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Strong selection in wheat populations during ten generations of dynamic management

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Abstract – Temporal evolution of genetic variability in a Dynamic Management programme of wheat populations was assessed for fitness-related traits and for 29 RFLP markers. Populations of the 1st, 5th and 10th generations were studied. Genetic correlation between plant height (PH) and kernel number (KN) or kernel weight (KW) per plant was high and positive in each population, due to an advantage for the taller plants in intergenotypic competition conditions. This led to a linear increase in PH over generations. On the other hand, KN and KW linearly decreased over generations certainly due to re-allocation of reproductive resources to vegetative functions in the taller plants. On the basis of temporal variation of allelic frequencies of RFLP markers, very low effective sizes (Ne) were estimated: 216 between the 1st and 5th generation, and 157 between the 5th and 10th. These values, much lower than expected from census sizes ($\approx$ 2650) demonstrated that selection strongly influenced the evolution of neutral loci either by direct hitch-hiking effects and/or by increasing variance of progeny size. The non-significantly different Ne estimates for both periods of time suggested that selection remained constant over the 10 generations. This result is consistent with the continuous evolution of the quantitative traits. A great heterogeneity of temporal variations was observed among loci, showing the heterogeneity of selective pressures over the genome. Detection of selected loci using genetic markers is discussed.

selection / genetic drift / molecular marker / fitness / competition

Résumé – Forte sélection dans des populations de blé durant 10 générations de gestion dynamique. La variabilité génétique de populations de blé menées en gestion dynamique est évaluée pour des caractères liés à la valeur sélective et pour 29 locus marqueurs RFLP neutres. L'étude porte sur des populations issues de la 1re, de la 5e et de la 10e génération de multiplication sans sélection intentionnelle. Au sein

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de chaque population, une corrélation génétique positive forte a été trouvée entre hauteur des plantes (PH) et nombre et poids de grain (KN, KW) par plante, traduisant l'avantage conféré aux plantes les plus hautes poussant en conditions de compétition dans des populations hétérogènes. Consécutivement, nous observons que la hauteur a augmenté linéairement au cours des générations. Par contre, KN et KW ont diminué. Ceci est interprété comme le résultat de la sélection de plantes qui allouent davantage de ressources à la fonction végétative et moins à la fonction reproductive. Sur la base des variations temporelles des fréquences alléliques, les marqueurs RFLP révèlent de faibles effectifs efficaces de reproduction (Ne) que l'on compare la génération 1 et la génération 5 ($Ne = 216$) ou la génération 5 et la génération 10 ($Ne = 157$). Ces valeurs sont très faibles comparées aux effectifs attendus sur la base des données démographiques ($\approx 2\,650$). Ces faibles effectifs efficaces sont interprétés comme une conséquence de la sélection qui, jouant sur les locus impliqués dans des caractères sélectionnés, pourrait faire évoluer par entraînement certains marqueurs RFLP étudiés ainsi qu'augmenter globalement les variations sur l'ensemble du génome en augmentant la variance du succès reproducteur. Les Ne estimés non significativement différents entre les générations 1 et 5 et les générations 5 et 10, laissent penser que l'intensité de la sélection a été comparable sur les deux périodes. Ce résultat est cohérent avec l'évolution continue et linéaire des caractères quantitatifs. L'examen du comportement des différents locus marqueurs montre que certains évoluent beaucoup et d'autre très peu, indiquant une hétérogénéité de l'action de la sélection sur l'ensemble du génome. La possibilité de repérer des locus sélectionnés grâce à des locus marqueurs neutres est discutée.

sélection / dérive génétique / marqueurs moléculaires / valeur sélective / compétition

1. INTRODUCTION

Dynamic management (DM) is a method complementary to genebanks for genetic resources conservation. Whereas genebanks maintain genotypes as samples of seeds, DM aims at maintaining the evolutionary mechanisms (selection, drift, recombination, mutation, migration) which are the sources of genetic variation and continuous evolution. For this, genetically heterogeneous populations are cultivated for subsequent generations isolated in different natural cropping environments. Genetic variability is expected to decrease in each population under the combined effects of drift and selection, but diversity is supposed to be maintained through the differentiation between populations. The evolution of a given population will depend among other things on its size and its mating system. Size determines the strength of genetic drift and the balance between genetic drift, selection and mutation governs genetic variability at each locus in the subsequent generations. Mating system controls gene associations, linkage disequilibrium evolution and possibility of transgressions.

Any finite population randomly loses genes with a correlated increase in inbreeding level due to the sampling of genes (genetic drift) from one generation to the other. Change in allelic frequencies due to genetic drift is in inverse

proportion to the size of the population. Other factors and especially selection also contribute to the variation in gene frequencies, even for non-selected genes. To quantify these variations and to be able to compare populations of different kinds, Wright [28] proposed the concept of effective size of drift (Ne). Ne is the size of an ideal finite panmictic population with no selection, no migration, no mutation, which would generate the same variations in gene frequencies as those observed in the studied population. It is of particular importance to study the effective size of the populations of DM programmes in order to predict the evolution of genetic diversity in the system.

In a previous study [12], Ne was computed for six wheat DM populations after 10 generations using the temporal variation of gene frequencies at RFLP markers. Values ranged from 37 to 187 for a true number of plants of 5000 (lower estimation) and an estimated demographic Ne of 2800. The discrepancy between genetic and demographic values raises two questions: which are the selective pressures that lead to increase so much variation in gene frequencies at marker loci in all the populations, and how long is it going to last? We suppose that the populations have been submitted to strong selective pressures at their installation in new environments but we expect that after a few generations they will be more adapted and that the selection effect on the Ne will decrease.

To test this hypothesis, we studied the evolution of allelic frequencies at marker loci (RFLP) and of the means and variances of phenotypic traits involved in fitness measured in the field. Evolutions between generations 1 and 5, and between generations 5 and 10 were analysed. Results indicating much greater changes between generations 1 and 5 than between 5 and 10 would be consistent with our hypothesis.

2. MATERIAL AND METHODS

2.1. The wheat DM populations

Two initial composite populations (PA and PB) were created by crossing 16 parental lines pyramidally [7, 26]. The genetic base of PB was wider than that of PA due to the presence in the former of more exotic lines among the parents. PA and PB are predominantly selfing (estimations of outcrossing rate in different populations ranged from 2.4 to 10.1% [10]).

In 1984, after three years of bulk multiplication, seed samples of the initial populations were distributed to the sites of a French multilocational experimental network. Since 1984, each of the local populations has been cultivated every year using seeds of the same population harvested the previous year in the same location under the same cultural conditions. A 100 m^2 cultivated area was generally used so as to obtain around 10,000–15,000 plants per population. All the populations were isolated from each other and from other wheat to avoid unwanted cross pollinations.

During the first eight generations, the populations were grown with no intentional selection. But since 1992, we have recommended cutting and discarding of the highest spikes before harvest in each population. This followed the results of the first studies in the programme. Indeed, the mean plant height of all PA and PB populations had increased compared to the initial situation [6,20]. This increase was interpreted as the result of the competition for light between plants of a local population. Because the founding populations contained both dwarf and non-dwarf alleles at two major loci (*Rht*1 and *Rht*2), there was large genotypic variability [24]. Plants taller than the tallest plants of the initial populations were also found, indicating that recombination and selection of quantitative polymorphic loci had occurred.

