Article

Genetic Diversity and Stability of Performance of Wheat Population Varieties Developed by Participatory Breeding

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Abstract: Modern agricultural systems rely on reduced crop genetic diversity, due in particular to the use of homogeneous elite varieties grown in large areas. However, genetic diversity within fields is a lever for a more sustainable production, allowing greater stability and resistance to biotic and abiotic stresses. In France, a Participatory Plant Breeding (PPB) project on bread wheat, involving farmers, facilitators and researchers, has led to the development of heterogeneous populations whose within-variety genetic diversity is expected to confer the ability to adapt to farmers' practices and environments. We studied the stability and local adaptation of ten of these farmers' populations as well as two commercial varieties in relation to their within-variety genetic diversity. Although no clear evidence of local adaptation was detected, we found that populations' grain yield and protein content were more stable over space and time respectively than those of commercial varieties. Moreover, the varieties' stability over time in terms of protein content was positively correlated with within-variety genetic diversity with no significant drawback on protein yield. These results demonstrate the wide adaptive potential of PPB populations, highlighting the importance of seed exchange networks for agrobiodiversity management and use. They emphasize the benefits of genetic diversity for stability over time, which is of great interest to farmers.

Keywords: agrobiodiversity; agroecology; decentralized selection; dynamic management; farmers varieties; local adaptation; participatory plant breeding; reciprocal transplant; temporal stability

1. Introduction

In recent decades, the increase in inter-annual climate variability has led to instabilities in agricultural production, sometimes leading to food shortages and rises in global food prices [1,2]). Projections predict an increase in frequency of extreme low yields due to adverse weather conditions [3,4], since current homogeneous varieties lack resilience to cope with climate instability as was demonstrated for European wheat varieties [5]. Therefore, it is necessary to build sustainable systems that can ensure food security through the stabilization of agricultural production [6].

Agroecology is one of the proposed alternatives to the mainstream system, advocating spatial and temporal diversification to support a sustainable and resilient agriculture based on natural

regulations [7–10]. One of the identified levers is the increase of genetic diversity at the field level which allows for better disease regulation [11,12], greater resilience to climate variability [13–15], and better ecosystems functioning [16–18]. Increased within-field diversity can be achieved by growing landraces or old varieties (i.e., in the French context, varieties cultivated before 1940 and generally showing some intrinsic genetic variability), by mixing or crossing varieties, and by growing Composite Cross Populations (CPP) or open-pollinated varieties [19]. Intraspecific diversity gives cultivated crops the ability to adapt to change and stabilize production [20,21]. The stabilizing effect is due to complementarity between genotypes exploiting resources from different ecological niches, facilitation, and sampling effects increasing the probability of having a genotype adapted to the conditions [22]. Overyielding and stability effects of variety mixtures were found to increase with components diversity [23,24]; however, no correlation was found with genome-wide genetic diversity for example in oat [25].

Genetic variability for traits involved in responses to environmental conditions is a prerequisite for populations to adapt to their environment. Local adaptation is one of the processes leading to a phenotypic differentiation of populations from the same origin but cultivated in different environments [26]. It can also be defined as the result of this process, a locally adapted population showing a greater fitness in its environment compared to populations from other environments [27]. Local adaptation was widely studied in natural populations using reciprocal transplant experiments [28,29] or common gardens [30]. Specific models are commonly used, as presented by Kawecki and Ebert [27], to study the superiority of resident populations over migrant populations, or the superiority of populations on their farm of origin compared with the same populations grown in other environments [31]. While most studies focused on natural populations, some studies assessing cultivated populations detected local adaptation for example in lentil [32] and common bean [33].

While conventional breeding produces genetically homogeneous varieties, such as pure lines in the case of selfing species, to meet the DUS (Distinction, Uniformity, Stability) requirements for variety registration and Plant Breeder Rights, alternative breeding methods such as decentralized Participatory Plant Breeding (PPB) are being used to develop more diverse varieties better adapted to organic and low-input systems [34]. Decentralized breeding aims at developing varieties adapted to the diversity of environments, taking into account Genotype $\times$ Environment interactions by breeding directly in the target environment [35,36]. Varieties can also be adapted to farmers' practices and needs by involving them in the breeding process [37], since they would select varieties with traits relevant to their particular conditions and objectives [38,39]. In France a PPB project on bread wheat, involving farmers and facilitators of the Réseau Semences Paysannes (RSP) and researchers from Diversity, Evolution and Adaptation of Populations (DEAP) team of the French National Institute for Agronomic Research (INRA), has been on-going since 2006 with the aim of developing heterogeneous varieties adapted to farmers' practices and needs, and restoring farmers' autonomy in terms of seed selection and management. The project has enabled the development of on-farm breeding tools and methods, such as experimental designs, statistical methods and collective organization between partners [40–42]. New populations have also been created and selected on-farm. Varieties bred in those PPB programs are often heterogeneous because farmers are interested in stability and adaptability to their local conditions. However, adaptation in this case has not been studied so far and although the stability of variety mixtures was demonstrated [43–45], little is known about the stability over time of evolving populations or mixtures derived from PPB, and the potential link to their genetic diversity.

To fill this gap, a two-year experiment was conducted to evaluate ten populations developed within the wheat PPB program, thereafter called *PPB populations*, compared with two commercial pure line varieties. An agronomic evaluation was carried out (for more information see Goldringer et al., [46]). The design is close to a reciprocal transplant experiment since some of the populations evaluated were tested both on their farm of origin and on other farms. In this study, we assessed the local adaptation of some of the early wheat PPB populations, as well as their genetic

diversity and spatio-temporal stability compared with the two commercial varieties. Hereafter, the term *variety* refers to both commercial varieties and PPB populations, and therefore is not used as in the UPOV definition.

2. Materials and Methods

2.1. Wheat PPB Populations and Commercial Varieties Studied

Ten wheat populations developed through the PPB project were proposed by five farmers and were evaluated on six farms (CHD, FLM, FRC, JFB, JSG, RAB), along with two commercial varieties (Renan, widely used in France by organic farmers and Hendrix, more recently released and bred for organic agriculture). These ten PPB populations, presented in Table 1, were developed with various methods based on genetically diverse varieties (selection within landraces, cross, mixtures of landraces and/or crosses) and evolved for different durations in their farm of origin. The crosses made in 2006 and subsequent years to generate new populations were based on parental varieties chosen by the farmers involved, and consisted of landraces, old lines and more recent varieties bred for organic farming.

Table 1. Varieties proposed by farmers and their make-up. Varieties included in the local adaptation analysis where the ones originated from the farms setting up the trials (X).

Variety	Farmer	Development Process	Creation Date	Evaluated in Their Farm of Origin
Saint-Priest	FLM	Derived from a Swedish variety (Progress)	2004	X
Rouge du Roc	JFB	Population derived from a mass selection within a landrace	2001	X
Savoysone	RAB	Population derived from a cross between two landraces	2010	X
Pop dynamique 2	FLM	Mixture of 3 landraces and 2 recent varieties	2010	X
Mélange du Sud-Ouest	JFB	Mixture of about 18 landraces	early 2000	X
Rocaloex	RAB	Mixture of 11 crosses	2012	X
Japhabelle	JFB	Mixture of 25 crosses	2009	X
Dauphibois	CHD	Mixture of 26 landraces and crosses	2012	X
Mélange 5 bourguignonnes	BER	Mixture of 11 landraces	2012	
Mélange1 13 pops	BER	Mixture of 13 crosses	2012	
Renan	INRA	Commercial pure line registered in 1989		
Hendrix	INRA	Commercial pure line registered in 2013		

2.2. Trial Locations

Trials were conducted during two growing seasons (2013-2014 and 2014-2015) in several locations in France, on four of the five farms from which the populations originated (CHD, Isère (38); FLM, Maine-et-Loire (49); JFB, Lot-et-Garonne (47); and RAB, Haute-Savoie (74)), and two other farms (JSG, Puy-de-Dôme (63); and FRC, Gard (30)). These farms presented different pedo-climatic conditions (Table 2 and Supplementary Material S1). Some farms presented deep and fertile soils (JSG and RAB) while others had very superficial soils (FRC, CHD). Moreover, one farm in southern France is located in a very dry and hot area (FRC) while CHD, RAB and JSG farms have colder temperatures during winter. Trials were managed by each farmer according to their own practices under organic management. The experimental design was a complete randomized block design with 2 replicates except in JSG farm in which 3 replicates were sown, and plots size ranged between 7 and 120 m^2.

