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Farmer-participatory *vs.* conventional market-oriented breeding of inbred crops using phenotypic and genome-enabled approaches: A pea case study

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ABSTRACT

Participatory plant breeding (PPB) has gained increasing importance in developing countries, but its value for market-oriented breeding programmes of countries with developed agriculture that are committed to pure line selection (as needed to comply with DUS requirements) is unknown. This study aimed to compare PPB *vs.* conventional plant breeding of pea (*Pisum sativum* L.) targeted to organic systems of Italy, exploring phenotypic and genome-enabled selection approaches. Priority values assigned on a 0–5 scale to 14 traits by 18 farmers from Northern and Central Italy and six breeders were used to define weights of farmer and breeder selection indexes. Farmers and breeders attributed outmost importance to a visual acceptability score assigned a few weeks before crop maturity on a 1–9 scale, followed in importance by grain yield and tolerance to lodging. However, breeders and farmers differed ($P < 0.05$) for trait importance in a few cases. Five phenotypic selection criteria (farmer selection index; breeder selection index; average of farmer and breeder selection indexes; grain yield; farmer acceptability score) were applied onto 306 lines evaluated in two researcher-managed experiments of Northern and Central Italy under organic crop management, selecting overall nine lines per criterion that were tested in four organically-managed environments of the same regions and one conventionally-managed site. The farmer selection index exhibited greater selection efficiency (+23% based on yield gains over elite commercial cultivars under organic farming) and farmer's acceptability of selected material than the breeder selection index. Breeding values based on the farmer selection index or the farmer acceptability score exhibited greater correlation with grain yields in independent environments than those from breeder selection criteria. Compared with grain yield-based selection, selection for the farmer acceptability score performed comparably in terms of yield gains, and somewhat better according to correlations of its breeding values with line grain yields in independent environments. The accuracy of genome-enabled predictions issued by a Bayesian Lasso model with 3443 SNP markers generated by genotyping-by-sequencing, estimated by averaging cross-environment correlations between predicted and observed values over two locations, was very high for the farmer acceptability score ($r_{Ac} = 0.77$), and high for grain yield ($r_{Ac} = 0.59$). Genomic selection for the farmer acceptability score ranked first in a preliminary comparison of eight genome-enabled or phenotypic selection criteria based on correlations of breeding values with grain yields in independent environments, suggesting its adoption for preliminary screening of genotype sets that are too numerous for field-based evaluation.

1. Introduction

Participatory plant breeding (PPB) alias client-oriented breeding, in which farmers select from segregating material, has gained increasing importance for field crop improvement in developing countries, where it showed greater farmer's acceptability and faster adoption of new cultivars than conventional breeding (Ashby, 2009; Witcombe and Yadavendra, 2014; Ceccarelli, 2015). PPB implies much greater impact of farmers' preferences on newly-released cultivars than participatory variety selection, in which farmers' preferences are expressed on genetically-fixed material previously selected by breeders (Witcombe et al., 1996). Comparisons of farmers *vs.* breeders for target traits

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Abbreviations: BL, Bayesian Lasso; BLUP, best linear unbiased prediction; GBS, genotyping-by-sequencing; GEI, genotype × environment interaction; GS, genomic selection; PPB, participatory plant breeding; RIL, recombinant inbred line; rrBLUP, Ridge regression BLUP

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revealed that both groups assigned top priority to higher crop yield, but sometime differed for other traits. For example, farmers attributed importance to straw characteristics and neglected disease tolerance for barley in West Asia and North Africa (Ceccarelli et al., 2001), whereas specific grain quality characteristics were sometime overlooked by breeders (*e.g.*, Asfaw et al., 2012). Comparisons of PPB *vs.* conventional breeding in terms of yield gain per unit of time and/or cost in farmers' fields did not provide univocal results, but mostly indicated the superiority of PPB when breeders selected on station but not when they selected on farm (Ceccarelli et al., 2001, 2003; Virk et al., 2003; Trouche et al., 2011). PPB may also provide other advantages relative to conventional breeding, such as farmer empowerment (Ashby, 2009) and greater biodiversity of cultivated material. For inbred crops, greater biodiversity may arise from independent farmer selection in many different farms according to a decentralized breeding approach (Ceccarelli and Grando, 2007), as well as from selecting evolutionary populations or pure line mixtures according to centralized approaches (where selection takes place in researcher-managed trials) or decentralized ones (Murphy et al., 2005; Döring et al., 2015). PPB-based selection of pure lines, however, does not necessarily increase biodiversity, particularly for crops targeted to markets rather than to subsistence (Witcombe et al., 1996).

Several reasons have contributed to the success of PPB in developing countries. Commercial or public breeding programmes often rely on poor infrastructure, and may lack sufficient technical skills. The occurrence of large genotype × environment interaction (GEI) between relatively favourable on-station selection environments and unfavourable farmer fields, and the presence of wide variation among target environments for prevailing abiotic or biotic stresses, favour the exploitation of positive GEI effects through decentralized farmer selection in many diversified target environments (Atlin et al., 2001; Ceccarelli et al., 2003). Informal seed systems, in which heterogeneous cultivars of inbred crops are fully acceptable, and farmer's self-production of seed, usually are very important in these countries (Almekinders et al., 1994). Hand sowing, which facilitates the on-farm assessment of many breeding lines, is widespread.

PPB has received modest attention in countries with developed agriculture, with the exception of potato breeding in the Netherlands (whose success has been favoured by various factors, such as the crop vegetative propagation, long-standing crop knowledge by farmers, early public support and the strong link with private breeding companies: Almekinders et al., 2014). In these countries, PPB has mostly been envisaged for organically-managed environments and, in inbred crops, for selecting heterogeneous material (Murphy et al., 2005; Wolfe et al., 2008; Dawson et al., 2011). While the possible variety registration of heterogeneous material is under evaluation in the European Union (Lammerts van Bueren et al., 2018), the value of PPB for market-oriented breeding programmes of developed countries aiming to select pure lines (as needed to comply with current DUS requirements for variety registration) is unknown. In general, PPB may prove less useful in these countries than in developing ones, because of the good infrastructure and efficiency of their conventional breeding programmes and the expected difficulty of their farmers to evaluate many lines (which contrasts with the widespread availability by breeding programmes of equipment that facilitates the researcher-managed evaluation of many lines). In addition, target environments of agriculturally developed regions tend to be less stress-prone and diversified than those in developing countries, thereby offering less opportunities for the exploitation of positive GEI effects. In this situation, a convenient option for PPB could be a centralized participatory approach, in which farmers display a "consultative" role by selecting within researcher-managed fields. This approach may well include different selection sites, in order to exploit repeatable GEI effects across contrasting subregions or to minimize poorly repeatable GEI (Annicchiarico, 2009). For selection environments that match well the target environments, such a centralized approach may prove as efficient as a decentralized one (Ceccarelli et al., 2001; Virk et al., 2003). On the other hand, however, properly chosen selection environments can effectively improve the value of researcher-based selections (Bänziger and Cooper, 2001; Ceccarelli et al., 2003; Rattunde et al., 2016).