2.2. Plant material

Generations 1, 5 and 10 of the PA and PB populations from Le Moulon were studied in the field trial whereas only the three generations of PA were studied for RFLP markers. The six populations will hereafter be referred to as PA1, PA5, PA10 and PB1, PB5 and PB10.

2.3. RFLP study

Random samples of 250, 232 and 213 individuals of PA1, PA5 and PA10 were analysed for RFLP markers. Total DNA was extracted from lyophilised young leaves following a rapid procedure adapted from Dellaporta *et al.* [8]. Enzyme restriction, electrophoresis, blotting onto Hybond N^+ membranes (Amersham) and non-radioactive hybridisations (DIG®Boehringer-Mannheim) were performed as described by Lu *et al.* [21]. Twelve RFLP probes (12 enzyme/probe combinations: *Fba*65, *Fba*127, *Fba*152, *Fba*242, *Fbb*12 and *Psr*144 with HindIII, *Fba*166, *Fba*204 and *Fbb*178 with DraI, *Fba*280, *Fba*69 and *Fbb*187 with EcoR1) which, except for *Psr*144, had all been obtained and mapped by the INRA-Génoblé group [22], were provided by P. Leroy (INRA Clermont-Ferrand, France). *Psr*144 had been mapped by Gale *et al.* [14] and was provided by K. Devos (John Innes Centre, Norwich, UK). Due to the hexaploid genome of wheat, most of the probes mapped simultaneously on the three homeologous genomes and the 12 enzyme/probe combinations corresponded to 29 polymorphic loci among which 24 were codominant. Two to four alleles were found per locus (2.3 alleles per locus on average).

2.4. Genetic analysis

Effective size (Ne) was estimated on the basis of temporal variation of allelic frequencies at RFLP loci between population PA1 and PA5, PA5 and PA10, PA1 and PA10. According to Waples [27], the expression of Ne for a population

between generations i and f depends on $\hat{F}_c$, the estimator of the standardised variance of allelic frequencies, S_i and S_f, the correction for sampling variance due to the collection of individuals at generations i and f (here for generations 1, 5 and 10, sample sizes were respectively 203.3, 223.4 and 185.6), and t, the number of generations between the two populations studied. For a selfing population, Ne can be written as:

$$\hat{N}e = \frac{t}{2\left[\hat{F}_c - \frac{1}{S_i} - \frac{1}{S_f}\right]}.$$

The fact that PA is mainly selfing only has implications for the sampling correction factors which are S_i and S_f instead of $2S_i$ and $2S_f$ in a panmictic population. Yet, the estimated genetic Ne should not be compared to the true number of plants grown in the population (5000, lower estimation) but to a value corrected for the mean inbreeding level [5]; here the demographic effective size of this PA population is 2650 (Apendix I, eq. (3)).

At each locus l with K alleles, $\hat{F}_c$ is given by:

$$\hat{F}_{c,l} = \frac{1}{K}\sum_{k=1}^{k} \frac{(p_{ki} - p_{kf})^2}{(p_{ki} + p_{kf})/2 - p_{ki}p_{kf}},$$

with $p_{ki}(p_{kf})$ the frequency of allele k at generation $i(f)$. The multilocus $\hat{F}_c$ is then calculated as the mean of the single locus $\hat{F}_{c,l}$ values. Confidence interval (CI) for $\hat{N}e$ was derived from that for $\hat{F}_{c,l}$, noting that it is actually a variance and that, if n is the number of degrees of freedom (number of alleles − number of loci), $n\hat{F}/E(\hat{F})$ follows a Chi^2 distribution [27]:

$$(1-\alpha)\text{CI for } \hat{F}_c = \left[\frac{n\hat{F}_c}{\chi^2_{\alpha/2,n}}, \frac{n\hat{F}_c}{\chi^2_{1-\alpha/2,n}}\right].$$

Expected distribution of F_c conditional on an Ne value were computed using the Chi^2 approximation. Expected distributions were computed for genetic and demographic ($\hat{N}e = 2650$) estimations.

2.5. Field experimentation

Seed samples of the six following populations PA1, PA5, PA10 and PB1, PB5, PB10 were sown at the beginning of November in 1997 and 1998 at Le Moulon. Four controls, Lutin, Renan, Soissons and Hyno-Précia, were included in the experiment each year to allow the estimation of environmental variances and covariances. Because the DM populations were known to be highly polymorphic, we chose a wide-based set of controls that would be more or less representative of the mean response induced by environmental variations

in the plants in the populations. Lutin is one of the parents of PA0. Renan is a quite tall cultivar related to an INRA genitor, VPM, which had widely contributed to the creation of PA0 and PB0. Soissons is a highly-productive short cultivar and Hyno-Précia a highly-productive hybrid.

All the DM populations and controls were sown each year at a density of 175 plants/m^2 in six row plots (3 m long and 1.5 m wide). The fertilisation was adjusted to fit a yield objective of 750 g/m^2 and the plots were treated against aerial fungal attacks. Because of the small available quantity of seeds for each population, the populations were sown each year in a single plot. This led each year to the confounding of the population effect with the plot effect. This confounding lessened the power of the experiment in the case of the comparison of means, but did not affect the estimation of within-population variances and covariances. Two hundred individual plants were measured in 1998 (150 in 1999) in each population and 50 plants for each control each year. To avoid border effects, plants were sampled in the four central rows of each plot on the 1.5 m central part of the plot.

The following traits were measured in plants individually harvested at full maturity (remaining grain moisture at about 11%) during the second week of August:

- Number of spikes per plant (NSP).
- Plant height (PH): from the base to the top, spike included but not awns.
- Number of kernels per plant (NKP).
- Number of kernels per spike (NKS) was computed as NKP/NSP.
- Kernel weight per plant (KWP).
- Mean kernel weight multiplied by 1000 (thousand kernels weight TKW).

2.6. Statistical analysis

Each year for each population, phenotypic variance (PV) and mean (PM) were calculated for each trait, as well as phenotypic covariances (PC) between traits. ANOVA was done for PV and PM using the following model:

$$\text{PV(or PM)} = \mu + Year + Pool + Generation + Pool^{*}Generation + R \qquad \text{Model 0}$$

The *Year* and the *Pool* effects each had two levels (1997, 1998 and PA, PB resp.), the *Generation* effect had three levels (1, 5, 10). *Pool* Generation* was the *Pool* by *Generation* interaction and R the residual.

To test whether the evolution of the variances and of the means was linear across generations, a model with *Generation* declared as a regressor (covariate) would be more powerful and would give additional information on the direction and the rate of evolution of the considered parameter in the populations. So, we also considered two models with *Generation* declared as a regressor. The first one (Model 1) supposed a parallel evolution for PA and PB (one regression slope estimated), and the second (Model 2) supposed two different rates of

Table I. $\hat{F}_c$ and $\hat{N}_e$ computed on the basis of the temporal variations of allelic frequencies at 29 RFLP marker loci.

