Heterosis indices: What do we really measure?

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Abstract

Heterosis (hybrid vigor) is a universal phenomenon of crucial agro-economic and evolutionary importance. We show that the most common heterosis indices do not properly measure the deviation from additivity because they include both a component accounting for the "real" heterosis and a term that has no link with heterosis since it depends only on the parental values. Therefore these indices are ineffective whenever the aim of the studies is to compare heterosis levels between traits, environments, genetic backgrounds or developmental stages, as these factors may affect not only heterosis but also the parental values. This observation argues for the careful choice of heterosis indices according to the purpose of the work.

Introduction

Non-linear processes are extremely common in biology. In particular, the genotype-phenotype or phenotype-phenotype relationships display frequently concave behaviours, resulting in dominance of "high" over "low" alleles (Wright, 1934) and in positive heterosis for a large diversity of polygenic traits (Fiévet *et al.*, 2018; Vasseur *et al.*, 2019). Quantifying properly the degree of non-additivity is an essential prerequisite for any interpretation and comparison of genetic studies and for predictions in plant and animal breeding. However, most of the classically used heterosis indices can hardly meet this requirement.

Recall first the way the degree of dominance is measured. There are two classical dominance indices: (i) Wright (1934) defined:

$$D_{\mathrm{W}} = \frac{z_2 - z_{12}}{z_2 - z_1}$$

where z_1, z_2 and z_{12} are respectively the phenotypic values of genotypes A_1A_1, A_2A_2 and A_1A_2, with $z_2 > z_1$. D_{W} varies from 0, when A_2 is fully dominant over A_1, to 1, when A_2 is fully recessive with respect to A_1. $D_{\mathrm{W}} = 0.5$ corresponds to semi-dominance or additivity ($z_{12} = \frac{z_1+z_2}{2}$) (Table 1). Note that D_{W} is strictly equivalent to the coefficient of dominance h used in evolutionary genetics (Crow & Kimura, 1970). (ii) Falconer (1960) proposed the following index:

$$D_{\mathrm{F}} = \frac{z_{12} - \bar{z}}{\frac{z_2 - z_1}{2}}$$

where $\bar{z} = \frac{z_1+z_2}{2}$. D_{F} varies in the reverse direction as compared to D_{W}: its value is 1 if $z_{12} = z_2$ (complete dominance of A_2 over A_1), -1 if $z_{12} = z_1$ (A_2 is fully recessive with respect to A_1) and 0 in case of additivity. In case of overdominance, $D_{\mathrm{W}} < 0$ and $D_{\mathrm{F}} > 1$, and in case of underdominance, $D_{\mathrm{W}} > 1$ and $D_{\mathrm{F}} < -1$ (Table 1).

The indices D_{W} and D_{F} are linearly related:

$$D_{\mathrm{F}} = 1 - 2D_{\mathrm{W}},$$

so it does not make any difference to quantify dominance with either of these indices: both give the position of the heterozygote relative to the parental homozygotes.

For polygenic traits, either index could be used to quantify non additivity, *i.e.* real heterosis, without any ambiguity. Actually D_{W} does not seem to have been used in this context, and D_{F} very little. In the literature one finds five heterosis indices, which are summarized in Table 1, with their characteristic values. Their expression in terms of genetic effects, namely additive, dominance, dominance-by-dominance epistasis and additive-by-additive epistasis effects, are shown in Supporting Table S1.

The two most popular indices are the best-parent (BP) and mid-parent (MP) heterosis indices (*e.g.* Gowen, 1952; Frankel, 1983):

$$H_{\mathrm{BP}} = \frac{z_{12} - z_2}{z_2}$$

$$H_{\mathrm{MP}} = \frac{z_{12} - \bar{z}}{\bar{z}}$$

where z_2, z_{12} and $\bar{z}$ are respectively the phenotypic values of parent 2 (with $z_2 > z_1$), of hybrid parent 1 × parent 2 and of the parental mean.

In some instances, the authors do not normalize the difference between the hybrid and the best- or mid-parent value:

$$H_{\mathrm{bp}} = z_{12} - z_2$$

$$H_{\mathrm{mp}} = z_{12} - \bar{z}$$

Finally, the so-called "potence ratio" (Mather, 1949) has the same expression as the Falconer's index of dominance:

$$H_{\mathrm{PR}} = \frac{z_{12} - \bar{z}}{\frac{z_2 - z_1}{2}}.$$

Its value is 0 in case of additivity, 1 if $z_{12} = z_2$ (hybrid value = best-parent value), -1 if $z_{12} = z_1$ (hybrid value = worst-parent value) and > 1 (resp. < -1) in case of best-parent (resp. worst-parent) heterosis. H_{PR}

includes the values of the three genotypes, whereas the other indices lack one of the parental values (H_{BP} and H_{bp}) or both (H_{MP} and H_{mp}). From a genetic point of view, H_{PR} is explicitly expressed in terms of the five genetic effects contributing to heterosis (Supporting information Table S1). Thus the potence ratio, which is yet by far the least used index, is the only one that informs us on the exact position of the hybrid value relative to the parental values. The Wright's index of dominance has the same property, but its inverse direction of variation, that makes comparisons less easy, probably explains why it is not used in this context.

Let us examine the possible interpretation fallacies resulting from the use of the common heterosis indices.