Field pea (*Pisum sativum* L.) is the most-grown cool-season grain legume in Europe, where it displays a key role as a source of feed proteins as well as to safeguard the sustainability of agricultural systems in terms of soil fertility, energy efficiency, greenhouse gas emissions and crop diversity (Watson et al., 2017). Pea is an inbred crop with relatively high rate of genetic yield gain, estimated as 1.3% per year based on international cultivars evaluated in Italy (Annicchiarico, 2017). Grain yield data from different sets of pea genotypes across conventionally-managed or organically-managed Italian environments highlighted a need to breed for wide adaptation over the country, because of the larger size of temporal GEI effects relative to spatial GEI effects associated with wide year-to-year variation for timing and extent of winter cold stress (Annicchiarico and Iannucci, 2008).

In large-scale breeding programmes, another challenge of PPB is its integration with genome-enabled selection tools. Genomic selection (GS), which is fully compatible with organic plant breeding (Nuijten et al., 2017), may enable breeders to predict complex, polygenic traits by means of a statistical model constructed from genome-wide marker information (Meuwissen et al., 2001; Heffner et al., 2010). Next generation sequencing techniques such as genotyping-by-sequencing (GBS; Elshire et al., 2011), which can provide thousands of single-nucleotide polymorphism (SNP) markers for a relatively low cost, have facilitated the application of GS to crops. Pioneer studies on grain legume species such as soybean (Jarquín et al., 2014) and pea (Annicchiarico et al., 2017a) have revealed the good ability of genome-enabled models to predict line breeding values for grain yield, and suggested the progressive adoption of GS as a partial substitute for phenotypic selection on the basis of greater predicted genetic gain per unit of time and/or cost of this selection procedure (Annicchiarico et al., 2017b).

A major objective of this study was to assess whether PPB can be beneficial for yield improvement of an inbred crop such as pea in a relatively large-scale, market-oriented breeding programme with a major focus on organic systems of Italy (whose extent has reached a share of 14.5% of the Italian cropping area according to EUROSTAT). We assessed phenotypic selection either based on individual traits such as grain yield and a farmer acceptability score or based on trait combinations as expressed by selection indexes defined according to priority traits for farmers and breeders, with farmer and breeder selections performed in researcher-managed trials under organic crop management. Concurrently, this study explored the variation among farmers and breeders with respect to priority traits for pea breeding. Another major aim of this study was to explore the ability of genome-enabled selection to predict pea line breeding values for grain yield and the farmer acceptability score, and to compare preliminarily these selection approaches with phenotypic ones.

2. Materials and methods

2.1. Assessment of priority traits for farmers and breeders

This assessment was based on responses from (i) six researchers, of whom three were current or past pea breeders belonging to public institutions, and three belonged to private seed companies that are routinely committed to evaluation in Italy of candidate varieties bred in France, and (ii) 18 organic pea growers selected by Associazione Italiana Agricoltura Biologica (AIAB), of whom nine were from Northern Italy and nine from Central Italy. All of them were asked to assess the importance of 14 traits listed in Table 1 on a scale ranging from 5 = very high to 0 = nil. One trait, namely, a visual acceptability score, implied its field observation by the actor (farmer or breeder). The other traits could be measured by a researcher for use in PPB or conventional breeding.

Table 1
Comparison of farmer *vs.* breeder groups for mean priority value attributed to 14 pea traits on a scale ranging from 5 = very high to 0 = nil. The reported values for selected traits were used as weights of a selection index defined for each group.

Trait	Farmers	Breeders	*t* test[a]
Visual acceptability score[b]	5	5	ns
Grain yield[b]	4.61	4.83	ns
Aerial biomass[b]	1.86	3.33	*
Cold tolerance	4.03	4.08	ns
Lodging tolerance[b]	4.22	4.58	ns
Ascochyta blight tolerance	2.22	3.75	*
Fusarium spp. tolerance	2.19	3.08	ns
Early flowering[b]	2.83	3.33	ns
Early maturity	3.17	3.17	ns
Plant height at flowering[b]	2.33	2.83	ns
Semi-leaflessness	2.56	4.50	*
Individual seed size[b]	0.86	0.83	ns
Grain protein content	4.22	3.92	ns
First pod height	3.45	3.67	ns

[a] Relative to 18 farmers and six breeders.

[b] Traits used for index definition, using data from Experiment 1 for aerial biomass and data averaged across Experiments 1 and 2 for the other traits (experiments are described in Table 2). Data for traits excluded from index definition were either unavailable or irrelevant.

Breeder *vs.* farmer groups were compared for mean priority value of each trait by *t* test. The variation among individual actors for the whole set of priority traits (which identified the target plant type) was synthetically displayed by actor scores on the first two axes of principal component analysis that held trait priority values as original variables. All statistical analyses of these data and of phenotypic data were performed using SAS/STAT® software (SAS Institute, 2011).

2.2. Genetic base for selections

The genetic base for performing phenotypic selection and defining GS models included 306 genotypes belonging to three connected recombinant inbred line (RIL) populations that originated from paired crosses between Attika (a European cultivar described as a spring-type), Isard (a French winter-type cultivar) and Kaspa (an Australian cultivar of Mediterranean type). According to Witcombe and Virk (2009), who recommended the use of relatively few carefully-chosen parent cultivars for PPB of inbred crops, these parent cultivars were selected among nearly 50 international cultivars that underwent extensive multi-environment testing. The three parent cultivars displayed high and stable grain yield and modest phenological differences across sites of Northern and Southern Italy (Annicchiarico, 2005; Annicchiarico and Iannucci, 2008). In addition, Attika showed outstanding adaptation to organic farming (Annicchiarico and Filippi, 2007). The RIL populations are coded henceforth as A × I, K × A and K × I from the initials of their respective parents. The population A × I included 102 lines; the population K × A, 100 lines; and the population K × I, 104 lines. Four F$_6$ plants per line were grown in a non-heated glasshouse to collect DNA samples for line genotyping and to produce seed, which underwent one additional generation of multiplication before being used for experiments.