Populations	$\hat{F}_c$	t	n	$\hat{N}e$	CI (5% level)
PA1–PA5	0.0186	4	37	216	$92 \leq Ne \leq 663$
PA5–PA10	0.0257	5	37	157	$75 \leq Ne \leq 344$
PA1–PA10	0.0415	9	37	144	$76 \leq Ne \leq 260$
PA0–PA10*	0.067	10	36	123	$58 \leq Ne \leq 277$

* data estimated with 30 RFLP loci in 78 individuals sampled in a single seed descent population derived from PA0 and in 77 of the 213 individuals sampled in PA10 (Enjalbert, 1999).
t is the number of the generation, n is the number of degrees of freedom.

evolution and led to the estimation of two different regression slopes, one for PA and one for PB.

Each year, phenotypic variance (PV_i) for each trait i and phenotypic covariances (PC_{ij}) between traits i and j were also estimated within each control. The mean over the four controls of the different PV_i (resp. PC_{ij}) was used as a unique estimate of the environmental variance (EV_i) (resp. environmental covariance (EC_{ij})). For each population, the difference ($PV_i - EV_i$) between the phenotypic variance and the environmental variance (resp. $PC_{ij} - EC_{ij}$) gave an estimate of the within-population genetic variance (GV_i) (resp. the within-population genetic covariance (GC_{ij})). The ratio GV_i / PV_i gave estimates of the broad-sense heritabilities (H_i^2) for all the traits in the different populations. The ratios $\frac{PC_{ij}}{\sqrt{PV_i \times PV_j}}$, $\frac{GC_{ij}}{\sqrt{GV_i \times GV_j}}$ and $\frac{EC_{ij}}{\sqrt{EV_i \times EV_j}}$ provided estimations of phenotypic, genetic and environmental correlations between traits i and j.

3. RESULTS

3.1. Variation of allelic frequencies at RFLP loci

The effective size estimated between PA1 and PA10 populations (Tab. I) was very low ($Ne = 144$) and very close to the value already found between PA0 and PA10 [9]. Hence, genetic Ne was significantly lower than expected on the basis of the demographic data (2650). Effective sizes estimated for intermediate periods (PA1-PA5 and PA5-PA10) were very close to the global one (Tab. I) and not significantly different from each other. Yet this is an average result over the 29 marker loci. In order to investigate further the behaviour of the different loci, we studied the distribution among loci of the observed variations in allelic frequency estimated with the F_c parameter.

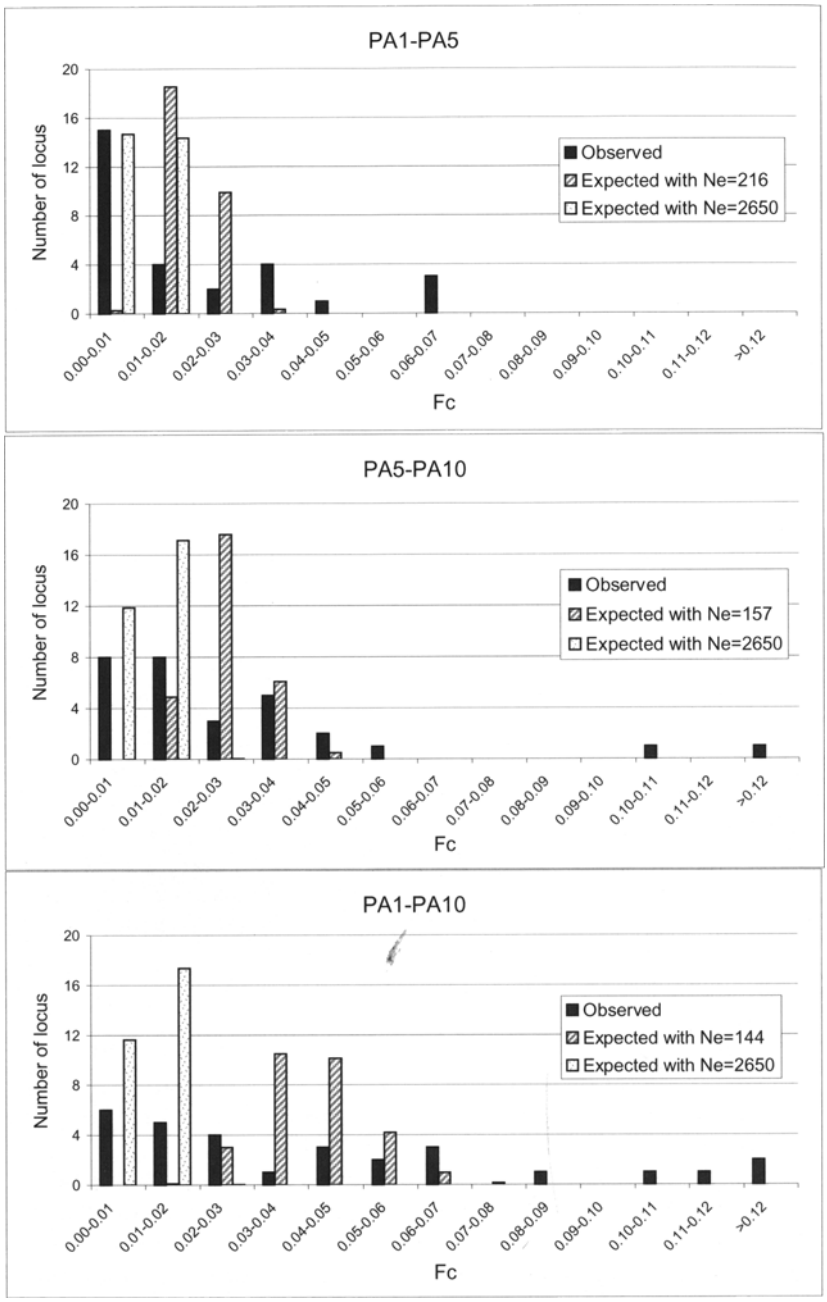

Figure 1. Comparison of the Chi^2 distributions ("expected") based on the estimated genetic Ne and based on the demographic Ne (2650) with the observed distribution of F_c (standardised variance of allelic frequency between two generations) for PA1–PA5, PA5–PA10 and PA1–PA10.

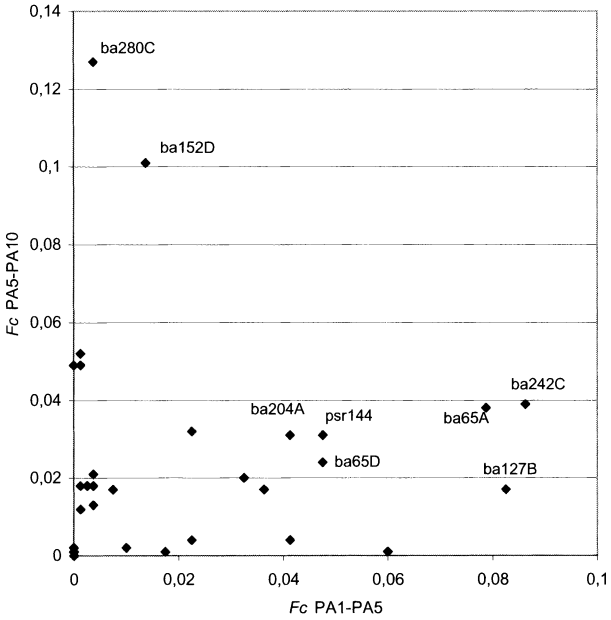

Figure 2. Relation between the F_c estimated from 29 marker loci for generations 1 to 5 and F_c estimated for generations 5 to 10; F_c are corrected for the number of generations.

