV, which is characterized by the desire to exacerbate G × E interactions, generalizing results is difficult, and even more so when E is considered in its widest sense. The main question that arises in participatory breeding is thus what should be centralized (in the experimental research station), and what should be decentralized, and at what cost. Our analysis of this question is based on breaking down the term E.

Centralizing or decentralizing B × C?

The efficiency of a trial location (B × C) is determined (i) by the genotypic correlation between the performance of a cultivar at this location and the performance obtained at the target location and (ii) by the precision (involved in heritability in the broadest sense, explained variance and power of discrimination) with which the performances of the cultivar are measured at the same location. A centralized breeding program enables local heritability to be maximized; while decentralized breeding enables the correlation to be maximized (Atlin et al. 2001). The question of centralizing or decentralizing E can also be seen as a compromise between bias and variance. The research station location is powerful for discriminating (i.e. for exacerbating or for estimating with a small variance varietal differences) but the more the selected trait depends on the environment, the greater the bias; the reverse is true of the farm location.

It is possible to achieve optimal results by giving preference to a large number of locations when there is an increase in bias. When the financial means are invariable, a plant breeder has to juggle with the number of locations and the number of repetitions at each location. In general, the search for a strong G × E interaction implies many trials with a limited number of repetitions and acceptance of the risk of unjustified expenditure if the interaction turns out to be weak (Gozé 1992).

The potential gap between the breeding location and B, the target agro-ecological environment, should be represented by the frequency deviation and the intensity deviation of the limiting factors. If this B cannot be simulated at the experimental station, then trials must be decentralized.

Crop management (C) depends on the farmers' objectives as a function of their constraints. It is defined by farmers' decision rules. It is difficult for an experimenter to represent the farmers' choices, and in this case decentralization also appears to be useful. However, if the decision rules are well clarified, it is possible to apply them at the research station and thus to control experimental bias. In the B of a breeding station and with a judicious range of C, it is possible to represent diverse range of target agro-ecological Es by diagnosing the limiting factors, and to predict G × E.

Prediction of G × E with the help of Gs One possible method for assessing the representivity of an experimental situation is by conducting an agricultural diagnosis using probe genotypes (Nolot 1994). This approach returns to the principle of measuring the environmental effect with the help of the plant itself. The use of well-known genotypes to reveal the characteristics of agro-ecological Es means any differences between environments will not be reduced to a single dimension. The variables measured on these genotypes can be used as environmental covariates for factorial regression (Desclaux 1996, 2000; Brancourt-Hulmel et al. 1999).

Prediction of G × E from environmental variables and ex-situ genotype parameters The technique of factorial regression (Denis 1988) permits to regress the interaction on the products of environment-by-genotype covariates. It opens the way to prediction for new environments where no experiments have been made. However, many environmental covariates (e.g. daily rainfalls) are themselves candidates for such regressions, and hence there is a need for reducing their number by regressing on synthetic variables. It has been shown that synthetic variables can be the outputs of an ecophysiological model (Dieng 2003). For instance; using the APLAT method (Dieng et al. 2006) it is possible to predict the G × E interaction in a given environment using only B and C without the need for prior observation of one or more genotypes in the concerned environment. These models enable breeding targets to be objectified by grouping Es that express combinations of related limiting factors, and ideotypes to be defined by the varietal parameters of the model that optimizes the result of crop in each target E. With the help of the G × E interaction prediction, the farmer can then choose a variety for the appropriate cropping system (which G for a particular E, or which E for a particular G).

Centralizing or decentralizing A, R, O and S?