2.3. Selection experiments

The 306 RILs and their parent cultivars underwent two selection trials in the seasons 2013-14, which are described as Experiment 1 and 2 in Table 2. The trials were performed in an organic farm of Lodi (45°19′N, 9°30′E), a site representative of the subcontinental climate typical of Northern Italy, and in a field with long-standing organic management in Perugia (43°06′N, 12°23′E), a location with a cool Mediterranean climate that is widespread in Central Italy and inland Southern Italy (Table 2). Each plot had 0.96 m^2 size, included four rows 1.2 m long and 0.2 m apart, and was sown at 62.5 seeds/m^2 density by a pneumatic seed drill. These and all following experiments were autumn-sown in October or November, were harvested in June, and were designed as a randomized complete block with three replications. Each parent line was replicated thrice within each block.

Farmer and breeder acceptability scores were attributed a few weeks before crop maturity by a scale ranging from 9 = very high to 1 = very low, allowing for half-unity values. Farmer scores were attributed by nine farmers from Northern Italy in Lodi and nine from Central Italy in Perugia. In each site, farmers were subdivided into three groups of three farmers each, and each group assessed one experiment replication. In front of each plot, farmers exchanged their opinions but eventually provided individual scores, which were averaged prior to statistical analyses. Breeder acceptability scores were attributed by three different breeders in each location. Each breeder assessed one replication in each site. Farmers and breeders were the same who defined priority traits for the respective groups.

The following traits were recorded on a plot basis: (i) dry grain yield, after combine-harvesting the plot and assessing seed moisture on a random sample of 250 seeds; (ii) onset of flowering, as the number of days from January 1 to when 50% of plants showed at least one open flower; (iii) mean plant height at flowering; (iv) lodging susceptibility, visually assessed at maturity on a 5-level scale ranging from 1 (lodging limited to the basal part of the stem) to 5 (complete lodging); (v) individual dry seed weight, assessed on the seed sample used for seed moisture determination; (vi) dry aerial biomass, recorded only in Lodi. Of the other possible target traits for farmer or breeder selection that are listed in Table 1, tolerance to winter low temperatures, ascochyta blight complex (*Peyronellaea pinodella* (L.K. Jones) Morgan-Jones & K.B. Burch., *Peyronellaea pinodes* (Berk. & A. Bloxam) Aveskamp, Gruyter & Verkelv, and *Ascochyta pisi* Lib.) and *Fusarium* spp. could not be assessed because of lack of sizeable stress, whereas maturity time and semi-leaflessness were irrelevant, the first because of lack of breeder *vs.* farmer group difference for priority score (Table 1), and the latter because all lines were semi-leafless. Finally, grain protein content and first pod height were not recorded (but group differences for these traits were very limited: Table 1).

The significance of genotypic and GEI effects across selection environments was verified separately for each RIL population by an analysis of variance (ANOVA) including the random factors genotype, environment, and block within environment. Genotypic (S_G^2) and GEI (S_{GE}^2) variance components for grain yield and the farmer and breeder acceptability scores were estimated by a restricted maximum likelihood method for each RIL population, assessing the genetic coefficient of variation across selection environments [$\mathrm{CV_g} = (S_G^2/m) \times 100$, where m = trait mean value] and the ratio of S_{GE}^2 to S_G^2. To get some insight into key traits associated with farmer and breeder acceptability scores, we assessed trait correlations for each RIL population using genotype data averaged across selection environments, averaging results across the populations.

Five phenotypic selection criteria were assessed, namely, farmer selection index, breeder selection index, average of farmer and breeder selection indexes (implying the co-selection by the two groups), grain yield, and farmer acceptability score. Mean priority values for farmer and breeder groups that are reported in Table 1 were used as weights of a selection index defined for farmer or breeder groups as described by Bänziger et al. (2000, p. 45). For a given index, its value for the line *i* was:

$$\mathrm{I_i} = \mathrm{w_1}\,\mathrm{T_{1i}} + \mathrm{w_2}\,\mathrm{T_{2i}} + \ldots\, \mathrm{w_n}\,\mathrm{T_{ni}}$$

where T_{ni} is the observed standardized value of the trait T_n for the line *i*, and w_n is the weight attributed by the relevant group to the trait (adopting negative weight value for lodging susceptibility, where lower values were actually desired). Line trait values were averaged across

Table 2

Climate and soil characteristics and mean grain yield of seven pea experiments. Experiments 1 and 2 were used for phenotypic selection according to five different criteria and for genomic selection modelling of grain yield and farmer acceptability score; the remaining experiments were used for comparison of selection criteria.

Item	Experiment 1[a]	Experiment 2[a]	Experiment 3[a]	Experiment 4[b]	Experiment 5[b]	Experiment 6[b]	Experiment 7[b]
Location	Lodi	Perugia	Lodi	Lodi	Perugia	Lodi	Perugia
Cropping year	2013-14	2013-14	2014-15	2014-15	2014-15	2015-16	2015-16
Crop management system	Organic	Organic	Conventional	Organic	Organic	Organic	Organic
Rainfall, Jan.-Mar. (mm)	343	280	198	198	223	258	194
Rainfall, Apr.-May (mm)	122	179	147	147	73	147	217
Absolute minimum daily temp. (°C)	–5.7	–3.6	–11.6	–11.6	–2.9	–12.0	–5.4
Mean of max. daily temp., May (°C)	23.2	23.4	23.9	23.9	26.0	21.8	22.7
Soil texture[c]	Silty-loam	Silty-clay-loam	Sandy-loam	Loam	Silty-clay-loam	Silty-loam	Silty-clay-loam
Soil pH	7.9	7.6	6.3	7.7	7.6	7.9	7.6
Grain yield (t/ha)	6.31	2.90	4.59	1.06	3.09	0.95	1.81

[a] Testing 306 recombinant inbred lines from three connected crosses (each including 100 to 104 lines) and three parent cultivars.

[b] Testing 31 lines, three parent cultivars and three elite commercial cultivars.

[c] According to FAO (2006).

locations (with the exception of aerial biomass, recorded only in Lodi) before standardization. For each selection criterion, we selected the three top-ranking lines within each RIL population, for evaluation in independent test environments.