Distribution of F_c (Fig. 1) appeared very flat with an aproximate L-shape for PA1-PA5 and PA5-PA10, and it was even flatter considering the complete period PA1-PA10. We can consider that about 2/3 of the loci for PA1-PA5, 1/2 for PA5-PA10 and 1/3 for PA1-PA10 did not vary much more than expected under genetic drift only (Fig. 1) based on the Chi^2 distribution with $Ne = 2650$. Moreover, only a few loci could fit the Chi^2 distribution with genetic Ne estimations and some loci were obviously out of these distributions at the right as well as at the left side.

To study the continuity of the evolutions of allelic frequencies at the different loci during the nine generations studied, we drew the relation between the F_c estimated at the 29 loci for PA1–PA5 on the one hand and for PA5–PA10 on the other hand. Correlation was close to zero. Yet some loci had strong F_c for both periods. For example, variation in allelic frequency at $Fba242C$ was the highest for PA1–PA5 and the 6^{th} for PA5–PA10 (Fig. 2), and it was the highest for the global period PA1–PA10 ($F_c = 0.190$). In fact, the situation was more complex because the F_c could be strong for both periods but the frequency might have evolved in the opposite direction. For example, the locus $Fba65A$ had strong F_c for PA1–PA5 and PA5–PA10 but not for PA1–PA10 because the frequency of allele 2 first increased and then decreased (Tab. II) so that PA1 and PA10 became very similar. Yet few cases could be found with inversion of frequency evolution after PA5: except for two loci ($Fba65A$ and $Psr144$)

among the 29, allelic frequencies were either stable over the whole period or changed during one period and were stable during the other or changed in the same direction during both periods (Tab. II).

3.2. Evolution of fitness-related traits

The results of the different ANOVAs for the phenotypic variances (PV) are presented in Tab. III. In Model 0, the only significant *Generation* effect was detected for plant height (PH), indicating a change in phenotypic variance across generations for this trait. For the number of kernels per spike (NKS), a *Pool* by *Generation* effect was significant at the 10% level indicating that evolutions of NKS in PA and PB were not parallel. Model 1 was able to detect a highly significant *Generation* effect for PH, and a significant *Generation* effect at the 10% level for number of kernels per plant (NKP) and kernel weight per plant (KWP). For these three traits, the fit of Model 1 to the data measured by the global F and its associated probability was improved compared to the fit of Model 0. Model 2 yielded no further significant improvement for these traits. For NKS, Model 2 appeared well adapted to the data and led to an estimated slope not significantly ($P = 0.51$) different from zero for PA and significant ($P = 0.01$) for PB. For all the traits that exhibited a significant evolution among generations, the estimated slopes associated with the *Generation* effect were all negative (data not shown) which indicated an evolution towards smaller variances along with the number of multiplication generations.

Estimated phenotypic variances and broad-sense heritabilities are given in Tab. IV. Evolution of the variances in PA and PB appeared clearly linear according to the generations for PH and in PB for NKS. The situation was a little more confused for NKP and KWP, which was in accordance with the *Generation* effect only significant at the 10% level. But the values of the phenotypic variances estimated in the tenth generation were always the smallest. The estimated heritabilities were high for PH (whatever the generation) and TKW, medium for NKS and medium to low for NSP, NKP and KWP. For the two last traits, the genetic variance appeared exhausted in PA10.

Analysing the phenotypic means (PM), Model 1 provided the best fit to the data for all traits (Tab. V). Four traits (PH, NKP, NKS and KWP) presented significant differences among generations. The evolutions of PH and NKS were the most significant and were detected by Model 0 and Model 1 at a level lower than 1%. Table VI presents the mean values of the traits for the two pools and the three generations and the estimated slopes of the evolution of the traits in the populations across generations. Whereas PH increased during generations of selection, NKP, NKS and KWP decreased. These evolutions were quite linear which was consistent with the good fit obtained with Model 1 for these traits. Increase in mean plant height according to the generation had already been found in the DM populations and was interpreted as a response to competition for light between plants within the population [20]. Here we showed that this

Table II. Allelic frequencies and confidence interval (CI) at the 5% level at 29 RFLP marker loci for three generations of a PA population.

Locus	ba127-A			ba127-D			ba127-B			ba127-C		
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)
PA1	456	**0.15** ↓	0.12 - 0.18	442	0.35	0.31 - 0.39	450	**0.78**	0.74 - 0.82	448	0.91	0.88 - 0.94
PA5	464	**0.10** ↓ -	0.07 - 0.12	464	**0.42** ↓	0.37 - 0.46	450	**0.88** ↓ +	0.85 - 0.91	452	0.89	0.87 - 0.92
PA10	420	**0.06** ↓ -	0.04 - 0.08	398	**0.33** ↓ -	0.28 - 0.38	270	0.83	0.78 - 0.87	270	0.93	0.89 - 0.96
Locus	ba127-E			ba152-A			ba152-B			ba152-C		
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)
PA1	448	0.83	0.79 - 0.86	436	0.36	0.32 - 0.41	446	**0.81** ↓ +	0.78 - 0.85	390	0.16	0.12 - 0.19
PA5	464	0.85	0.82 - 0.88	464	0.31	0.26 - 0.35	462	**0.89**	0.86 - 0.92	464	0.21	0.17 - 0.25
PA10	270	0.90	0.86 - 0.93	422	0.29	0.25 - 0.34	420	0.90	0.87 - 0.93	306	0.23	0.19 - 0.28
Locus	ba152-D			ba65-B			ba65-D			bb12		
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)
PA1	432	0.96	0.94 - 0.98	450	0.84	0.81 - 0.88	442	**0.16** ↓	0.12 - 0.19	414	0.32	0.28 - 0.37
PA5	462	**0.94** ↓	0.91 - 0.96	464	0.86	0.83 - 0.89	446	**0.09** ↓ -	0.06 - 0.12	450	0.34	0.30 - 0.39
PA10	422	**0.99** ↓ +	0.99 - 1.00	426	0.89	0.86 - 0.92	426	0.05	0.03 - 0.07	376	0.41	0.36 - 0.46
Locus	ba242-B			ba242-C			ba166-A			ba166-B		
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)
PA1	420	0.27	0.23 - 0.31	336	**0.19** ↓	0.15 - 0.23	380	0.76	0.72 - 0.80	388	0.89	0.85 - 0.92
PA5	464	0.28	0.23 - 0.32	462	**0.09** ↓ -	0.07 - 0.12	452	**0.77**	0.73 - 0.81	462	0.90	0.87 - 0.92
PA10	426	0.29	0.25 - 0.33	426	**0.04** ↓ -	0.02 - 0.06	268	**0.86** ↓ +	0.82 - 0.90	270	0.85	0.81 - 0.89
Locus	ba204-A			ba204-C			ba204-D			ba280-A		
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)
PA1	272	0.55	0.49 - 0.61	340	0.98	0.97 - 1.00	256	0.97	0.95 - 0.99	462	**0.91**	0.89 - 0.94
PA5	462	**0.46** ↓	0.41 - 0.50	460	0.98	0.97 - 0.99	464	**0.97** ↓	0.96 - 0.99	384	**0.96** ↓ +	0.94 - 0.98
PA10	420	**0.37** ↓ -	0.32 - 0.41	420	0.99	0.98 - 1.00	420	**1.00** ↓ +	1.00 - 1.00	270	0.97	0.95 - 0.99
Locus	ba280-B			ba187-A			psr144					
(2 alleles)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)	n	f(A1)	CI (5% level)			
PA1	460	0.67	0.63 - 0.71	372	0.73	0.69 - 0.78	438	**0.48** ↓	0.43 - 0.52			
PA5	414	0.66	0.62 - 0.71	424	**0.74** ↓	0.70 - 0.78	424	**0.38** ↓ -	0.33 - 0.42			
PA10	420	0.65	0.61 - 0.70	270	**0.64** ↓ -	0.58 - 0.69	364	**0.47** ↓ +	0.42 - 0.52			

Table II. Continued.