Beyond the functional categories of actors (A) usually considered in PPB (farmer, breeder, manufacturer, etc.), the representatives of relational positions can be involved directly either at the research station or on their farms. Their participation also can take the form of individual interviews, working groups, debates, etc. In all cases, specific principles and procedures are needed to facilitate critical participation, and not merely passive attendance (Friedberg 1988). These principles, based on empathy, include transparency, democracy, open doors and respect of the individual (Desroches 1976), and suppose that rules are explicitly negotiated. Plant breeding by farmers, on their own farms, facilitates this type of critical participation by enabling the participants to recognize the constraints and limits of plant improvement (Chiffoleau and Desclaux 2006). Experimental varieties and plots can be used as an "intermediary object" (Vinck 1999) to link the actors in the network as well as to facilitate the expression and sharing of knowledge and agreements about what constitutes a feasible innovation and for whom.

Two stages can be envisaged to deal with target markets and outlets (O), and with the economic and political, sectoral and territorial coordinating structures (R). In-situ audits and joint information-gathering should enable the listing and weighting of criteria that subsequently can be used as entry variables in economic simulations. Moreover, in Model IV, the existing regulations concerning registration in the catalogue (R) have to be changed to enable the creation and use of the diversity of Gs needed in order to respond to the diversity of (B × C × A × O).

Finally, concerning societal dynamics (S), insofar as "one cannot relocate society" (Cauderon 2003), the challenge is to take into consideration the individuals who make up society both as actors and as owners of diverse values capable of constructing relevant rules for both global and territorial contexts (Pecqueur 2007) and of making "the cultural effort to take part in the debate". S thus promotes a technical and proximate democracy that enables us to make not only genetic progress but also ethical and social progress.

Diversification of E and call for diversity of G

The diversity of E leads to a desire for (and even a claim for) a diversity of Gs (Kastler 2006). This could be derived diversity from between or within-species × between or within variety diversity (composite crosses, populations, variety mixtures, etc.).

Within-variety heterogeneity has a number of agronomic advantages, including disease control and better adaptation to uncontrolled variability of the climate-soil environment (Wolfe 1997; Pope de Vallavieille et al. 2007). Heterogeneity is also an economic necessity when it enables the diversification or differentiation of final products and markets, particularly in the case of organic farming and of products that valorize particular specifications (as in Model II) or a particular local territory labeled with a Geographical Indication (as in Model III).

The desired diversity of G may imply a search for new Gs, or a search for different functions of G, or for the adaptation of existing or newly-used Gs to the public's taste today. For example, certain types or components of G (such as genetic engineering, cytoplasmic male sterility, or hybrids) are rejected by some people, sometimes as a way of expressing their desire for a distinct social identity (Bourdieu 1979). At the same time, the search continues for multifunctional Gs: as a contribution to (i) enhancement of the landscape (e.g. through color), (ii) health (by nutrients, etc.), (iii) balanced agro-ecological system (capacity for myccorhization, competition, remediation of polluted soils, etc.).

The challenge is thus to design new plant improvement systems and to claim to a change in variety registration legislation, as there is an increasing gap between uniformity inherited from the productivist model (i.e. the U in DUS) and the requirements of sustainable agricultures, in particular of organic agriculture, in which heterogeneity is a key factor for management and further development of organic agro-ecosystems.

Conclusion

The standardization of Es encouraged by the productivist model in agriculture has resulted in the standardization of Gs. G × E under this model is perceived as an inconvenience and therefore plant breeders have sought to reduced G × E effects.

Consequent to the assertion of new societal values, agriculture in Europe is in the process of diversifying to fit contrasted environments, represented in this paper by Models I–IV. Each model, by profoundly modifying the representation of Gs and Es, give a new status to the G × E interaction. G × E becomes a complex objective that plant breeder attempt to predict and valorize (Table 3).