2.4. Comparison of phenotypic selection criteria

All the lines selected according to each criterion were evaluated in four organically-managed test environments described as Experiments 4 to 7 in Table 2, which were represented by site-year combinations relative to Lodi and Perugia in the seasons 2014-15 and 2015-16. The selected lines were less than the possible maximum number of 45 (5 criteria × 3 lines × 3 RIL populations), because many of them were selected according to more than one criterion. The experiments included also some additional high-yielding lines that were selected from the same RIL populations (for a total of 31 lines), the three parent cultivars, and three reference cultivars, *i.e.*, Spacial, Pepone and Fraser, which displayed excellent adaptation across organically-managed environments of Northern and Central Italy in recent variety trials (Pecetti et al., 2014). These experiments had 6.5 m^2 plot size and adopted 105 seeds/m^2 sowing density (as allowed for by the availability of greater seed amounts for these trials). The farmer acceptability score was attributed by six farmers from Northern Italy in Lodi and six from Central Italy in Perugia, of whom four participated in the selection trials and two were novel participant farmers in each site. Dry grain yield, onset of flowering, plant height at flowering, and lodging susceptibility, were recorded as described earlier.

Differences among germplasm selected according to different criteria and other reference germplasm were assessed by an ANOVA that included the fixed factors germplasm (with seven variants, of which five were relative to sets of lines selected according to each criterion, and two were relative to parent germplasm and elite cultivar germplasm, respectively) and genotype within germplasm, and the random factors environment and block within environment. Accordingly, GEI acted as the error term for testing the variation in germplasm mean values.

The same 31 lines and the parent cultivars were also evaluated for dry grain yield in a conventionally-managed test environment relative to Lodi in 2014-15, described as Experiment 3 in Table 2. This trial adopted same plot size and sowing density as the selection experiments, along with pre-sowing mineral fertilization (24 kg/ha N, 72 kg/ha P_2O_5, and 72 kg/ha K_2O) and chemical weed control [(Stomp® 330 E (a.i. Pendimethalin at 307 g/L)]. Differences among germplasm groups were assessed by an ANOVA including the factors germplasm, genotype within germplasm, and block.

We compared the five phenotypic selection criteria, the additional phenotypic criterion represented by the breeder acceptability score, and two genome-enabled criteria relative to GS for grain yield and farmer acceptability score (described later on), in terms of correlation of line breeding values estimated (phenotypic criteria) or modelled (genome-enabled criteria) from data averaged across the selection environments (Experiments 1 and 2) with line grain yields observed (i) across four independent organically-managed test environments (Experiments 4 to 7, for 31 lines), and (ii) in the conventionally-managed test environment represented by Experiment 3 (averaging results for the three RIL populations). Differences between pairs of correlation coefficients were verified as described by Dagnelie (1975, p. 321).

2.5. Genotyping and genotype SNP calling

Details on DNA isolation, GBS library construction and sequencing of the 306 lines were provided in Annicchiarico et al. (2017a). In brief, DNA was extracted from green tissue that was collected from bulked stipules of four F_6 plants per line using the CTAB method described by Rogers and Bendich (1985), checking its quality on 1% agarose gel. We adopted the GBS protocol based on the *Ape*KI restriction enzyme that was described by Elshire et al. (2011), with modifications. After quantification by a Quant-iT™ PicoGreen® dsDNA assay kit (Life Technologies, P7589), each DNA sample (100 ng) was digested with *Ape*KI (NEB, R0643 L) and then ligated to a unique barcoded adapter plus a common adapter. Equal volume of the ligated product was pooled and cleaned up with QIAquick PCR purification kit (QIAGEN, 28,104) for subsequent amplification. In PCR, 50 ng template DNA was mixed with two primers and KAPA Library Amplification Readymix (KAPA Biosystems KK2611). Amplification was carried out on a thermocycler for 10 cycles with 10 s of denaturation at 98 °C, followed by 30 s of annealing at 65 °C and 30 s extension at 72 °C. Each library was sequenced in two lanes on Illumina HiSeq 2000 at the Genomic Sequencing and Analysis Facility of the University of Texas, Austin, TX.

We used the UNEAK pipeline for SNP discovery and genotype calling, filtering the raw reads (100 bp, single end read) to keep only reads having a barcode and a single cut site and no missing bases in the useful part of the sequence (first 64 bases). All reads beginning with the expected barcodes and cut site remnant were trimmed to 64 bp, grouping identical reads into one tag, and using tags with 10 or more reads across all individuals for pairwise alignment aimed to find tag pairs that differed by one bp. For each SNP marker, the read distribution of the paired tags in each individual was used for SNP genotype calling. A further quality filter, implemented through *ad hoc* Python scripts, removed markers with fewer than 4 aligned reads. The data set was filtered for five possible data configurations that were relative to maximum thresholds of allowed genotype missing values per SNP marker equal to 10%, 20%, 30%, 40%, or 50%. Markers that were monomorphic or with minor allele frequency < 2.5% were removed. Following Nazzicari et al. (2016), we estimated missing data by Random Forest imputation (Breiman, 2001) using the R package MissForest (Stekhoven and Bühlmann, 2012) with the configuration ntree = 100, maxiter = 10, and encoding genotypes as categorical data (factors).

2.6. Assessment of genomic selection criteria

GS was explored for grain yield and the farmer acceptability score using best linear unbiased prediction (BLUP) values from Experiments 1 and 2 computed according to DeLacy et al. (1996). We assessed two GS models that stood out for predictive ability in a previous comparison of models for pea grain yield (Annicchiarico et al., 2017a), namely, Ridge regression BLUP (rrBLUP; Searle et al., 2009), and Bayesian Lasso (BL; Park and Casella, 2008). Details on the implementation of these models were given in Annicchiarico et al. (2017a), where a brief model description was also reported. The impact of population structure, which may improve the predictive ability of GS models (Guo et al., 2014), was taken into account by the possible addition in the model of a RIL population fixed factor as a $3 \times n$ incidence matrix, where n is the number of samples. Overall, we assessed for each trait 20 GS models produced by the factorial combination of BL or rrBLUP models by absence or presence of imputed population structure by maximum missing data thresholds per SNP marker of 10%, 20%, 30%, 40%, or 50%.