Table 2. Trials information.

Farm	Growing Season	Soil Type	Sowing Date	Sowing Density	Plot Size
CHD	2013–2014	Clay-limestone	13 November 2013	300 grains/m^2	22.5 m^2
CHD	2014–2015	Clay-limestone	29 October 2014	300 grains/m^2	10 m^2
FLM	2013–2014	Sandy hydromorphic	27 November 2013	300 grains/m^2	10 m^2
FLM	2014–2015	Sandy hydromorphic	November 2014	300 grains/m^2	10 m^2
FRC	2013–2014	Clay-limestone dry	1 November 2013	23 g/m^2	10 m^2
FRC	2014–2015	Clay-limestone dry	18 December 2014	250 grains/m^2	10 m^2
JFB	2013–2014	Clay-limestone	12 December 2013	12.5 g/m^2	8 m^2
JFB	2014–2015	Clay-limestone	13 November 2014		10 m^2
JSG	2013–2014	Clay-limestone	27 November 2013	350 grains/m^2	7 m^2
JSG	2014–2015	Clay-limestone	31 October 2014	350 grains/m^2	7.8 m^2
RAB	2013–2014	Loam	2 November 2013	20 g/m^2	22.5 m^2
RAB	2014–2015	Clay-loam	29 October 2014	15 g/m^2	120 m^2

2.3. Measured Traits

Several characters were measured at the plot level: thousand kernel weight (TKW, determined on 20g of cleaned seed samples per plot), grain yield (GY, in qx/ha) and protein content (PC, in % of protein in the grain measured with NIRS technology at INRA Clermont Ferrand France on grain using near infrared spectroscopy (FOSS NIRSystem 6500)). Others traits were measured on individual plants sampled randomly (25 plants per plot) such as plant height (PH), spike weight (SW, measured on spikes after harvest, moisture under 15%) and length (SL), last leaf to spike distance (LLSD, corresponding to the peduncle length), number of spikelets per spike (NSPK), proportion of sterile spikelets (NSPK_st, which are small spikelets at the bottom and top of the spike that do not contain seeds), and spikes morphological characters (colour, presence of awns and curve). These last three traits were determined by using visual scales from 0 to 20 (possible values were 0, 5, 10, 15 and 20). For colour the scale ranged from white to dark red. For the presence of awns it went from no awns to abundant and long awns all along the spike. Curve was measured as the angle between the spike and the straw, from no curve to a 180° angle.

2.4. Genotypic Data

Ninety plants per population were sampled on five farms in 2015 (eighteen per farm) for PPB populations and thirty plants per commercial variety (six per farm). The seeds were sown at Le Moulon experimental station in autumn 2015 and a piece of leaf was collected from each seedling at the 2-leaf stage for genotyping. For each plant, total DNA was extracted from 200 mg of young leaves, using 96 well plate Whatman unifilter 800 GF/B (Whatman Ref 7700-2803) and following a protocol derived from the Qiagen's DNeasy 96 Plant Kit (Qiagen, Basel, Switzerland). 86 markers using the KASP™ method (LGC Biosearch Technologies) [47] were assessed, including 52 in non coding region of the genome (neutral zones) and 34 in candidate genes for heading precocity. These markers are presented in Appendix B. The analyses were done on polymorphic markers: 50 for neutral ones and 30 for markers in candidate genes.

2.5. Genetic Diversity

All the analysis were carried out using R software [48], and the genetic analysis using adegenet package [49]. Euclidian distances (Roger's distance) between varieties were calculated and a clustering was done using the Ward method. Within-variety diversity was assessed by computing the expected (*He*) and observed (*Ho*) heterozygosity. The former was estimated as the Nei diversity index based on the allelic frequencies at each locus [50], and the latter was estimated as the proportion of heterozygous individuals at each locus averaged over all loci that were polymorphic within the studied variety.

2.6. Local Adaptation

Local adaptation is frequently studied in ecological experiments on natural populations using translocation experiments, in which populations from different origins are sown both in their environment of origin and in other environments. Specific models are used to characterize (i) the superiority of residents over migrants in their home environment ("Local vs. Foreign") and (ii) the superiority of populations when grown in their home environment compared to other environments ("Home vs. Away") [27]. These models, which were implemented in the PPBstats package [51], were applied to a subset of the agronomic data which included PPB populations evaluated on their farm of origin (all PPB populations except Mélange1 13 pops and Mélange 5 bourguignonnes, see Table 1), and trials conducted on farms where the populations were developed (FLM, JFB, RAB and CHD).

2.6.1. Local vs. Foreign

The model used to detect a superiority of residents in their farm of origin compared to populations coming from other farms was the following type III ANOVA:

$$
\begin{aligned}
Y_{ijklm} = {} & \mu + pop_i + farm_j + year_l + MR_{ij} + (farm \times year)_{jl} + (MR \times farm)_{ij} \\
& + rep(farm \times year)_{kjl} + (MR \times farm \times year)_{ijl} + R_{ijklm}
\end{aligned}
\tag{1}
$$

with Y_{ijklm} the phenotypic value of population i in farm j, replicate k, year l, and individual m for variables measured at the individual level, pop_i the effect of population i, $farm_j$ the effect of the farm j, $year_l$ the effect of year l, MR_{ij} the status (Migrant or Resident) of population i in farm j, and R_{ijklm} the residual.

The comparison of values for all populations in sympatry vs. allopatry situation is characterized by the MR effect that gives a global measure of local adaptation [31]. The $(MR \times farm)_{ij}$ interaction term provides information on adaptation patterns specific to each farm, while the triple interaction effect detects if this adaptation is specific to the year.

2.6.2. Home vs. Away

The model used to detect a superiority of populations grown on their farm of origin compared with the same populations cultivated on other farms was the following type III ANOVA:

$$
\begin{aligned}
Y_{ijklm} = {} & \mu + pop_i + farm_j + year_l + MR_{ij} + (farm \times year)_{jl} + (MR \times pop)_{ij} \\
& + rep(farm \times year)_{kjl} + (MR \times pop \times year)_{ijl} + R_{ijklm}
\end{aligned}
\tag{2}
$$

with Y_{ijklm} the phenotypic value of population i in farm j, replicate k, year l, and individual m for variables measured at the individual level, pop_i the effect of population i, $farm_j$ the effect of the farm j, $year_l$ the effect of year l, MR_{ij} the status (Migrant or Resident) of population i in farm j, and R_{ijklm} the residual.

As in model 1, the MR effect tests for a global local adaptation of populations to their original farm. Here the interaction term $(MR \times pop)_{ij}$ provides information on adaptation patterns specific to each population, while the triple interaction effect detects if this adaptation is specific to the year.

2.7. Temporal Stability

To study varieties' stability over years in a given farm, the following model was applied to each variable and variety:

$$
Y_{ijkl} = Year_i + Farm_j + (Farm \times Year)_{ij} + \epsilon_{ijkl}
\tag{3}
$$

with Y_{ijkl} the phenotypic value of the studied variety, $Year_i$ the effect of year i, $Farm_j$ the effect of farm j, $(Farm \times Year)_{ij}$ the interaction effect of year i and farm j, k is the replicate, l is the individual plant

for variables measured at the individual level, and ϵ_{ijkl} is the residual. All effects were considered random and therefore variances associated with the effects were estimated using the REML procedure.

For each variety and each effect (*Year*, *Farm*, *Farm × Year* and the residual) a coefficient of variation was calculated as the standard deviation associated with the effect divided by the mean of the variety across all farms and years. These coefficients of variation were used to compare the variation due to each effect between varieties. Stability over years in a given farm was characterized by the sum of the *Year* and (*Farm × Year*) coefficients of variation, while the Residual coefficient of variation was used to characterize the phenotypic variability of a variety for traits measured at the individual level. Mean comparisons between PPB populations and commercial varieties stability was done using the Mann-Whitney test. Correlation coefficients were then calculated between genetic diversity (*He*), phenotypic variability (either for each trait measured at the individual level or for an index calculated as the mean of the coefficients of variation of each trait measured at the individual level, the latter used to represent the overall heterogeneity of the variety) and stability (taken here as $(-1) \times$ coefficient of variation associated with the *Year* and (*Farm × Year*) effects).