Locus	ba65-A					ba242-A				
(3 alleles)	n	f(A1)	CI (5% level)	f(A2)	CI (5% level)	n	f(A1)	CI (5% level)	f(A2)	CI (5% level)
PA1	450	**0.97** ↓ -	0.95 - 0.99	**0.02** ↓ +	0.00 - 0.03	450	0.06	0.04 - 0.08	0.85	0.81 - 0.88
PA5	464	**0.90** ↓ -	0.87 - 0.93	**0.09** ↓ +	0.06 - 0.11	464	0.10	0.07 - 0.13	**0.86**	0.83 - 0.89
PA10	426	0.94	0.92 - 0.96	**0.03** ↓ -	0.01 - 0.04	426	0.06	0.04 - 0.08	**0.91** ↓ +	0.89 - 0.94

Locus	bb178					ba204-B				
(3 alleles)	n	f(A1)	CI (5% level)	f(A2)	CI (5% level)	n	f(A1)	CI (5% level)	f(A2)	CI (5% level)
PA1	328	0.11	0.07 - 0.14	0.33	0.28 - 0.38	278	0.52	0.46 - 0.58	0.45	0.39 - 0.51
PA5	406	0.08	0.06 - 0.11	0.33	0.28 - 0.38	462	0.47	0.42 - 0.51	0.51	0.46 - 0.55
PA10	414	0.06	0.03 - 0.08	0.41	0.37 - 0.46	418	0.45	0.40 - 0.50	0.53	0.48 - 0.58

Locus	ba280-C						
(4 alleles)	n	f(A1)	CI (5% level)	f(A2)	CI (5% level)	f(A3)	CI (5% level)
PA1	448	0.50	0.45 - 0.55	0.32	0.28 - 0.36	0.17	0.14 - 0.21
PA5	378	**0.50** ↓ -	0.45 - 0.55	**0.33**	0.28 - 0.38	0.16	0.13 - 0.20
PA10	258	**0.29** ↓ -	0.24 - 0.35	**0.56** ↓ +	0.50 - 0.62	0.15	0.10 - 0.19

Table III. Results for different ANOVA models applied to the phenotypic variances (PV) estimated in 1997 and 1998 (*Year* effect) in pools A and B (*Pool* effect) after 1, 5 and 10 years of multiplication (*Generation* effect).

Effects in the Model	d. f.	NSP	PH	NKP	NKS	KWP	TKW
Model 0							
Year (F/*Proba.*)	1	2.42 / 0.18	0.5 / 0.51	2.54 / 0.17	0.52 / 0.50	5.72 / 0.06	15.72 / 0.01
Pool (F/*Proba.*)	1	0.00 / 0.95	3.16 / 0.14	1.19 / 0.32	3.53 / 0.12	2.71 / 0.16	1.08 / 0.35
Generation (F/*Proba.*)	2	0.14 / 0.88	42.29 / 0.0007	1.63 / 0.28	2.58 / 0.17	2.13 / 0.21	0.53 / 0.62
Pool*Generation (F/*Proba.*)	2	0.70 / 0.54	1.29 / 0.35	1.2 / 0.37	4.00 / 0.09	2.07 / 0.22	1.16 / 0.39
Model (F/*Proba.*)	6	0.69 / 0.67	15.15 / 0.005	1.61 / 0.3	2.78 / 0.14	2.86 / 0.13	3.36 / 0.10
Residual	5						
Model 1							
Year (F/*Proba.*)	1	2.90 / 0.13	0.48 / 0.51	2.65 / 0.14	0.24 / 0.63	4.85 / 0.06	15.82 / 0.004
Pool (F/*Proba.*)	1	0.02 / 0.90	3.06 / 0.12	1.34 / 0.28	1.72 / 0.23	2.41 / 0.16	0.93 / 0.36
Generation (F/*Proba.*)	1	0.08 / 0.78	(*)**88.05 / 0.0001**	**3.48 / 0.10**	1.83 / 0.21	**3.66 / 0.09**	0.42 / 0.53
Model (F/*Proba.*)	3	1.01 / 0.44	**30.33 / 0.0001**	**2.59 / 0.13**	1.3 / 0.34	**3.79 / 0.06**	5.7 / 0.02
Residual	8						
Model 2							
Year (F/*Proba.*)	1	2.57 / 0.15	0.67 / 0.44	2.43 / 0.16	0.54 / 0.48	4.67 / 0.07	18.22 / 0.004
Pool (F/*Proba.*)	1	0.06 / 0.81	7.16 / 0.03	1.07 / 0.33	11.96 / 0.01	2.28 / 0.175	3.40 / 0.11
Generation(Pool) (F/Proba.)	2	0.11 / 0.90	59.55 / 0.0001	1.7 / 0.25	**6.10 / 0.03**	2.06 / 0.20	1.41 / 0.31
Model (F/*Proba.*)	4	0.71 / 0.61	30.74 / 0.0002	1.82 / 0.23	**4.06 / 0.05**	2.87 / 0.11	3.39 / 0.08
Residual	7						

NSP: Number of spikes per plant, PH: Plant height, NKP: Number of kernels per plant, NKS: Number of kernels per spike, KWP: Kernel weight per plant, TKW: Thousand kernels weight.

_: underlined: values significant at least at the 10% level.

(*) In bold: model considered as the most adapted for the explanation of the generation effect in each pool.

Table IV. Estimations of the phenotypic variances (PV) and of the broad-sense heritabilities (H^2) in PA1, PA5, PA10, PB1, PB5 and PB10 for the different traits (means for the two years).