We assessed the cross-environment predictive ability (r_{ab}) of each model as Pearson's correlation between the breeding values predicted by the model built in one site and the phenotypic values in the other site of independent lines selected by a stratified cross validation scheme keeping 90% of lines for modelling and 10% for validation that was repeated 50 times, averaging the individual results obtained for each RIL population. These r_{ab} values were used to estimate predictive accuracy (r_{Ac}) values according to Lorenz et al. (2001) as: $r_{Ac} = r_{ab} / H$, where H is the square root of the broad-sense heritability on a genotype mean basis (H^2) in the validation environment. H^2 value was estimated as: $H^2 = S_G^2 / (S_G^2 + S_e^2 / n)$, where S_G^2 and S_e^2 are variance components for genotype and experimental error, respectively, and n is the number of experiment replications. Regression models, cross-validations and predictive ability estimation were carried out using the R package GROAN (Nazzicari and Biscarini, 2017).

Genome-enabled predictions of grain yield and farmer acceptability score of the 306 lines were finally implemented by the top-performing model represented by BL with imputed population structure and maximum missing data threshold of 30%, using line phenotypic data averaged across the two selection environments. As anticipated, these GS criteria and six phenotypic selection criteria were compared in terms of correlation of line breeding values estimated or modelled from data of Experiments 1 and 2 with line grain yields across the organically-managed Experiments 4 to 7 or the conventionally-managed Experiment 3.

3. Results

3.1. Assessment of priority traits for farmers and breeders

On average, farmers attributed significantly ($P < 0.05$) lower importance than breeders to greater aerial biomass, to ascochyta blight tolerance and the semi-leaflessness trait, on the ground of mean priority values reported in Table 1. Both groups attributed outmost importance to their own visual acceptability score, which was followed in importance by grain yield and tolerance to lodging (Table 1). Individual seed size was unanimously ranked as the least important trait.

The overall variation for priority trait values between and within farmer and breeder groups is graphically represented by scores of individual actors in the space of the first two PC axes (Fig. 1), which summarized 49% of the total variation. Based on trait eigenvectors, PC 1 mainly indicated greater importance attributed to semi-leaflessness and to tolerance to ascochyta blight, *Fusarium* spp. and lodging, whereas PC 2 indicated relatively greater preference for higher grain yield and lower biomass (data not reported). The variation among farmers was partly accounted for by geographic provenance, as farmers from Central Italy tended to display lower PC 1 score than those from Northern Italy (Fig. 1). Breeders, which tended to belong to the right lower corner of the graph, showed greater mismatch for overall targeted plant type with farmers from Central Italy than with those from Northern Italy (Fig. 1).

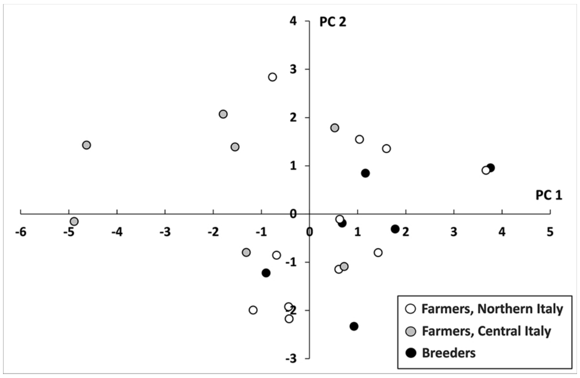

Fig. 1. Scores of 18 farmers from Northern and Central Italy and six breeders on the first two axes (PC) of principal component analysis performed on priority values attributed to 14 pea traits (priority ranging from 5 = very high to 0 = nil; traits listed in Table 1; PC 1 and PC 2 explaining 32% and 17%, respectively, of the overall variation).

3.2. Comparison of phenotypic selection criteria

Lodi's selection environment, while featuring the expected lower level of winter low temperature relative to Perugia's, was definitely milder-winter and higher-yielding than Lodi's test environments used for comparing selection criteria in the following two years (Table 2). Crop mean yield in these latter environments was particularly low under organic management, because of plant mortality and plant damage caused by low winter temperatures, severe weed competition exerted in spring on less dense and vigorous pea stands and, to some extent, because of apparently outstanding weed occurrence in the chosen fields. Perugia's selection environment matched more closely the climatic conditions of this site in the following years (Table 2).

ANOVAs for each RIL population unanimously showed significant GEI across selection environments for grain yield, onset of flowering and seed weight ($P < 0.05$), and no GEI for the farmer and breeder acceptability scores and tolerance to lodging. Accordingly, the GEI to genotypic variance component ratio was close to zero for the farmer and breeder scores, while being moderately high for grain yield (Table 3).

On average, farmer and breeder groups visiting the selection experiments rated the lines on the 1–9 acceptability scale with similar severity on the basis of group means over lines and locations (4.47 *vs.* 4.89). However, the distinctly lower genetic CV of the farmer score relative to the breeder score (11.7 *vs.* 17.3%; Table 3) indicated that extreme positive or negative values were less frequent in the farmer assessment.

Farmer and breeder acceptability scores averaged across selection environments exhibited moderately high correlation ($r = 0.78$), according to results averaged across RIL populations. The farmer score tended to be somewhat more correlated with grain yield ($r = 0.66$) than the breeder score ($r = 0.60$). In contradiction with the higher interest for greater aerial biomass stated by breeders relative to farmers (Table 1), the correlation with aerial biomass was slightly higher for the farmer score ($r = 0.59$) than the breeder score ($r = 0.52$). Finally and specifically for the test genetic base, the preference for early-flowering material that was declared by farmers and breeders (Table 1) contrasted with the correlation of the farmer and breeder scores with later onset of flowering ($r = 0.62$ for both groups).

Table 3
Genetic coefficient of variation and ratio of genotype × environment interaction (GEI) to genotypic variance for grain yield and farmer and breeder acceptability scores.

Item[a]	Grain yield	Farmer acceptability	Breeder acceptability
Genetic coefficient of variation	14.6	11.7	17.3
GEI / Genotypic variance ratio	0.50	0.03	0.05

[a] Across Experiments 1 and 2 described in Table 2. Average value for three recombinant inbred line populations, each including 100–104 lines. G variance ≠ 0 for each trait and population ($P < 0.01$); GEI variance ≠ 0 only for grain yield, in each population ($P < 0.05$).

Significant ($P < 0.05$) variation among germplasm groups (five groups relative to lines selected according to different criteria, and two groups relative to parental or reference cultivars) and within germplasm groups was found for all traits assessed across the four organically-managed test environments ($P < 0.05$). However, no difference among selection criteria was found for seed size ($P > 0.05$). The interaction with environments of germplasm groups and lines within groups was always significant ($P < 0.05$), except for grain yield of germplasm groups.