2.8. The Participatory Dimension

Researchers, farmers and facilitators involved in the PPB project meet regularly between field visits, usually during winter when farmers have more time, to discuss ongoing research projects, new results and perspectives. At a meeting in winter 2015–2016, the raw results were first presented to farmers and facilitators and the discussion led to ideas for further analysis and testing of the data set. Farmers were particularly interested in the temporal stability of the different varieties and its possible link with genetic diversity and intravarietal phenotypic diversity. The results of the new analyses were then presented at a meeting a few months later, which allowed for discussion and a common understanding of the new results. This is what is presented here.

3. Results

3.1. Genetic Diversity

3.1.1. Genetic Distances between Varieties

The two commercial varieties appeared clearly distinct from the PPB populations grouped together, as shown in Figure 1. Some of the PPB populations appeared quite similar, probably because these mixtures have common components. For example, Mélange1-13 pops, Dauphibois, Rocaloex and Japhabelle mixtures are partly composed of the same crosses whose parents were mixed in Mélange-du-Sud-Ouest population. One of Savoysone's parents (Blanc de Saône) is very close genetically to three of Mélange-5-Bourguignonnes' landrace components (Blé de la Saône, Blanc hâtif de la Saône and Blanc de haute Saône), which may explain the genetic proximity of these two PPB populations.

3.1.2. Within-Variety Genetic Diversity

As expected, pure line commercial varieties exhibited low to no genetic diversity, while PPB populations with the highest level of diversity were mixtures (Table 3). Hendrix showed a little genetic diversity, which was due to one individual that exhibited differences for three markers in neutral zones. This punctual diversity is most probably due to a residual variability within the variety.

He was lower for markers in candidate genes (CA) than in neutral zones (NE), and the ranking of populations was not the same, meaning that these populations were under different levels of selection pressure on these zones of the genome. Savoysone, a population derived from a cross between two landraces, proved to be as diverse as Mélange-5-Bourguignonnes, a mixture of landraces, when looking at He_{NE}. This population also exhibited more heterozygous individuals than all other varieties for NE and CA markers (0.011 and 0.010 respectively), probably due to the fact that the cross was made more

recently than those of Mélange1 13 pops, Rocaloex, Japhabelle and Dauphibois that were created in 2006, and was probably still segregating.
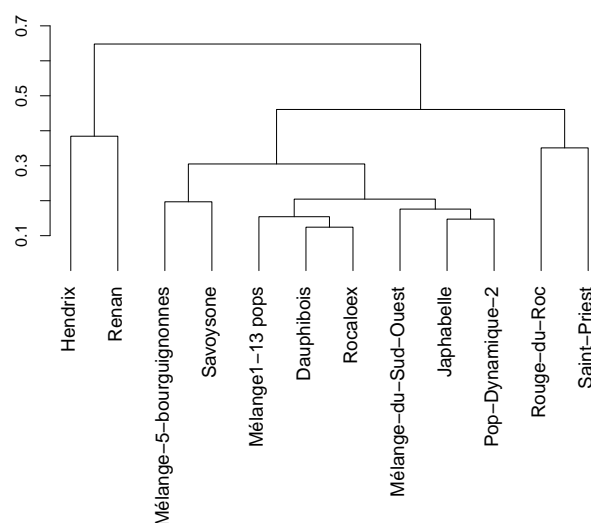

Figure 1. Clustering of the PPB populations and the two commercial pure lines on the Rogers' distances using the Ward clustering method. The length of the branches represent the distance between two varieties.

Table 3. Expected heterozygosity (*He*) and observed heterozygosity (*Ho*) of each variety for neutral markers (NE) and markers in candidate genes (CA). "-" means all locus were monomorphic for the variety.

Population	Number of Individuals	*He*		*Ho*	
		NE	CA	NE	CA
Renan	30	0.000	0.000	-	-
Hendrix	29	0.004	0.000	0.000	0.000
Rouge-du-Roc	90	0.084	0.062	0.001	0.000
Saint-Priest	90	0.129	0.081	0.005	0.007
Mélange-5-bourguignonnes	90	0.283	0.128	0.010	0.004
Savoysone	90	0.290	0.109	0.011	0.010
Pop-Dynamique-2	90	0.361	0.205	0.006	0.006
Mélange-du-Sud-Ouest	90	0.363	0.233	0.010	0.009
Rocaloex	90	0.377	0.157	0.002	0.001
Japhabelle	90	0.388	0.146	0.008	0.004
Mélange1-13 pops	90	0.396	0.150	0.007	0.002
Dauphibois	90	0.402	0.198	0.004	0.002

3.1.3. Correlations between Genetic Diversity and Phenotypic Variability

For most traits the correlation between phenotypic variability, estimated as the residual coefficient of variation in eq.3, and genetic diversity, both for NE and CA markers, was high and significant, except for SW, NSPK_st and to a lesser extent curve, for which commercial varieties seemed to be as variable as PPB populations (Table 4). This has already been observed in another study [52], in which the phenotypic variance of commercial varieties for spike weight and non morphological traits was large, which showed the sensitivity of these varieties to environmental heterogeneity. The correlations between mean traits variability and He_{NE} (0.699, $p = 0.011$) on the one hand, and He_{CA} (0.607, $p = 0.036$) on the other hand, were also highly positive and significant.

Finally, there were rather high correlations between varieties' genetic diversity and their average trait value for PH (NE: 0.71, $p = 0.010$; CA: 0.73, $p = 0.0072$), which was due to the fact that the two

homogeneous commercial varieties were also the shortest. For all other traits, there was no correlation between genetic diversity and average trait value.

Table 4. Correlation between phenotypic variability estimated as the residual coefficient of variation (eq. 3) and genetic diversity for neutral markers (NE) and markers in candidate genes (CA) for the 12 varieties for variables measured at the individual level. **Bold**: significant at 5%, *Italic*: significant at 10%. PH: plant height; LLSD: last leaf to spike distance; SL: spike length; SW: spike weight; NSPK: number of spikelets per spike; NSPK_st: proportion of sterile kernels.

	NE	**CA**
PH	**0.862**	**0.815**
LLSD	**0.832**	**0.891**
awns	**0.876**	**0.869**
color	**0.865**	**0.773**
curve	*0.556*	*0.507*
SL	**0.717**	**0.580**
SW	−0.243	−0.235
NSPK	**0.814**	**0.716**
NSPK_st	0.355	0.203

3.2. Local Adaptation

Tables 5 and 6 present the ANOVA results for all characters. Information on mean and standard error of each variety for each farm and year is available in Supplementary Material S2. The MR effect was significant for all characters except GN, either as main effect or involved in interactions with other factors: SL, SW, NSPK_st and PC for both models (Tables 5 and 6) and NSPK, TKW and GY only in the Home vs Away model (Table 5).

Table 5. ANOVA results of the Local vs. Foreign analysis: spike length (SL); spike weight (SW); number of spikelets per spike (NSPK); proportion of sterile kernels (NSPK_st); thousand kernel weight (TKW); protein content (PC); number of grains per m^2 (GN); grain yield (GY). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. [a]: individual data; [b]: plot data.