	NSP		**PH**		**NKP**		**NKS**		**KWP**		**TKW**	
	PV	H^2	PV	H^2	PV	H^2	PV	H^2	PV	H^2	PV	H^2
PA1	1.52	0.31	345	0.97	2668	0.21	89	0.48	6.0	0.17	57	0.83
PA5	2.16	0.51	260	0.96	3569	0.41	84	0.45	8.0	0.38	51	0.81
PA10	1.39	0.24	145	0.92	1970	0.00	93	0.50	4.7	0.00	77	0.87
PB1	1.72	0.39	286	0.96	4424	0.52	124	0.63	11.2	0.55	76	0.87
PB5	1.51	0.31	236	0.95	2820	0.25	97	0.52	6.6	0.24	69	0.86
PB10	1.79	0.41	150	0.93	2733	0.23	85	0.46	6.7	0.25	68	0.86

evolution seemed to continue at the same rate in the first four generations and in the following ones, although the higher plants had been eliminated from the 8^{th} generation. This increase in PH was also correlated with a decrease in mean NKP, NKS and KWP, which was rather important. This led us to investigate further the relation between PH and the three latter traits. Whereas the within-population phenotypic correlations between PH on the one hand and NKP, NKS and KWP on the other hand were always positive and very similar in the different populations (Tab. VII), the between-generation correlations calculated for the same pairs of traits were negative. Hence, competition in heterogeneous populations selects for the highest plants although this induces a decrease in the global grain production of the populations.

4. DISCUSSION

The effective size between PA1 and PA10 was very low ($Ne = 144$) compared to the expected demographic value ($Ne = 2650$). Though it is classical for Ne to be lower than N, the actual census size, to our knowledge there are few studies in which demographic and genetic Ne are simultaneously estimated in the same population. Frankham [13] reviewed 192 experiments and analysed the Ne/N ratios measured in animal and plant natural populations. The mean ratio was about 0.10, and the first most important variables influencing the value of this ratio were the fluctuation in population size and variance in family size. In the different experiments, Ne was estimated either by demographic or by genetic methods, and interestingly we noted that the genetic methods based on variation in gene frequency or heterozygosity yielded even lower ratios. So, our estimated Ne (ratio genetic $Ne/N = 0.03$) appeared rather low but not unusual compared to bibliographic data. Yet, the PA population is not a natural population and the number of individuals was under control, so that very few fluctuations might have happened. The role of the variation in family size will be considered later in this chapter.

Table V. Results of different ANOVA models applied to the phenotypic means estimated in 1997 and 1998 (*Year* effect) in pools A and B (*pool* effect) after 1, 5 and 10 years of multiplication (*Generation* effect).

Effects in the Model	d. f.	NSP	PH	NKP	NKS	KWP	TKW
Model 0							
Year (F/*Proba.*)	1	10.8/0.02	12.8/0.16	3.89/0.105	0.00/0.975	7.74/0.04	14.3/0.013
Pool (F/*Proba.*)	1	1.23/0.32	46.9/0.001	6.91/0.05	23.9/0.0045	6.19/0.055	1.10/0.34
Generation (F/*Proba.*)	2	0.47/0.65	26.1/0.002	3.30/0.12	11.6/0.01	2.67/0.16	0.57/0.57
Pool*Generation (F/*Proba.*)	2	2.64/0.17	0.26/0.78	1.75/0.265	1.35/0.34	1.75/0.265	0.38/0.69
Model (F/*Proba*)	6	3.07/0.12	18.5/0.003	3.63/0.09	8.63/0.016	3.93/0.08	2.90/0.13
Residual	5						
Model 1							
Year (F/*Proba.*)	1	8.13/0.02	18.5/0.003	3.54/0.10	0.00/0.99	7.13/0.03	16.72/0.0035
Pool (F/*Proba.*)	1	0.99/0.35	66.7/0.0001	6.67/0.03	19.24/0.002	5.98/0.04	1.26/0.29
Generation (F/*Proba.*)	1	0.60/0.46	(*)**75.1/0.0001**	**6.14/0.04**	**16.26/0.004**	**5.03/0.055**	0.16/0.70
Model (F/*Proba*)	3	3.33/0.08	**52.8/0.0001**	**5.66/0.022**	**11.99/0.0025**	**6.30/0.017**	6.16/0.018
Residual	8						
Model 2							
Year (F/*Proba.*)	1	7.5/0.03	17.6/0.004	3.11/0.12	0.00/0.97	6.4/0.04	15.6/0.006
Pool (F/*Proba.*)	1	1.03/0.34	26.9/0.001	2.21/0.18	2.56/0.15	2.66/0.15	1.31/0.29
Generation(Pool) (F/*Proba.*)	2	0.44/0.66	36.4/0.0002	2.71/0.14	8.89/0.01	2.33/0.17	0.28/0.76
Model (F/*Proba*)	4	2.38/0.15	38.2/0.0001	3.73/0.06	9.48/0.006	4.27/0.05	4.39/0.04
Residual	7						

NSP: Number of spikes per plant, PH: Plant height, NKP: Number of kernels per plant, NKS: Number of kernels per spike, KWP: Kernel weight per plant, TKW: Thousand kernels weight.

_: underlined: effects in the model significant at least at the 10% level.

(*) In bold: model considered as the most adapted for the explanation of the generation effect in each pool.

Table VI. Estimated means of the *Pool* and *Generation* effects and estimated slope of the regression when Generation is declared as a regressor.

	NSP	PH	NKP	NKS	KWP	TKW
Pool A	2.92	110 cm	90.3	30.1	3.98 g	43.1 g
Pool B	3.06	119 cm	108.2	34.7	4.87 g	44.2 g
Generation 1	3.07	109 cm	108.7	34.3	4.92 g	44.3 g
Generation 5	2.96	114 cm	101.3	33.7	4.43 g	43.0 g
Generation 10	2.94	120 cm	87.8	29.3	3.91 g	43.7 g
Estimated slope	–0.014 spike/year	1.26 cm/year	$-2.35 kernel/year$	$-0.58 kernel/year$	−0.11 g/year	
Probability ($P = 0.0001$) $P = (0.055)$	($P = 0.70$, NS)					−0.05 g/year
	($P = 0.0.46$, NS)		($P = 0.04$)	($P = 0.004$)		

Table VII. Values of the pooled within-population correlations and values of the between-generation correlations. Minimum and maximum estimated values are given for the phenotypic within-population correlations. All the within-population correlations are significantly different from 0.

	PH-NKP	PH-NKS	PH-KWP
Within-population correlations:			
[1]Pooled phenotypic correlation	0.37	0.35	0.41
[2]Min.	0.31	0.31	0.36
[2]Max.	0.46	0.44	0.50
[1]Pooled environmental correlation	0.225	0.22	0.24
[1]Pooled genotypic correlation	0.61	0.45	0.69
Between-generation correlations:			
PA: Value and (*Proba.*)	−0.79 (0.42)	−0.92(0.25)	−0.79 (0.42)
PB: Value and (*Proba.*)	−0.85 (0.35)	−0.99 (0.08)	−0.81 (0.40)
Pooled PA-PB: Value and (*Proba.*)	−0.81(0.10)	−0.93(0.025)	−0.78(0.13)

[1] Pooled means obtained as the ratio of the mean covariance (mean over all the populations) by the square root of the products of the mean variances of the two traits.

[2] Min and Max are the minimum and maximum values of the phenotypic correlations observed in the different populations.

Since the estimated Ne between PA1 and PA5 and between PA5 and PA10 were not significantly different, we concluded that allelic variations at marker loci were of the same order when passing from the first four generations to the following ones.