On average, all selections exhibited a distinct progress in terms of grain yield and farmer's acceptability across the four organically-managed test environments not only relative to the parent cultivars but also relative to the elite commercial cultivars, although the latter cultivars were earlier-flowering and more tolerant to lodging (Table 4). Interestingly, the germplasm selected by the farmer index was top-yielding and out-yielded the material selected according to the breeder index by 5.7% (1.824 *vs.* 1.726, $P < 0.05$; Table 4). When assessing the selection efficiency of the selection criteria in terms of actual yield gain over the mean of the elite commercial cultivars, the farmer index-based criterion was 23% more efficient than the breeder index-based criterion (0.523 *vs.* 0.425 t/ha yield gain), and showed no increase in efficiency from its integration with the breeder index-based criterion (Table 4). However, germplasm selection based only on grain yield was nearly as efficient as the farmer index-based selection (Table 4), whereas the selection based on a simple criterion such as the farmer acceptability score was about 8% less efficient (0.479 *vs.* 0.523 t/ha yield gain) but not statistically worse than the farmer index-based selection (Table 4). Breeder selections, compared with farmer selections based on the selection index or the appreciation score, were less appreciated by farmers ($P < 0.05$) and showed a slight trend towards shorter stature and earlier flowering (Table 4). However, the particularly high importance attributed by breeders to tolerance to lodging (Table 1) resulted in greater tolerance to lodging of breeder index-based selections relative to selections based on the farmer score or grain yield (Table 4).

In the experiment performed in one conventionally-managed test environment, the breeder index-based selections were out-yielded by farmer selections based on the appreciation score ($P < 0.05$), and tended to display lower yield than selections based on the other criteria (Table 4).

3.3. Assessment of genomic selection criteria

The UNEAK pipeline applied to GBS data produced a gross total of 95,740 SNP markers. The actual number of polymorphic markers available for GS increased as a function of the allowed genotype missing data threshold, ranging from 462 for 10% missing rate to 7521 for 50% missing rate. For both grain yield and the farmer acceptability score, the results summarized in Fig. 2 indicated: (i) the similar accuracy of BL and rrBLUP models without or with imputed population structure, with some advantage of population structure only for predicting grain yield in Lodi based on data from Perugia; (ii) a plateau of predictive ability achieved around 30% genotype missing data threshold, with nil or negligible improvements thereafter; (iii) the similar value of each site providing phenotyping data (GS model training site) for predicting responses in the other site. The BL model with imputed population structure and 30% genotype missing data threshold displayed a slight advantage over the other models when averaging results across traits. The predictive accuracy of this model averaged across RIL populations and cross-environment validations was very high for the farmer acceptability score ($r_{Ac} = 0.77$), and high for grain yield ($r_{Ac} = 0.59$). This model was selected for the final modelling of genotype breeding values for the two traits based on phenotypic data averaged across the two sites.

Table 4
Mean value of pea germplasm selected according to five selection criteria (farmer selection index; breeder selection index; average of farmer and breeder selection indexes; grain yield; farmer acceptability score), three parent cultivars and three elite commercial cultivars, for dry grain yield and other traits in independent experiments.

Germplasm[a]	Average of four experiments[b]					One experiment[c]
	Grain yield (t/ha)	Farmer acceptability score (1 = lowest, 9 = highest)	Plant height at flowering (cm)	Onset of flowering (dd from Jan 1)	Lodging susceptibility (1 = lowest, 5 = highest)	Grain yield (t/ha)
Selected by farmer index	1.824 a	4.68 a	60.7 ab	107.4 ab	1.87 ab	5.966 ab
Selected by breeder index	1.726 b	4.36 b	58.4 b	106.6 b	1.79 b	5.227 b
Selected by farmer + breeder indexes	1.811 a	4.65 a	61.6 a	108.0 a	1.88 ab	5.882 ab
Selected by grain yield	1.819 a	4.63 a	59.9 ab	107.4 ab	2.05 a	6.025 ab
Selected by farmer acceptability score	1.780 ab	4.61 a	60.8 ab	108.4 a	2.06 a	6.227 a
Three parent cultivars	1.285 c	3.53 c	47.2 c	102.8 c	2.07 a	3.489 c
Three commercial cultivars	1.301 c	3.08 d	44.1 d	103.5 c	1.46 c	–
Least significant difference ($P < 0.05$)	0.071	0.22	1.9	1.1	0.22	0.841

[a] Selection index weights are given in Table 1. For each selection criterion, selection of three top-performing lines from each of three recombinant inbred line populations issued from three connected crosses (each including 100 to 104 lines), based on pooled data from the organically-managed Experiments 1 and 2 described in Table 2. Column means with different letter differ at $P < 0.05$ according to Duncan's test.

[b] Organically-managed Experiments 4–7 described in Table 2. Error term for mean comparison is germplasm × environment interaction.

[c] Conventionally-managed Experiment 3 described in Table 2.