	SL [a]			**SW** [a]			**NSPK** [a]			**NSPK_st** [a]		
	Df	**SS**	**F**	**Df**	**SS**	**F**	**Df**	**SS**	**F**	**Df**	**SS**	**F**
farm	3	75,850.5	111.42 ***	3	116.3	97.89 ***	3	2085.3	151.19 ***	3	0.3	23.15 ***
pop	7	35,836.1	22.56 ***	7	50.9	18.36 ***	7	1849.9	57.48 ***	7	1.2	39.48 ***
year	1	66,707.2	293.96 ***	1	113.5	286.65 ***	1	8.3	1.81	1	1.8	405.72 ***
MR	1	297	1.31	1	0.1	0.23	1	8.3	1.82	1	0	9.56 **
farm × year	3	69,552.6	102.17 ***	3	20.3	17.11 ***	3	357.1	25.89 ***	3	0.4	26.91 ***
farm × MR	3	2578.8	3.79 *	3	2.6	2.16	3	13.4	0.97	3	0.1	4.8 **
rep/farm × year	8	18,186.1	10.02 ***	8	21.1	6.67 ***	8	165.6	4.5 ***	8	0.2	6.29 ***
farm × year × MR	4	3718.8	4.1 **	4	9.6	6.05 ***	4	26	1.42	4	0.1	5.87 ***
Residuals	3100	703,478.4		3080	1219.4		3080	14,160.1		3076	13.4	

	TKW [b]			**PC** [b]			**GN** [b]			**GY** [b]		
	Df	**SS**	**F**	**Df**	**SS**	**F**	**Df**	**SS**	**F**	**Df**	**SS**	**F**
farm	3	189.8	15.81 ***	3	48.9	44.85 ***	3	2,218,503.5	92.06 ***	3	5485.3	96.82 ***
pop	7	604.7	21.58 ***	7	31.6	12.42 ***	7	39,4951.2	7.02 ***	7	400.6	3.03 **
year	1	158.1	39.5 ***	1	152.4	419.4 ***	1	252,074.2	31.38 ***	1	870.7	46.11 ***
MR	1	5.7	1.42	1	2.8	7.58 **	1	177.3	0.02	1	0.4	0.02
farm × year	3	100	8.32 ***	3	82.5	75.66 ***	3	1,214,761.2	50.41 ***	3	2717.9	47.97 ***
farm × MR	3	3	0.25	3	3.3	3.06 *	3	47,465.2	1.97	3	95.4	1.68
rep/farm × year	8	59.8	1.87	8	4.3	1.48	8	165,843.4	2.58 *	8	249	1.65
farm × year × MR	4	14.2	0.89	4	1.2	0.82	4	49,122.2	1.53	4	81.3	1.08
Residuals	95	380.4		94	34.2		89	714,887.2		89	1680.7	

Migrants exhibited significantly higher PC than residents only in two farms and for two populations (Figure 2). For all other characters the results were contrasted with either migrants or residents showing superiority depending on the farm or population. While residents exhibited a higher NSPK_st in RAB farm for both years, results in FLM farm showed opposite effect regarding MR

status depending on the year (Figure 3a). Moreover, only the two populations developed in RAB farm presented a higher NSPK_st for both years (Savoysone and Rocaloex), while for other populations the differences were either insignificant or inconsistent from one year to the next (Figure 3b). For SW (Figure 4), the superiority of residents over migrants depended on the farm, the year and the population, with no consistent trend, except that on JFB's farm the resident populations had a larger SW, and that two JFB's populations (Japhabelle and Rouge du Roc) showed a significantly larger SW on their farm of origin. Finally, Rouge du Roc exhibited a lower PC at home than in foreign environments, which could be explained by a dilution effect since this population also presented a higher SW at home.

Table 6. ANOVA results of the Home vs. Away analysis: spike length (SL); spike weight (SW); number of spikelets per spike (NSPK); proportion of sterile kernels (NSPK_st); thousand kernel weight (TKW); protein content (PC); number of grains per m^2 (GN); grain yield (GY). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. [a]: individual data; [b]: plot data.

	SL [a]			SW [a]			NSPK [a]			NSPK_st [a]		
	Df	SS	F	Df	SS	F	Df	SS	F	Df	SS	F
farm	3	75,850.5	112.65 ***	3	116.3	101.03 ***	3	2085.3	151.94 ***	3	0.3	23.52 ***
pop	7	35,836.1	22.81 ***	7	50.9	18.95 ***	7	1849.9	57.77 ***	7	1.2	40.1 ***
year	1	66,707.2	297.21 ***	1	113.5	295.84 ***	1	8.3	1.81	1	1.8	412.1 ***
MR	1	297	1.32	1	0.1	0.24	1	8.3	1.82	1	0	9.71 **
farm × year	3	69,552.6	103.29 ***	3	20.3	17.66 ***	3	357.1	26.02 ***	3	0.4	27.33 ***
pop × MR	7	5048.4	3.21 **	7	15.4	5.72 ***	7	59.7	1.86	7	0.1	3.78 ***
rep/farm × year	8	18,223.1	10.15 ***	8	21.1	6.89 ***	8	165.4	4.52 ***	8	0.2	6.38 ***
pop × year × MR	15	12,269.9	3.64 ***	15	40.4	7.02 ***	15	118.5	1.73 *	15	0.3	5.03 ***
Residuals	3085	692,420.7		3065	1175.8		3065	14,021.4		3061	13.1	

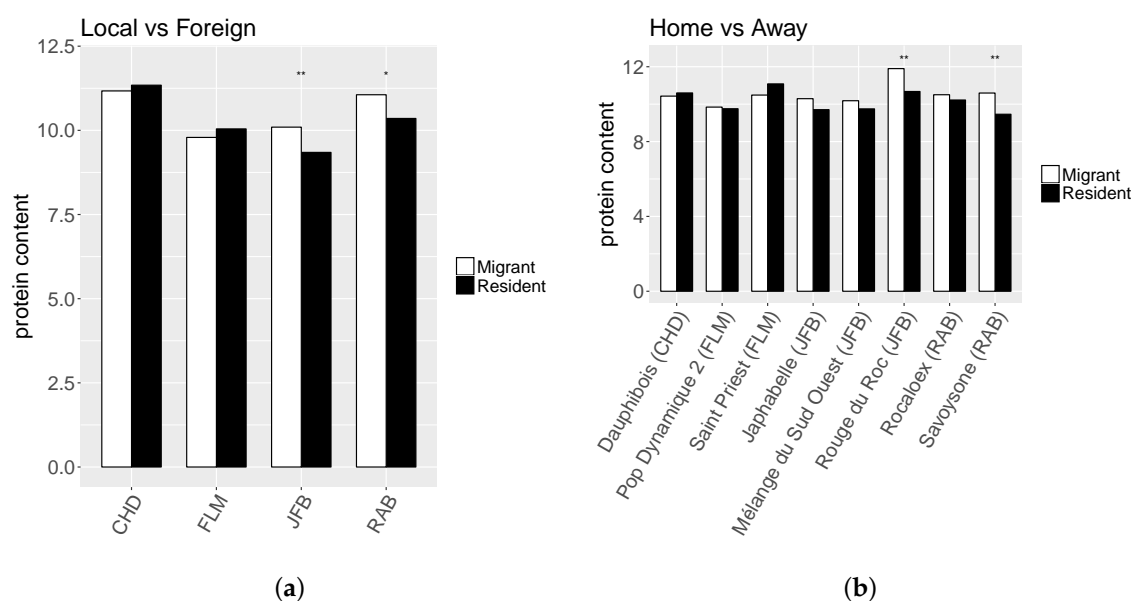|	TKW [b]			PC [b]			GN [b]			GY [b]		
	Df	SS	F	Df	SS	F	Df	SS	F	Df	SS	F
farm	3	189.8	17.85 ***	3	48.9	45.27 ***	3	2,218,503.5	96.92 ***	3	5485.3	111.27 ***
pop	7	604.7	24.37 ***	7	31.6	12.54 ***	7	394,951.2	7.39 ***	7	400.6	3.48 **
year	1	158.1	44.61 ***	1	152.4	423.35 ***	1	252,074.2	33.04 ***	1	870.7	52.98 ***
MR	1	5.7	1.61	1	2.8	7.65 **	1	177.3	0.02	1	0.4	0.02
farm × year	3	100	9.4 ***	3	82.5	76.38 ***	3	1,214,761.2	53.07 ***	3	2717.9	55.13 ***
pop × MR	7	7.8	0.31	7	6.2	2.47 *	7	70,444.7	1.32	7	170.9	1.49
rep/farm × year	8	59.8	2.11 *	8	4.3	1.5	8	166,093.2	2.72 *	8	248.9	1.89
pop × year × MR	15	106.2	2 *	15	4	0.75	15	176,163.7	1.54	15	470.7	1.91 *
Residuals	80	283.6		79	28.4		74	564,616.3		74	1216	