Continuous evolution was also found for the phenotypic traits involved in individual fitness, indicating strong selection effects. Mean plant height had the most significant change across generations, and number of kernels per plant (NKP), number of kernels per spike (NKS) and kernel weight per plant (KWP) have also significantly evolved (Tab. III). For these traits, the evolution of means appeared to follow a steady rate with no slowing down between generations 5 and 10. Evolution of mean PH was associated with a significant decrease in variance but the level of broad sense heritability was kept at a rather high level, indicating that variability was still available for selection in future generations. The low estimated heritabilities for NKP and KWP in PA10 (Tab. IV) suggested that the speed of evolution of these traits might be reduced in the future in PA. If fitness is defined as the product of the number of seeds per plant and the mean viability of the seeds, NKP is the measured trait the most directly related to plant fitness. Hence, selection intensity might lessen in the future generations of PA and correlatively Ne should increase.

Increase in the mean plant height of the population can be explained by the advantage of higher plants over the shorter ones when they are grown side by side, which is well documented in a number of cultivated species (wheat: [15,19]; barley: [16, 25]; rice: [18]; kale: [4]). Hence, this was a general trend in all wheat DM populations and competition for light appeared to be the driving evolutionary force of the system. Surprisingly, this was clearly not the case in the barley composite cross populations created by Harlan and Martini [17] and grown in Davis, California. Allard [1] observed that the changes in mean height were small until about the 25^{th} generation when a generally increasing trend started that led to an increase in mean height of about 5% by generation 53. This is a very small change considering the ratio over generations. Possible but unverified explanations are (i) the initial genetic variability for plant height in the barley composite crosses was very limited and mean plant height was already high, (ii) growing conditions were different and sowing density was much lower so that competition intensity was low or even negligible.

At each generation in a given population, the tallest individuals have benefited from between-plant competition effects and they contributed more to the next generation. Yet, at the population level, a population of tall plants would be less productive than a population of short plants as shown by the negative between-population correlation between PH and NKS or NKP (Tab. VII). This can be explained by a trade-off between allocation of resources to the vegetative traits and to the reproductive ones.

Low effective size can be explained by strong differences in the reproductive contribution of each individual to the next generation. This variance of the reproductive contribution may be due either to nonherited causes, which would lead to an increase in genetic drift over the whole genome, or to herited causes. In the latter case, selection would also increase the variance of reproductive contribution (indirect effect) but in addition would modify the frequency of the genes involved in the control of the fitness-related traits so that the regions around these genes should be submitted to stronger variations of allelic frequency than the rest of the genome due to hitch-hiking effects (direct effect).

Using the analytical formulae ([5] and eq. (2), Appendix 1) for the calculation of Ne in the case of non-herited variation in the reproductive contribution, we found that only unrealistic variances (75 compared to 2 if the differences in contributions of parents are exclusively due to sampling) could explain the discrepancy we observed between the estimated Ne and the demographic size of the populations (Appendix I). Theory [5] as well as some experimental results [2] showed that low level of correlation between the effective family sizes for successive generations may have a strong impact on the evolution of the gene pool of a population. As wheat is mainly a selfing species, all the individuals in the DM populations are close to a pure line and the correlation between two generations can be approximated by broad-sense heritability. So, we suspected that the effective family size was correlated across successive generations based on the broad sense heritability values found for NKP. This led us to conclude

that differences in parental contributions were due to inherited genetic causes and that in other terms limited effective size in the PA population was due to selection. Yet, true parent-offspring correlation needs to be more precisely investigated and experiments are now being carried out to evaluate directly the correlations for NKP, NKS and KWP measured in related plants of two successive generations.

The comparison of the observed F_c distribution with the expected Chi^2 distribution based on the estimated genetic Ne gave evidence that drift effects were not homogeneous over the whole genome and that some genome regions had been submitted to high hitch-hiking effects. The different above mentioned arguments led us to the conclusion that some marker loci were certainly dragged by selected genes linked to them. But assuming that selection acted on the same traits during the subsequent generations, then we would expect to find a positive correlation between the variations during the first four generations and the variations during the five following ones. The lack of correlation between shifts during the first period of time and shifts during the following one can be explained by different mechanisms: (i) the fixation of the favourable allele at the selected locus responsible for hitch-hiking effects in the first generations, (ii) the increase in the weight of a gene in the variation in the selected trait due to the previous fixation of genes with larger effects, (iii) low linkage disequilibrium between marker loci and selected genes. The latter case may lead to the situation observed for $Fba65A$ and $Psr144$. Both loci revealed important F_c during the two periods, but the frequencies of the different marker alleles varied in opposite directions during the two periods. The case of $Psr144$ is quite interesting because this RFLP marker had been mapped by Gale *et al.* [14] on chromosome 4B very close to the dwarfing locus $Rht1$ (5–20 cM). We know that $Rht1$ was polymorphic in PA, that plant height has been strongly selected and that the frequency of dwarfing alleles has decreased across generations [20]. Hence, this strongly suggests that the large variations in allelic frequency at $Psr144$ were the result of a hitch-hiking effect of the $Rht1$ locus with no initial linkage disequilibrium between $Rht1$ and $Psr144$.

Using an SSD population derived from PA0, nulli-tetrasomic lines and information based on synteny, the other marker loci were mapped by Enjalbert *et al.* [11]. In order to find possible explanations for the large shifts in frequency of some markers, we sought genes located around the mapping positions of these markers. Such information is of course incomplete, particularly in wheat, but among the four marker loci ($ba65A$, $ba242C$, $ba204A$ and $ba280C$), two cases seemed interesting. The $ba204A$ locus was found to map on chromosome arm 7DL at less than 10 cM of locus $Pch1$ (major gene of resistance to eyespot). The frequency of the $Pch1$ resistance gene was assessed in this PA population by Paillard [23], and the value did not differ from the frequency in the initial PA population (PA0). Yet, the sample size for this estimation was very small (11) and this should be further investigated in order to achieve a more precise estimation. The second case was that of locus $ba280C$, which mapped

on chromosome arm 2AS at about 20 cM of loci $Yr17$ and $Lr37$. Both loci are located on an interspecific introgression from Aegilops ventricosa [3]. $Yr17$ (resp. $Lr37$) is a specific gene of resistance to yellow rust (resp. to leaf rust). None of them was overcome during the 10 first generations of DM. Moreover, Paillard [23] showed that these genes had been selected and that their frequencies had increased in most of the PA populations studied. Unfortunately, PA Moulon was not among the populations studied. To acquire more arguments in favour of a role of $Yr17-Lr37$ in the evolution of $ba280C$, individuals of PA Moulon should be characterized for the presence of resistance alleles at these loci.

Hence if we wish to identify chromosomic regions carrying genes involved in the variation in selected traits using the variation in allelic frequencies at marker loci in multi-parental populations, it appears necessary to have a sufficient set of highly polymorphic marker loci such as SSR. This would enhance the probability of linkage disequilibrium between the marker and the selected loci. Yet the finite size of the populations and their high rate of selfing should increase this probability even with a low density of markers. The behaviour of $Fba65a$ and $Psr144$ also suggested that the information on the evolutions between more than two different generations should be taken into account in order to be more powerful.

The very low effective size estimated in the DM populations and its relation with a high and probably heritable variation in individual contribution to the next generation showed the necessity of managing larger population sizes during the installation in new environments. In heterogeneous populations, the main selective pressure is competition between plants and in the DM populations individual fitness appeared to be mostly related to plant height. Hence, when devising the protocol of a DM programme, particular attention should be paid to the control of the evolution of plant height and more generally of traits involved in competition ability in order to limit hitch-hiking and genetic drift effects.