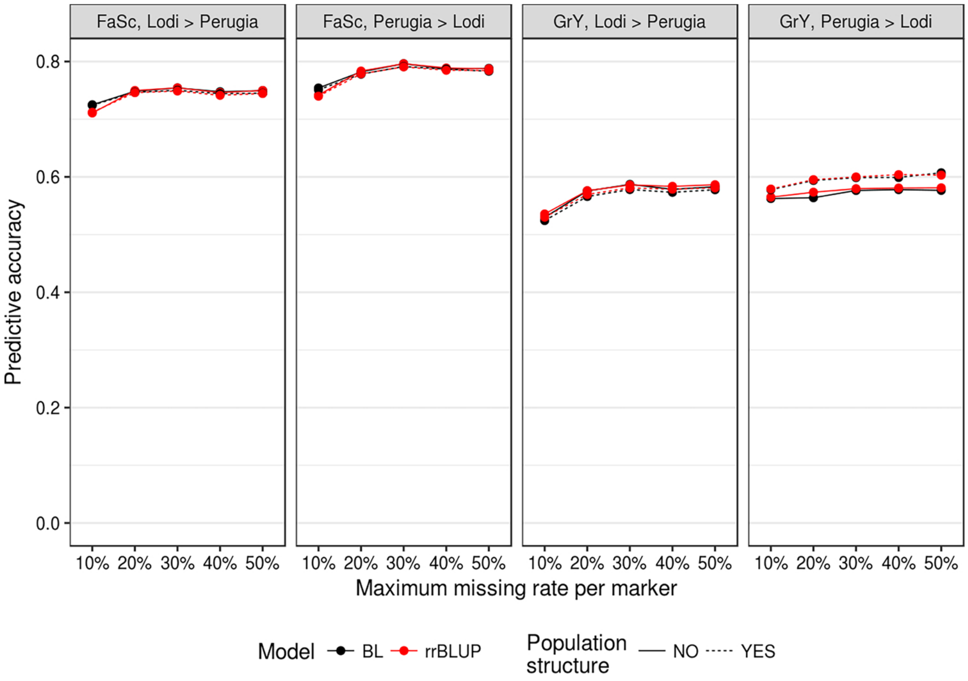

Fig. 2. Cross-environment predictive accuracy of genomic selection using Bayesian Lasso (BL) or Ridge regression BLUP (rrBLUP) models without or with imputed population structure as a function of five genotype missing data thresholds, relative to predictions in Lodi for Perugia (Lodi > Perugia) and *vice versa* (Perugia > Lodi) of a farmer acceptability score (FaSc) and grain yield (GrY). Results averaged across three pea recombinant inbred line populations (each including 100–104 lines) and 50 repetitions of 10-fold stratified cross validations per individual analysis.

Table 5
Correlation of pea line breeding values for each of eight selection criteria with pea grain yield in independent experiments.

Selection criterion[a]	Average of 4 experiments[b]	One experiment[c]
Farmer selection index	0.458[d]	0.268[d]
Breeder selection index	0.370[d]	0.242[d]
Farmer + breeder selection indexes	0.418[d]	0.257[d]
Grain yield	0.348[d]	0.328[d]
Farmer acceptability score	0.645	0.409
Breeder acceptability score	0.479	0.342[d]
Genomic selection for grain yield	0.679	0.453
Genomic selection for farmer acceptability score	0.769	0.564

[a] Using data averaged across the organically-managed Experiments 1 and 2 described in Table 2.

[b] Organically-managed Experiments 4–7 described in Table 2. Test lines are 31.

[c] Conventionally-managed Experiments 3 described in Table 2. Results averaged across three recombinant inbred line populations, each including 100–104 lines.

[d] Correlation coefficient significantly lower ($P < 0.05$) than that relative to genomic selection for farmer acceptability score.

Table 5 reports results for the preliminary comparison of eight phenotypic or genome-enabled selection criteria based on correlations between line breeding values obtained or modelled from selection experiments and line grain yields observed in independent test environments. Both the correlation assessment based on genotype yields averaged across four organically-managed experiments (which had larger and more meaningful sampling of the target environment), and that based on one conventionally-managed environment (which had larger germplasm sampling), revealed higher correlations for selection criteria that exploited genome-modelled data in comparison with those that exploited phenotypic data of a given trait (grain yield or the farmer acceptability score) (Table 5). The selection criterion based on genome-enabled prediction of the farmer score ranked consistently first for correlation value (Table 5). It significantly ($P < 0.05$) out-performed any phenotypic selection criterion in at least one assessment, with the exception of the phenotypic farmer score, which ranked first among the phenotypic criteria according to correlation results. Breeding values estimated according to the farmer selection index or the farmer acceptability score displayed higher correlation with line yields in independent environments than values estimated according to the corresponding breeder-based criteria, particularly across organically-managed test environments (Table 5).

4. Discussion

4.1. Priority traits for farmers and breeders

Various studies showed that farmers value, and would select for, several plant characteristics (Weltzien and Christinck, 2009). Accordingly, we envisaged multi-trait phenotypic selection by farmers and breeders based on selection indexes whose weight would reflect the priority assigned by these groups to different traits. Considering that breeders targeted also conventional systems beside organic ones (unlike farmers), the relatively greater importance that they attributed to two traits of putatively high interest under organic farming, *i.e.*, tolerance to ascochyta blight and greater aerial biomass [where the latter can confer greater pea competitive ability against weeds: McDonald (2003); Annicchiarico and Filippi (2007)], was not expected. However, the occurrence of ascochyta blight and *Fusarium* spp. was visually limited in all experiments, and the modest impact of these diseases in Central Italy reported by farmers from this region contributed to the difference for overall targeted plant type between these farmers and the farmers from Northern Italy or the breeders. An attitude by PPB-contributing farmers to neglect tolerance to diseases with a modest impact on crop yields was reported for barley by Ceccarelli et al. (2003). The lower importance attributed by current farmers to aerial biomass relative to breeders was actually contradicted - and likely counterbalanced in their selection index - by the somewhat higher correlation with this trait of the farmer acceptability score relative to the breeder score. Finally, the inconsistency between stated preference for early-flowering material and greater score attributed to late-flowering lines should not be seen as a real contradiction, because the current plant material tended to be intrinsically early. However, a PPB initiative may envisage a circularity process between farmers' criteria for index-based selection and farmer acceptability, by which trait preferences are periodically re-assessed in view of the specific characteristics of the genetic base and the actual desiderata suggested by the acceptability score.

4.2. Phenotypic selection criteria

Climatic data, particularly those for Lodi, confirmed the remarkable year-to-year variation for extent of winter cold stress that justified the breeding of pea for wide adaptation across geographically-contrasting Italian locations (Annicchiarico and Iannucci, 2008). Adopting just one mild-winter cropping year for multi-site selection was a limitation of this study, but the nearly identical importance attributed by breeders and farmers to cold tolerance (Table 1) suggests that a meaningful assessment of this trait in a colder selection year would have hardly affected the comparison of farmer-based *vs*. breeder-based selection indexes. Despite the lack of cold tolerance selection, the selected germplasm displayed a remarkable yield progress not only over the parent cultivars but also over the set of elite commercial cultivars across partly cold-prone independent environments. The matching of selection and target environments with respect to organic crop management conditions probably contributed to this result.