Figure 2. Least-square means for the interaction effects between "migrant vs resident" status and (**a**) farm ("Local vs Foreign") or (**b**) population origin ("Home vs Away", the farm of origin of each population is indicated in brackets) for protein content (PC).
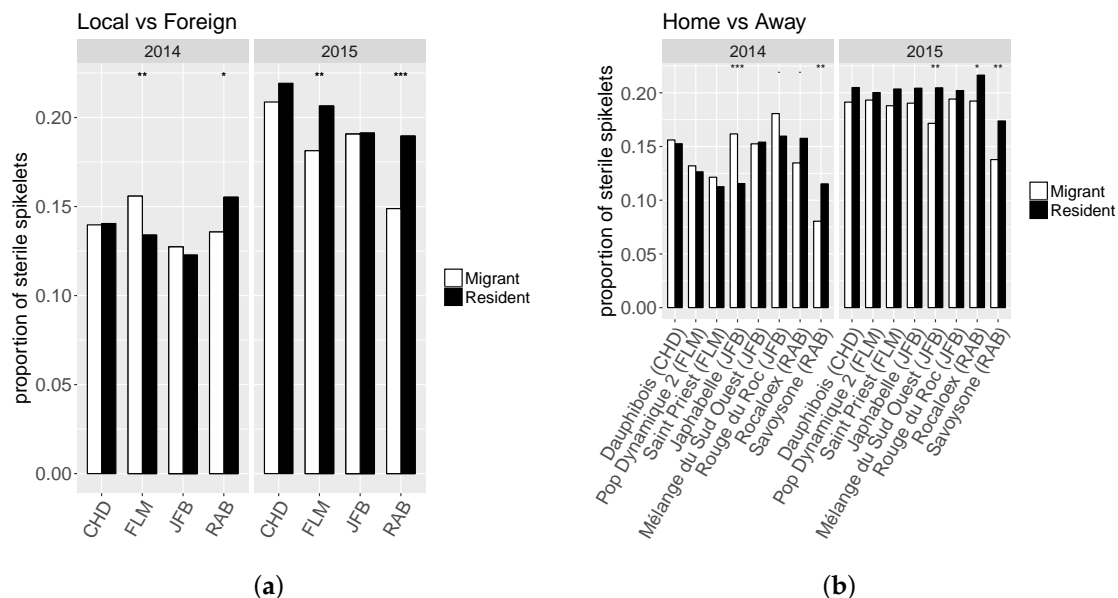
Figure 3. Least-square means for the interaction effects between "migrant vs resident" status and (**a**) farm ("Local vs Foreign") or (**b**) population origin ("Home vs Away", the farm of origin of each population is indicated in brackets) for the proportion of sterile kernels (NSPK_st).
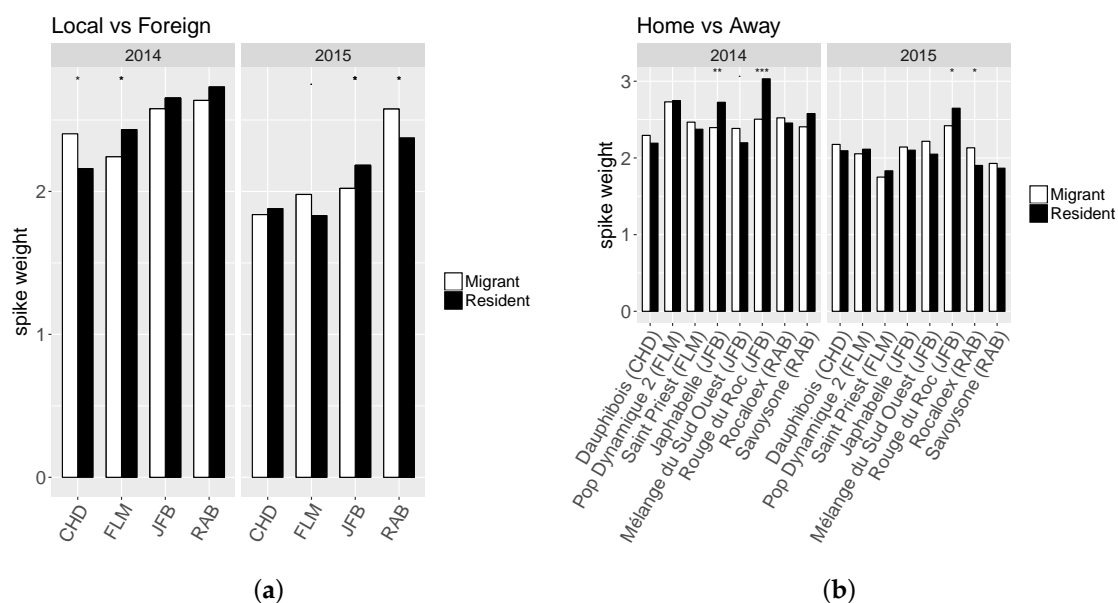

Figure 4. Least-square means for the interaction effects between "migrant vs resident" status and (**a**) farm ("Local vs Foreign") or (**b**) population origin ("Home vs Away", the farm of origin of each population is indicated in brackets) for spike weight (SW).

3.3. Spatio-Temporal Stability and Its Link with Genetic and Phenotypic Variability

3.3.1. Spatio-Temporal Stability

Stability over time within a farm can be characterized for each trait by the sum of the *Year* and (*Farm × Year*) coefficients of variation. Table 7 shows, for each variety, characters for which the variability explained by at least one effect is higher than that of the residuals (which correspond to the intra-environment variability). The results for the other traits are presented in Appendix A. The average temporal stabilities of PPB populations and commercial varieties were close for PH (0.113 and 0.132 respectively) and TKW (resp. 0.050 and 0.052). However, PPB populations were more stable over time than commercial varieties for PC (resp. 0.238 and 0.346, $p = 0.030$) and tended to be more

stable for GN (resp. 0.256 and 0.330, $p = 0.27$) and GY (resp. 0.284 and 0.353, $p = 0.27$) although not significantly. Considering stability across farms, only GN and GY showed significant differences as commercial varieties were more strongly varying than PPB populations (resp. 0.368 and 0.218, $p = 0.030$ for GN and 0.366 and 0.228, $p = 0.030$ for GY). These two traits presented similar patterns of responses to all effects, which indicates that yield stability was probably mainly due to stability in grain number setting and therefore a stability in tillering capacity. We noticed that for PC none of the variety types (PPB or commercial) were sensitive to the *Farm* effect. Variability due to intra-environment heterogeneity (Residuals) was sometimes higher for commercial varieties than for PPB populations (GY, GN, LLSD, SW, NSPK_st, see Appendix A), but it was only marginally significant for LLSD and GY ($p = 0.06$).

Table 7. Coefficients of variation for each effect. Y: Year; F: Farm; FY: Farm × Year interaction; Res: Residual. PPB: PPB populations; CV: Commercial varieties. **Bold**: significant at 5%, *Italic*: significant at 10%. [a]: individual data; [b]: plot data. PH: plant height; TKW: thousand kernel weight; PC: protein content; GN: number of grains per m^2; GY: grain yield.