In Model I, R (regulations for registration) impose a uniform G. C (the crop management) has to enable expression of the potential of G under the constraints imposed by the biophysical environment B and the rules associated with B (such as organic specifications, or agro-environmental measures). In Model II, the challenge of controlling outlets (O) and associated traits of interest (G) determines the choice of the cropping area and of crop management (B × C), which are then defined in contract specifications. In Model III, the direct, exclusive relation established between farmers and consumers, presumes that over time, G adapts naturally to changes in the bio-physical environment (B), and that the actors (A) accept the limited control over these changes. In Model IV, where the objective is sustainable and efficient plant improvement, complex interactions are promoted throughout the plant breeding process, facilitating a shared acceptance of the end product. Here, it is the S, representing the dynamic participation of representative actors of each relational position that defines the organization of roles, responsibilities and resources (A), as well as the breeding objectives G × O × (C × B), and the rules (R).

The difference in the nature of the main components of E envisaged in the four models (Table 3) modifies breeding objectives and the ways in which plant improvement is conceived. The order of the five breeding stages of Model I is thus called into question by Model II, their interest is questioned by Model III, and their status is modified by Model IV. Compartmentalized stages succeed one another in Model I, become functions that are envisaged as cyclic and iterative in Model IV, and are interlinked by numerous feedback loops (Desclaux 2005). In terms of participation, Model IV operationalises the concept to include the sharing of the decision-making among the actors involved, and the specific users' expertise and capacities for innovation (Von Hippel 2005).

In Models I and II the definition and development of the "most suitable" G (Boltanski and Thévenot 1991) is driven by the market and/or regulation, and

Table 3 Difference in the nature of G, E, G × E and objectives according to the four models represented in Fig. 1

Model	Target *G*	Major component of *E*	Objective	Target *G* × *E*
I	Genetic progress	*R* Regulation	Adapt *G* to *R*; (*B* × *C*) to *G*	$R \Rightarrow G \Rightarrow (C \times B)$
II	Specific traits	*O* Segmented use	Adapt *G* to *O*	$O \Rightarrow G \Rightarrow (C \times B)$
III	Patrimonial and political issue	*A* Farmer and consumer	*A* adapts to *G*; *G* adapts to *M*	$B \Rightarrow G \Rightarrow A$
IV	Diverse and relevant towards a project	*S* Technical participatory democracy	Adapt (*G* & *C*) to (*S*, *O*, *B*) and *R* to all the above	$S \Rightarrow A \times (G \times O \times (B \times C)) \Rightarrow R$

A, actors; *B*, bio-physical context; *C*, crop management; *O*, outlets, markets; *G*, genotypes; *E*, environment; *R*, regulations structures (public policies, public or private standards, etc.)

the G × E relation is dominated by the market and its actors. Models III and IV offer a fundamental challenge to these assumptions and conceptualizations. The artisanal outlets or direct marketing channels identified in Models III and IV enable better valorization and recognition of specific and contrasted Gs, from the plot to the final product. However, given the pressure of supermarkets, logistical problems, and official regulations, it remains difficult to develop such niches on a large scale (Rastoin 2007).

This heuristic modeling of G, E and G × E has enabled us to better understand the basic concept of representivity. Representivity clearly should include consideration not only of classic parameters such as the experimental location (proximity of B × C breeding sites and target B × Cs) but also that of the socio-economic positions of the actors. Representivity also at some level connects to deep-seated perception of the meaning of the relation between people and nature.

Taking complex relations like G × (A × O × S × R) into account provides a framework for the construction of sectors (which are often territorial) based on both socio-economic and agro-ecological criteria, and enables long-term evaluation of the variety coherence (economic performance and social acceptability).

Paillotin (2006) argued that “Improvement means exploiting a range of phenotypes; current breeding tends to eliminate the phenotype and conserve only the genes”). We understand this statement as a call for renewal of systems for varietal selection, particularly through participatory breeding, with the aim of integrating the phenotype (P) in a much larger “project or challenge” of sustainability that enables plant breeders to account for the systemic and heterogeneous realities of Es. A phenotype P can become a ‘P object’ at the heart of social-technical networks (Callon et al. 2001) which bring sustainable development projects into existence. The key component is neither the gene, nor the environment, but regulatory feedback. As Le Guyader (2006) neatly states: “We no longer speak about progress or improvement but about emergence”.

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