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APPENDIX I

In a review [5], Caballero developed the prediction of effective size in numerous cases. Here, for a better understanding of our results, we show some

useful expressions for Ne. For the derivation of these expressions, see [5]. In an idealised population, differences in the contributions of parents are only due to sampling and the number k of successful gametes contributed by each parent is binomially distributed with mean $m_k = 2$ and variance:

$$\sigma_k^2 = 2\left(1 - \frac{1}{N}\right) \cdot \tag{1}$$

Yet, in real populations parental contributions should vary more than expected just by chance and σ_k^2 should be higher. Let us consider a population of constant size N over generations ($m_k = 2$) with a mixed mating system. Effective size can be derived using the sampling drift approach. Ne depends on the variance of family size (S_k^2) and on α, the inbreeding coefficient (Wright *Fis* [28]).

$$Ne = \frac{4N}{2(1-\alpha) + S_k^2(1+\alpha)} \cdot \tag{2}$$

In the PA population studied, mean α was 0.89. If the true number of individuals is 5000, then, $Ne = 144$ implies that $S_k^2 = 73$, to be compared with 2 (eq. (1)).

At inbreeding equilibrium, α and (S_k^2) can be expressed as a function of t (outcrossing rate in the population), and Ne reduces to:

$$Ne = \frac{N}{1+\alpha} \cdot \tag{3}$$

REFERENCES

[1] Allard R.W., Genetic changes associated with the evolution of adaptedness in cultivated plants and their wild progenitors. J. Hered. 79 (1988) 235–238.

[2] Austerlitz F., Heyer E., Social transmission of reproductive behavior increases frequency of inherited disorders in a young-expanding population, Proc. Natl. Acad. Sci. USA 95 (1998) 15140–15144.

[3] Bariana H.S., McIntosh R.A., Cytogenetic studies in wheat XV. Chromosome location of rust resistance genes in VPM1, Genome 36 (1993) 476–482.

[4] Bradshaw J.E., Competition between cultivars of fodder kale (*Brassica oleracea* L.) in yield trials with single-row plots, Euphytica 35 (1986) 433–439.

[5] Caballero A., Developments in the prediction of effective population size, Heredity 73 (1994) 657–679.

[6] David J.L., Savy Y., Trottet M., Pichon M., Méthode de gestion dynamique de la variabilité génétique. Exemple d'un réseau expérimental de populations composites de blé tendre, in: Complexes d'espèces, flux de gènes et ressources génétiques. BRG, Paris, 1992, pp. 337–350.

[7] David J.L., Zivy M., Cardin M.L., Brabant P., Protein evolution in dynamically managed populations of wheat: adaptive responses to macro-environmental conditions, Theor. Appl. Genet. 95 (1997) 932–941.

[8] Dellaporta S., Wood J., Hicks J., A plant DNA minipreparation version II, Plant Mol. Biol. Report 1 (1983) 19–21.

[9] Enjalbert J., Diversité génétique et régime de reproduction de populations de blé tendre (*Triticum aestivum* L.) menées en gestion dynamique, Thèse de doctorat de l'Institut national agronomique, Paris Grignon, 1999.

[10] Enjalbert J., Goldringer I., David J.L., Brabant P., The relevance of outcrossing for the dynamic management of genetic resources in predominantly selfing *Triticum aestivum* (bread wheat), Genet. Select. Evol. 30 (suppl. 1) (1998) 197–211.

[11] Enjalbert J., Bœuf C., Belcram H., Leroy P., Use of multiparental inbred populations to determine allelic relationships of molecular markers, Plant Breeding 118 (1999) 88–90.

[12] Enjalbert J., Goldringer I., Paillard S., Brabant P., Molecular markers to study genetic drift and selection in wheat populations, J. Exp. Bot. 50, No 332 (1999) 283–290.

[13] Frankham R., Effective population size / adult population size ratios in wildlife: a review, Genet. Res. Camb. 66 (1995) 95–107.

[14] Gale M.D., Atkinson M.D., Chinoy C.N., Harcourt R.L., Jia J., Li Q.Y., Devos K.M., Genetic maps of hexaploid wheat, in: 8^{th} International Wheat Genetics Symposium, Beijin, China, 1997 pp. 29–40.

[15] Goldringer I., Brabant P., Kempton P., Adjustment for competition between genotypes in single-row-plot trials of winter wheat (*Triticum aestivum* L.), Plant Breeding 112 (1994) 294–300.

[16] Hamblin J., Donald C.M., The relationship between plant form, competitive ability and grain yield in a barley cross, Euphytica 23 (1974) 535–542.

[17] Harlan H.V., Martini M.L., A composite hybrid mixture, J. Am. Soc. Agron. 21 (1929) 487–490.

[18] Jennings P.R., Aquino R.C., Studies on competition in rice. III. The mechanism of competition among genotypes, Evolution 22 (1967) 529–542.

[19] Jensen N.F., Federer W.T., Adjacent row competition in wheat, Crop Sci. 4 (1964) 641–645.

[20] Le Boulc'h V., David J.L., Brabant P., De Vallavieille-Pope C., Dynamic conservation of variability: responses of wheat populations to different selective forces including powdery mildew, Genet. Select. Evol. 26 Suppl 1, (1994) 221–240.

[21] Lu Y.H., Merlino M., Isaac P.G., Staccy J., Bernard M., Leroy P., A comparative analysis between ^{32}P and digoxigenin-labelled single-copy probes for RFLP detection in wheat, Agronomie 14 (1994) 33–39.

[22] Nelson J.C., Sorrells M.E., Van Deynze A.E., Lu Y.H., Atkinson M., Bernard M., Leroy P., Faris J.D., Anderson J.A., Molecular mapping of wheat: major genes and rearrangements in homoeologous group 4, 5 and 6, Genetics 141 (1995) 721–731.

[23] Paillard S., Evolution des résistances à différentes maladies dans des populations de blé tendre (*Triticum aestivum* L.) menées en gestion dynamique, thèse de doctorat de l'Institut national agronomique, Paris Grignon, 1999.

[24] Pontis C., Utilisation de marqueurs génétiques pour le suivi de la variabilité de 3 composites de blé tendre d'hiver (*Triticum aestivum* L.) menées en gestion dynamique, thèse de doctorat de l'Institut national agronomique, Paris Grignon, 1992.

[25] Powell W., Caligari P.D.S., Goudappel P.H., Thomas W.T.B., Competitive effects in monocultures and mixtures of spring barley (*Hordeum vulgare*), Theor. Appl. Genet. 71 (1985) 443–450.
[26] Thomas G., Rousset M., Pichon M., Trottet M., Doussinault G., and Picard E., Méthodologie de l'amélioration de blé tendre (*Triticum aestivum* L.). I. Création par croisements et analyse d'une population artificielle à 16 parents, base de cette étude méthodologique, Agronomie 11 (1991) 359–368.
[27] Waples R.S., A generalized approach for estimating effective population size from temporal changes in allelic frequency, Genetics 121 (1989) 379–391.
[28] Wright S., Evolution in Mendelian populations, Genetics 16 (1931) 97–159.