	PH [a]				TKW [b]							
	Y	F	FY	Res	Y	F	FY	Res				
Dauphibois	0.000	*0.140*	**0.100**	0.099	0.031	0.042	**0.062**	0.042				
Japhabelle	0.000	*0.139*	**0.101**	0.087	0.000	0.043	**0.063**	0.031				
Mélange-1	0.000	0.148	**0.118**	0.089	0.000	0.065	**0.065**	0.031				
Mélange-5	0.044	**0.173**	**0.090**	0.082	0.012	0.076	**0.053**	0.034				
Mélange-SO	0.000	0.148	**0.121**	0.086	0.025	*0.075*	0.038	0.039				
Pop-Dyn-2	0.000	*0.131*	**0.093**	0.076	0.003	**0.085**	0.000	0.034				
Rocaloex	0.000	**0.150**	**0.086**	0.091	0.006	0.066	**0.046**	0.032				
Rouge-du-Roc	0.000	0.143	**0.127**	0.074	0.000	0.060	0.050	0.060				
Saint-Priest	0.018	**0.137**	**0.081**	0.072	0.011	**0.073**	0.019	0.036				
Savoysone	0.037	0.147	**0.112**	0.078	0.000	**0.083**	0.016	0.036				
Hendrix	0.000	0.138	**0.125**	0.075	0.000	0.055	**0.068**	0.041				
Renan	0.000	0.119	**0.140**	0.083	0.000	*0.059*	**0.035**	0.031				
Mean PPB	0.010	0.146	0.103	0.083	0.009	0.067	0.041	0.038				
Mean CV	0.000	0.128	0.132	0.079	0.000	0.057	0.052	0.036				
	PC [b]				GN [b]				GY [b]			
	Y	F	FY	Res	Y	F	FY	Res	Y	F	FY	Res
Dauphibois	*0.155*	0.069	*0.097*	0.072	0.000	0.228	**0.234**	0.115	0.000	0.223	**0.236**	0.133
Japhabelle	*0.142*	0.000	**0.105**	0.053	0.000	0.217	**0.292**	0.173	0.000	0.204	**0.326**	0.162
Mélange-1	*0.120*	0.000	**0.103**	0.040	0.134	0.221	0.196	0.246	0.152	0.208	0.242	0.258
Mélange-5	0.101	0.000	**0.100**	0.061	0.000	0.264	0.146	0.212	0.063	0.286	0.162	0.207
Mélange-SO	**0.173**	0.000	*0.089*	0.081	0.000	0.240	**0.234**	0.139	0.000	0.235	**0.255**	0.113
Pop-Dyn-2	0.088	0.000	*0.096*	0.076	0.000	0.149	**0.343**	0.176	0.000	0.216	**0.343**	0.175
Rocaloex	**0.162**	0.000	**0.100**	0.054	0.000	0.198	**0.307**	0.125	0.000	0.205	**0.308**	0.113
Rouge-du-Roc	*0.139*	0.051	**0.096**	0.065	0.000	0.270	0.225	0.286	0.000	0.266	0.226	0.243
Saint-Priest	**0.135**	0.000	**0.095**	0.053	0.000	0.149	**0.229**	0.170	0.000	0.183	**0.272**	0.150
Savoysone	*0.174*	0.000	**0.113**	0.052	0.000	0.247	**0.222**	0.134	0.000	0.257	**0.246**	0.142
Hendrix	**0.249**	0.000	**0.123**	0.058	0.000	0.331	*0.382*	0.266	0.000	0.337	**0.404**	0.261
Renan	**0.247**	0.000	**0.073**	0.047	0.000	0.404	*0.279*	0.271	0.000	0.395	**0.302**	0.254
Mean PPB	0.139	0.012	0.099	0.061	0.013	0.218	0.243	0.178	0.022	0.228	0.262	0.170
Mean CV	0.248	0.000	0.098	0.052	0.000	0.368	0.330	0.268	0.000	0.366	0.353	0.258

3.3.2. Correlations between Diversity and Stability

For most traits, stability over time was not significantly correlated with neutral genetic diversity (Table 8), except for PC with a correlation between temporal stability and He_{NE} of 0.582 ($p = 0.047$). This correlation was even greater when considering markers located in candidate genes for precocity: 0.632 ($p = 0.028$). This greater temporal stability for PC was not linked to a lower variety effect in protein production since the correlation was 0.384 ($p = 0.218$). Although there was a trend towards greater temporal stability of PC associated with higher mean phenotypic variability, the correlation was not significant (0.483, $p = 0.11$). There were negative but moderate correlations between temporal stability and variety effect for GN (-0.581, $p = 0.048$) and GY (-0.537, $p = 0.072$), which makes it possible to identify PPB populations that present a good trade-off between productivity and temporal stability.

Considering stability across farms, only three traits presented significant correlations between stability and genetic diversity: NSPK (NE: -0.578, $p = 0.049$), GN (NE: 0.646, $p = 0.023$; CA: 0.678, $p = 0.015$) and GY (NE: 0.730, $p = 0.007$; CA: 0.711, $p = 0.0095$). This greater stability in GY and GN linked to a higher genetic diversity is very interesting considering the fact that this stability is not correlated with a lower variety effect (-0.152, $p = 0.638$ for GN; -0.435, $p = 0.157$ for GY). For NSPK the differences in stability between varieties were very small (Table A1), so this correlation probably has little biological significance.

Table 8. Correlation between temporal and spatial stability (-cv) and genetic diversity (He_{NE}), and between temporal and spatial stability and variety effect. PH: plant height; LLSD: last leaf to spike distance; SL: spike length; SW: spike weight; NSPK: number of spikelets per spike; NSPK_st: proportion of sterile kernels; TKW: thousand kernel weight; PC: protein content; GN: number of grains per m^2; GY: grain yield. **Bold**: significant at 5%, *Italic*: significant at 10%.

	Temporal			Spatial		
	Diversity		Variety Effect	Diversity		Variety Effect
	NE	CA		NE	CA	
PH	0.455	0.487	0.233	-0.408	-0.337	*-0.568*
LLSD	-0.185	-0.147	**-0.770**	-0.270	-0.143	-0.242
SL	0.222	0.287	0.135	-0.049	-0.069	*0.503*
SW	0.374	0.444	0.136	0.302	0.260	0.153
NSPK	0.480	0.361	0.475	**-0.578**	-0.426	-0.342
NSPK_st	0.300	0.427	**0.775**	0.135	-0.033	-0.290
TKW	-0.182	-0.124	-0.062	-0.068	-0.187	0.194
PC	**0.582**	**0.632**	0.384	-0.033	-0.111	-0.425
GN	0.072	0.140	**-0.581**	**0.646**	**0.678**	-0.152
GY	0.060	0.190	*-0.537*	**0.730**	**0.711**	-0.435

4. Discussion

4.1. Genetic and Phenotypic Diversity

Populations developed through the French wheat PPB programme were diverse with different levels of genetic diversity, which corroborates the fact that PPB programs usually lead to the development of a wide diversity of varieties [53]. On the contrary, commercial varieties were genetically homogeneous as expected. These different levels of genetic diversity in PPB populations reflect their history and farmers' practices, as the most diversified mixtures in terms of number and type of components also had larger within-variety genetic diversity.

Since phenotypic variability estimated on the basis of the residual coefficient of variation is influenced by the means of the traits, it is difficult to compare commercial varieties with PPB varieties for PH and LLSD based on the coefficient of variation because the mean values for Renan and Hendrix are much lower. Visually, plots of commercial varieties appeared more homogeneous for PH and LLSD which makes the identification of potential off-types easier during fixation or multiplication. For the other traits, phenotypic variability measured on individual plants was not necessarily lower for commercial pure lines than for PPB varieties under organic conditions despite the strict evaluation for homogeneity they undergo for the registration to the official catalogue. This is in line with the findings of Serpolay et al., [52], and highlights the sensitivity of these commercial varieties to heterogeneous conditions, as organic farming is characterized by environmental heterogeneity.

4.2. Detection of Local Adaptation

Decentralized selection is based on the fact that varieties bred in a specific environment will adapt to this environment, under the effect of both human and natural selection. As such, local adaptation is expected in these populations selected on-farm. However, although genetic [54,55]

and phenotypic (plant height, earliness [56,57]) differentiation between populations evolving in contrasted environments were already demonstrated [58,59], our analysis did not detect general local adaptation patterns on these PPB varieties. Several factors could explain these results.

First of all, the experimental design was not optimized to study local adaptation as the varieties used were of very diverse origins (an old variety, a selection of a plant within a landrace, a cross and several mixtures) with a wide range of within-variety genetic diversity, and were selected and cultivated for contrasting numbers of years on their original farms. The most recent ones might not have had enough time to adapt to their environment. This is inherent of participatory research where a compromise has to be found between farmers' wishes and the experimental design format. The population that showed the strongest sign of local adaptation for spike weight was Rouge du Roc, the population that was cultivated the longest in its farm of origin.