This study indicated that PPB can be useful also for a large-scale, market-oriented breeding programme performed on an inbred crop in a country with developed agriculture. One result supporting this conclusion was the distinct superiority of the farmer selection index criterion over the breeder index-based criterion both in terms of selection efficiency (+23% based on yield gains over elite commercial cultivars) and in terms of farmer's acceptability of the selected material. A second supporting result was the greater correlation with grain yield in independent environments of breeding values issued by the farmer selection index or the farmer acceptability score relative to the corresponding breeder-based criteria. These results emerged for organically-managed environments and, albeit to a somewhat lower extent, also for a conventionally-managed environment. Recalling that the acceptability score was the trait with highest impact on the selection index of farmers or breeders, a reason contributing to these results was the somewhat greater ability of the farmer acceptability score relative to the breeder score to predict genotype yields in selection and in independent environments. Actually, a simple selection criterion such as the farmer acceptability score performed quite well in terms of yield gains or correlation of breeding values with grain yields in independent organically- or conventionally-managed environments. While earlier studies usually contemplated farmer acceptability scores with three (*e.g.*, Virk et al., 2003; Asfaw et al., 2012) to five levels (*e.g.*, Ceccarelli and Grando, 2007), we proposed a nine-level score which, on the proposal of farmers and breeders to use also half values, became a 17-level score - a complexity level that may have contributed to its high sensitivity and selection efficiency. The smaller variation in genotype acceptability score values issued by farmers relative to breeders may be due to greater prudential attitude by farmers (as reported by Virk et al., 2003) and/or the fact that the farmer score assigned to each plot was actually the average of three acceptability scores expressed by farmers with possibly different views of the ideal plant type (in the presence of fairly large variation among farmers in this respect: Fig. 1).

The grain yield-based selection criterion, which is the most widespread phenotypic criterion in conventional breeding programmes, performed nearly as well as the farmer index-based criterion, while implying a lower cost for trait recording. In general, a comparison of index-based *vs*. yield-based selections merely in terms of yield progress is not completely fair, because index-based selections accounted for other traits whose importance may not emerge from the yield responses of the selected material in the test environments (or the yield responses at all). For example, the high priority attributed by breeders to tolerance to lodging did result in greater tolerance of breeder index-based selections relative to yield-based ones. In the low-cost scenario of selection based on a single trait, a cost-efficient PPB alternative to yield-based selection proved to be the selection based on the farmer acceptability score, which performed comparably in terms of yield gains under organic or conventional farming and somewhat better on the basis of correlations of its line breeding values with line yields in independent environments - while seemingly implying lower costs. A further advantage of this farmer-based criterion over grain yield was its lower susceptibility to GEI as indicated by results for the two selection environments, which was not quite expected considering that different scoring farmers in the two environments may have contributed to GEI for this selection trait. Low GEI can be particularly important for a selection criterion recorded in very few test environments.

4.3. Genomic selection criteria

This study confirmed for both target traits the similar predictive ability of BL and rrBLUP models, the negligible increase of predictive ability arising from imputing RIL structure information, and the peak of predictive ability in the range of 20–40 % maximum missing rate, that were reported for pea grain yield in Annicchiarico et al. (2017a). A peak of predictive ability is expected from the trade-off between increased information (more markers) and increased noise (higher imputation errors) arising from increasing missing rate.

Annicchiarico et al. (2017a) reported high GS predictive ability for pea grain yield, which averaged 0.72 across three RIL populations, under conditions of severe terminal drought in a phenotyping platform. Those conditions implied ecologically simple adaptive responses, which relied largely on drought stress escape *via* early onset of flowering. In addition, their assessment of GS predictions was based on intra-experiment cross-validations rather than the current, more conservative criterion based on cross-validations across independent test sites. The high predictive accuracy of GS for grain yield observed in this study highlights the interest of GS also for pea yield improvement across cropping environments, such as those of Northern and Central Italy, that are less unfavourable climatically and ecologically more complex in terms of genotype adaptive responses.

This study provided the first attempt to model genomically a complex trait such as farmer's acceptability. Our results were beyond expectation in this respect, indicating greater predictive accuracy for this trait than grain yield. Furthermore, GS for higher farmer acceptability score ranked consistently first in our preliminary comparison of eight genome-enabled or phenotypic selection criteria based on correlations of line breeding values with grain yields in independent environments. Interestingly, such correlations were higher for genome-modelled than phenotypically-estimated breeding values, for both the farmer acceptability score and grain yield. A study of wheat grain yield (Michel et al., 2017) reported already the higher correlation with phenotypic data in independent environments of genome-modelled yield data relative to the phenotypic data used to construct the genomic model. A possible reason for that could be the ability of the genome-based modelling process to reduce the noise of trait data - in a similar manner as done, for example, by proper modelling of GEI effects for yield data (Gauch et al., 2008).

High GS predictive ability was reported for a few pea traits of possible interest to farmers, such as onset of flowering and individual seed weight (Burstin et al., 2015) and biomass and straw production (Annicchiarico et al., 2018).

5. Conclusions

One key conclusion from this study is the high value of PPB for the market-oriented breeding of an inbred crop targeted to a country with developed agriculture. The adoption of PPB across geographically-contrasting researcher-managed selection environments based on a farmer selection index or a farmer acceptability score out-performed index-based or acceptability score-based selection by breeders in terms of yield progress and farmer's acceptability of novel cultivars. Phenotypic selection based on the farmer acceptability score proved to be a cost-efficient alternative to conventional grain yield-based selection, and may prove particularly valuable for early stages of field-based selection, in which grain yield evaluation is hindered by small plot size.

A second important conclusion from this study is the opportunity to support and complement PPB by genome-enabled selection for pea breeding value as expressed by farmer's acceptability and crop grain yield. In particular, GS for higher farmer's acceptability (as established from prior multi-environment farmer data) may be the most cost-efficient criterion for pea yield improvement targeted to Italian organic systems, although this finding requires confirmation, *e.g.*, from assessments based on actual yield gains. GS for the farmer acceptability score could be particularly valuable for preliminary selection within very large genotype sets, whose field-based evaluation would be prevented by its high cost.

While we envisaged pure line selection from RIL population material, our conclusions may hold true for other breeding schemes, *e.g.*, the evaluation of segregating lines within a bulk-pedigree method (Witcombe et al., 1996), or that of pure lines extracted from evolutionary populations (Murphy et al., 2005). More generally, the current success of PPB approaches highlights the high importance of knowledge exchange and mutual learning between researchers and farmers also in the context of plant breeding and in countries with developed agriculture. Also, the integration of farmers in selection programmes can be a component of a system-based breeding approach that favours the attainment of various agro-ecological and socio-economic targets (Lammerts van Bueren et al., 2018). The described PPB effort has produced one variety proposed for registration.

Declaration of interest

None.

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