Secondly, here only the farm effect was studied. However, agricultural systems are different from natural ones. We can expect cultivated populations to adapt not only to pedo-climatic conditions but also to farmers' practices that were not taken into account in this analysis. Although the environments had contrasted soil and climate characteristics, these characteristics and farmers' practices may not have been sufficiently contrasted to detect local adaptation, which is better detected at large spatial scales [60]. It is also possible that climatic variability tempered local adaptation if this variability was larger than spatial variability between environments [30].

Farmers select their populations based on an overall assessment of their behaviour or a combination of traits, rather than on individual traits. Although grain yield is of importance to farmers and summarizes the global vigor of the population, it might not always be the primary trait farmers select for, and trade-off between traits may have limited their maximization. Moreover, depending on their context and their objectives, farmers have different selection targets (yield, quality, resistance to lodging, morphological characteristics, . . .) and selection practices, so that populations will not evolve the same way under farmers' selection. Another study assessing local adaptation of wheat landraces using different kinds of design and models [61] found that varieties in different farms evolved inconsistently across farms, and not necessarily towards an improvement of agronomic performance. Finally, the analysis was done on traits associated with but not directly corresponding to fitness, and these traits may not be the most relevant to measure local adaptation [52].

However, the fact that foreign populations behave as well, sometimes better, than local ones, shows the flexibility of these varieties [62], which depends more on their inherent diversity than their local adaptation. This is highly relevant information for farmers collectives as it underlines the importance of seeds and information exchanges within their network so that each farmer can benefit from the work of the collective. It also supports the statement that farmers should be encouraged to collectively organise and test many varieties in order to select a few that can best fit their practices and pedoclimatic conditions. This selection can be organized in the framework of a PPB programme developing the most appropriate methods and tools for this task [40–42,63].

4.3. Spatio-Temporal Stability of PPB Populations and Commercial Varieties

Farmers are looking for stability in production over time, especially in organic farming where biotic and abiotic stresses cannot be tempered by chemical inputs. In France, this has resulted in an increased use of variety mixtures in recent years [64] by farmers in organic as well as in conventional farming. In another approach studying stability on the same experiment [46] using dynamic indicators (Wricke's ecovalences), it was found that all PPB populations were more stable over farms than commercial lines for GY, and some of them were more stable for PC than the two commercial lines. All PPB populations were also more stable in time than the two commercial lines for PC. However these indicators are not the most relevant for farmers as they consider the relative response with regards to the mean per farm or year. Here, using a static indicator of stability, results show that PPB populations were more stable in time than commercial varieties for protein content, and that this stability was linked to the genetic diversity within populations. Despite the fact that only two

commercial varieties were studied here, they are very commonly used by organic farmers in France, especially Renan for its rusticity. Results showed that PPB populations were more stable over time than Hendrix for grain yield; however, Renan's temporal stability was closer to the ones of populations. This might explain why this variety has been, and continues to be, widely cultivated by organic farmers in France, representing 15% of organic wheat acreage in 2015 [65].

Results showed that commercial varieties were less stable across farms in terms of grain yield than PPB populations, which highlights the fact that homogeneous commercial varieties are sensitive to poor conditions but valorize better fertile environments [46]. This productivity stability of PPB populations seems to be associated with greater stability in tillering capacity rather than in grain filling as indicated by the more stable grain number per m^2. Raggi et al. [66] obtained similar results when comparing a Composite Cross Population (CCP) and a mixture of lines selected within this CCP with control lines selected under high input conditions, the heterogeneous varieties showing higher static and dynamic stability over environments than the homogeneous controls.

No correlation was found between stability of grain yield and genetic diversity, while studies showed that more varietal diversity usually leads to greater stability [45,67]. While general genetic diversity at neutral markers is not correlated with yield stability, this stability might be well explained by the diversity in specific loci involved in traits related to plant competition for resources [25].

5. Conclusions

The analyses presented in this study show that PPB populations are flexible enough to behave well in contrasted environments, and that they present temporal and spatial stability for protein and grain yield respectively. Thus, this kind of varieties seems suitable for organic or agroecological practices in a context of climate change in which heterogeneity is present both in space and time. The development of populations relying on diversity and the reappropriation of on-farm breeding knowledge by a collective of farmers, facilitators and research teams contribute to other important aspects of agroecology that are seed sovereignty [68] and farmers empowerment. The autonomy conferred by the on-farm selection and production of seeds, together with the combination of farmers' knowledge [69] with scientific approaches, contributes to the development of varieties compatible with a sustainable agriculture. Finally, given the within- and between-variety genetic diversity of these varieties, their deployment in agricultural landscapes is expected to increase the cultivated genetic diversity at the landscape level. This should also contribute to stabilizing the agricultural production since diversity at larger spatial scales offers a buffer against biotic and abiotic stresses [10,70].

Abbreviations

The following abbreviations are used in this manuscript:

GY	grain yield
LLSD	last leaf to spike distance
TKW	thousand kernel weight
GN	number of grains per m^2
NSPK	number of spikelets per spike
PC	protein content
PH	plant height
PPB	Participatory Plant Breeding
NSPK_st	proportion of sterile kernels
SL	spike length
SW	spike weight

Appendix A. Temporal Stability for Remaining Traits

Table A1. Variation coefficients for each factor. Y: Year; F: Farm; FY: Farm × Year interaction; Res: Residual. PPB: PPB populations; CV: Commercial varieties. **Bold**: significant at 5%, *Italic*: significant at 10%. [a]: individual data; [b]: plot data. LLSD: last leaf to spike distance; SL: spike length; SW: spike weight; NSPK: number of spikelets per spike; NSPK_st: proportion of sterile kernels.

	LLSD [a]				SL [a]							
	A	**F**	**AF**	**Res**	**A**	**F**	**AF**	**Res**				
Dauphibois	0.112	0.205	**0.152**	0.252	0.065	0.041	**0.075**	0.171				
Japhabelle	0.089	0.166	**0.180**	0.223	*0.083*	0.056	**0.061**	0.154				
Mélange-1	0.087	0.209	**0.166**	0.247	0.075	0.023	**0.103**	0.172				
Mélange-5	0.195	0.185	**0.176**	0.240	*0.078*	0.049	**0.055**	0.145				
Mélange-SO	0.104	0.211	**0.169**	0.244	0.077	0.033	**0.093**	0.145				
Pop-Dyn-2	0.000	0.132	**0.195**	0.266	**0.106**	0.052	**0.057**	0.146				
Rocaloex	0.133	*0.239*	**0.144**	0.237	0.080	0.039	**0.071**	0.182				
Rouge-du-Roc	0.152	0.170	**0.195**	0.162	0.048	0.000	**0.096**	0.143				
Saint-Priest	0.092	0.188	**0.194**	0.149	**0.104**	0.050	**0.061**	0.128				
Savoysone	0.180	*0.241*	**0.144**	0.176	*0.133*	0.000	**0.099**	0.149				
Hendrix	0.000	0.160	**0.170**	0.285	*0.118*	0.083	**0.078**	0.118				
Renan	0.000	0.196	**0.214**	0.256	0.063	0.000	**0.108**	0.148				
Mean PPB	0.114	0.195	0.172	0.220	0.085	0.034	0.077	0.154				
Mean CV	0.000	0.178	0.192	0.270	0.090	0.042	0.093	0.133				
	SW [a]				NSPK [a]				NSPK_st [a]			
	A	**F**	**AF**	**Res**	**A**	**F**	**AF**	**Res**	**A**	**F**	**AF**	**Res**
Dauphibois	0.075	*0.132*	**0.086**	0.321	0.011	0.038	**0.072**	0.111	0.115	0.060	**0.124**	0.396
Japhabelle	**0.156**	0.102	**0.091**	0.305	0.030	*0.073*	**0.045**	0.116	**0.180**	0.000	**0.106**	0.385
Mélange-1	0.108	0.142	**0.140**	0.312	0.000	0.070	**0.073**	0.114	*0.184*	0.036	**0.172**	0.386
Mélange-5	0.129	0.143	**0.111**	0.277	0.000	0.084	**0.069**	0.116	**0.138**	0.000	**0.074**	0.386
Mélange-SO	0.091	0.138	**0.127**	0.295	0.022	0.058	**0.069**	0.116	*0.147*	0.083	**0.117**	0.395
Pop-Dyn-2	**0.194**	**0.163**	*0.052*	0.287	0.044	0.050	**0.068**	0.106	**0.200**	0.039	**0.114**	0.374
Rocaloex	**0.144**	**0.165**	0.035	0.315	0.036	0.048	**0.070**	0.121	*0.149*	0.000	**0.139**	0.435
Rouge-du-Roc	0.082	0.152	**0.123**	0.301	0.041	0.000	**0.089**	0.089	0.115	0.016	**0.120**	0.333
Saint-Priest	**0.219**	**0.180**	*0.049*	0.267	0.043	0.049	**0.053**	0.075	**0.246**	0.000	**0.143**	0.402
Savoysone	**0.222**	**0.192**	0.060	0.265	0.032	0.071	**0.072**	0.098	**0.327**	0.000	**0.222**	0.557
Hendrix	*0.155*	0.140	**0.086**	0.323	0.014	0.055	**0.067**	0.092	**0.259**	0.127	**0.143**	0.359
Renan	0.135	0.167	**0.143**	0.298	0.041	0.012	**0.092**	0.102	0.131	0.000	**0.261**	0.465
Mean PPB	0.142	0.151	0.087	0.294	0.026	0.054	0.068	0.106	0.180	0.023	0.133	0.405
Mean CV	0.145	0.154	0.114	0.310	0.028	0.034	0.080	0.097	0.195	0.064	0.202	0.412

Appendix B. Markers Used for Genotyping

Appendix B.1. Markers in Neutral Zones

Table A2. Markers in neutral zones used for genotyping, chromosome position (chr) and references (ref).

Marker Name	Chr	Ref	Marker Name	Chr	Ref
wsnp_BE443995B_Ta_2_2	3A	9K	wsnp_Ex_c11265_18216936	5B	9K
wsnp_Ex_c1255_2411550	1A	9K	wsnp_BE445506B_Ta_2_4	7B	9K
wsnp_BE489326B_Ta_2_1	3B	9K	wsnp_Ex_c18616_27481826		9K
wsnp_Ex_c18800_27681277	7B	9K	wsnp_Ex_c26312_35558700	5B	9K
wsnp_Ex_c38105_45710671	5B	9K	wsnp_Ex_c62701_62229607	5A	9K
wsnp_Ex_c18965_27868480	6A	9K	wsnp_Ex_c8588_14419007	1A	9K
wsnp_Ex_c9502_15748469	6A	9K	wsnp_Ex_c9763_16125630	6A	9K
wsnp_Ex_rep_c102707_87814407	7B	9K	wsnp_Ex_rep_c103087_88123733	1A	9K
wsnp_BF484606A_TA_2_3	1A	9K	wsnp_Ex_rep_c66389_64588992	1B	9K
wsnp_Ex_rep_c70036_68988728	6B	9K	wsnp_BG606986A_TA_2_4	1A	9K
wsnp_JD_c19925_17854742	7A	9K	wsnp_JD_c20555_18262260	7A	9K
wsnp_BM136727B_Ta_2_6	6B	9K	wsnp_BM140362A_Ta_2_2	1A	9K
wsnp_BQ161779B_Ta_2_4	6B	9K	BS00077147 [m]	7D	Kaspar db
wsnp_Ku_c3151_5892200	5B	9K	BS00022478	2B	Kaspar db
wsnp_Ku_c3929_7189422	7A	9K	BS00021865	2D	Kaspar db
wsnp_Ku_rep_c70220_69775367	5B	9K	BS00060226	4A	Kaspar db
wsnp_Ku_rep_c73198_72796386	3B	9K	BS00064002	4D	Kaspar db
wsnp_Ra_c107797_91270622	2A	9K	BS00022277	5D	Kaspar db
wsnp_Ku_c13204_21105694	3D	9K	BS00080040	6D	Kaspar db
wsnp_JG_c625_379570	5B	9K	BS00096478 [m]	7D	Kaspar db
wsnp_Ku_c33335_42844594	3B	9K	BS00026412	2B	Kaspar db
wsnp_Ku_c51039_56457361	5A	9K	BS00023211	2D	Kaspar db
wsnp_Ku_rep_c72211_71920520	5B	9K	BS00065607	4A	Kaspar db
wsnp_Ra_c1020_2062200	1D	9K	BS00068103	4D	Kaspar db
wsnp_CAP12_c7952_3403722	5B	9K	BS00085191	5D	Kaspar db
wsnp_Ra_c4254_7755493	6B	9K	BS00087343	6D	Kaspar db

[m]: monomorphic. 9K: 9K iSelect assay. Kaspar db: Kaspar database. Chromosomic positions are from Cavanagh et al. [71].

Appendix B.2. Markers in Candidate Genes for Precocity

Table A3. Markers in candidate genes for precocity, chromosome position (chr) and references (ref).

Candidate Gene	Associated Trait	Chr	Polymorphism	Ref	Marker Name
PHYA	photoreceptors	4A	SNP	9K	wsnp_Ex_c1563_2987002
ZTL	photoreceptors	6B	SNP	9K	wsnp_Ex_c18382_27210656
VIL2	vernalization	6B	SNP	9K	wsnp_Ex_c39304_46635517
SMZ	photoperiod	1B	SNP	9K	wsnp_BE_403956B_Ta_2_3
Vrn1B	vernalization	1A	SNP	9K	wsnp_Ex_c645_1273901
Vrn1B	vernalization	6A	SNP	9K	wsnp_Ex_c7546_12900094
SMZ	photoperiod	1B	SNP	9K	wsnp_Ex_c9063_15093396
PHYA	photoreceptors	4A	SNP	9K	wsnp_Ex_rep_c66600_64897324
C04	photoperiod	5B	SNP	9K	wsnp_Ex_rep_c67690_66354931
Vrn1B	vernalization	6A	SNP	9K	wsnp_Ex_rep_c69901_68864080
CO1	photoperiod	7A	SNP	9K	wsnp_JD_c15333_14824351
TaHd1A	photoperiod	5A	SNP	9K	wsnp_Ku_c15816_24541712
CO1	photoperiod	3B	SNP	9K	wsnp_Ku_c48167_54427241
SMZ	photoperiod	4A	SNP	9K	wsnp_CAP11_c3346_1639010
SOC1	photoperiod	3A	SNP	9K	wsnp_Ra_c16053_24607526
C04 [out]	photoperiod	7A	SNP	9K	wsnp_CAP12_c1461_744121
ZTL	photoreceptors	6B	SNP	9K	wsnp_Ra_c3766_6947953

Table A3. *Cont.*

Candidate Gene	Associated Trait	Chr	Polymorphism	Ref	Marker Name
Vrn1A	vernalization	5A	SNP	[72]	
Vrn1A	vernalization	5A	SNP	[72]	
Vrn1B	vernalization	5B	SNP	[72]	
Vrn1B	vernalization	5B	SNP	[72]	
Vrn1A	vernalization	5A	SNP	[73]	
Vrn1B	vernalization	5B	SNP	[74]	
Vrn3B [m]	vernalization	7B	SNP	[75]	
Vrn1B [m]	vernalization	5B	6849bp indel	[72]	
TaGI3	photoperiod	3B	SNP	[76]	wsnp_Ex_rep_c67404_65986980
LDDA	photoperiod	5A	SNP	[76]	wsnp_Ku_c1102_2211433
CO-B	photoperiod	5B	SNP	[77]	
FTA	flowering	7A	SSR	[78]	
Ppd-D1 [m]	photoperiod	2D	2kb indel	[79]	
Vrn1A	vernalization	5A	SNP	[73]	
Vrn1D	vernalization	5D	4kb indel	[72]	
TaGW2	grain size	6A	SNP	[80]	
Ppd-D1	photoperiod	2A	305bp indel	[81]	

[m]: monomorphic. [out]: did not work. 9K: 9K iSelect assay [71,82,83]. Associated traits are from Higgins et al. [84]. Chromosomic positions are from Cavanagh et al. [71].

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