Relationships between the potence ratio and other heterosis indices

It is easy to show that the relationship between H_{PR}, hereafter noted h_{P} for simplicity, and the other indices is (with $z_2 > z_1$):

$$H_{\mathrm{MP}} = h_{\mathrm{P}} \left(\frac{z_2 - z_1}{z_1 + z_2} \right) = h_{\mathrm{P}} z_{\mathrm{m}} \tag{1}$$

$$H_{\mathrm{BP}} = \left(\frac{-1 + h_{\mathrm{P}}}{2} \right) \left(\frac{z_2 - z_1}{z_2} \right) = \left(\frac{-1 + h_{\mathrm{P}}}{2} \right) z_{\mathrm{b}} \tag{2}$$

$$H_{\mathrm{mp}} = h_{\mathrm{P}} \left(\frac{z_2 - z_1}{2} \right) = h_{\mathrm{P}} \bar{z} z_{\mathrm{m}} \tag{3}$$

$$H_{\mathrm{bp}} = \left(\frac{-1 + h_{\mathrm{P}}}{2} \right) (z_2 - z_1) = \left(\frac{-1 + h_{\mathrm{P}}}{2} \right) z_2 z_{\mathrm{b}} \tag{4}$$

where $z_{\mathrm{m}} = \frac{z_2 - z_1}{z_1 + z_2}$ is the coefficient of variation (σ/μ) of the trait in the parents and $z_{\mathrm{b}} = \frac{z_2 - z_1}{z_2}$ is the difference between parents normalized by the best-parent value (or $z_{\mathrm{b}} = 2\sigma/z_2$).

For a given h_{P} value, the indices H_{MP} and H_{BP} are linearly related to z_{m} and z_{b}, respectively, *i.e.* they depend on the scale of parental values.

The relation between H_{MP} and z_{m} is negative when $h_{\mathrm{P}} < 0$ and positive when $h_{\mathrm{P}} > 0$, while the relation between H_{BP} and z_{b} is negative when $h_{\mathrm{P}} < 1$ and positive when $h_{\mathrm{P}} > 1$. Recalling that z_{m} and z_{b} are positive, we see from equation 1 that for $h_{\mathrm{P}} \neq 0$, we have

$$\begin{aligned} 0 < H_{\mathrm{MP}} < h_{\mathrm{P}} \quad & \text{if } h_{\mathrm{P}} > 0 \ \ \text{(positive mid-parent heterosis)} \\ h_{\mathrm{P}} < H_{\mathrm{MP}} < 0 \quad & \text{if } h_{\mathrm{P}} < 0 \ \ \text{(negative mid-parent heterosis)} \end{aligned}$$

and we see from equation 2 that for $h_{\mathrm{P}} \neq 1$, we have

$$\begin{aligned} 0 < H_{\mathrm{BP}} < \left(\frac{-1 + h_{\mathrm{P}}}{2}\right) \quad & \text{if } h_{\mathrm{P}} > 1 \ \ \text{(positive best-parent heterosis)} \\ \left(\frac{-1 + h_{\mathrm{P}}}{2}\right) < H_{\mathrm{BP}} < 0 \quad & \text{if } h_{\mathrm{P}} < 1 \ \ \text{(negative best-parent heterosis)} \end{aligned}$$

If $h_{\mathrm{P}} = 0$ (resp. $h_{\mathrm{P}} = 1$), H_{MP} (resp. H_{BP}) $= 0$.

Numerical applications performed with nine h_{P} values, from $h_{\mathrm{P}} = -2$ to $h_{\mathrm{P}} = 2$, show that a given H_{MP} or H_{BP} value can be observed with contrasted h_{P} values (Supporting information Fig. S1). For instance, $H_{\mathrm{MP}} \approx 0.4$ can both correspond to mid-parent heterosis ($h_{\mathrm{P}} = 0.5$, $z_{\mathrm{m}} \approx 0.8$) and to best-parent heterosis ($h_{\mathrm{P}} = 2$, $z_{\mathrm{m}} \approx 0.21$).

This can also be illustrated from experimental data in maize. We measured six traits (flowering time, plant height, ear height, grain yield, thousand-kernel weight and kernel moisture) in four crosses (B73×F252, F2×EP1, F252×EP1, F2×F252) and three environments in France (Saint-Martin-de-Hinx in 2014, Jargeau in 2015 and Rhodon in 2015). We computed h_{P}, H_{MP} and H_{BP} for the 72 trait-cross-environment combinations. Fig. **1a,b** shows that the relationship between h_{P} and either index is very loose, if any. A given h_{P} value can correspond to a large range of H_{MP} or H_{BP} values, and vice versa. We performed the same analyses from the data published by Shang *et al.* (2016), who measured in cotton five traits in two crosses and three environments. The same loose relationship between h_P and either heterosis index was observed (Fig. **1c,d**). This means that the coefficients of variation of the traits or the normalized difference between parents, which have no link with heterosis since they do not include the hybrid values, affect markedly H_MP and H_BP.

Regarding the indices H_mp and H_bp, which are not dimensionless, they give no other information than the sign of heterosis. For a given h_P value, H_mp can vary from $-\infty$ to 0 when $h_\mathrm{P} < 0$ and from 0 to $+\infty$ when $h_\mathrm{P} > 0$, and H_bp can vary from $-\infty$ to 0 when $h_\mathrm{P} < 1$ and from 0 to $+\infty$ when $h_\mathrm{P} > 1$ (equations 3 and 4).

The pitfalls of the commonly used indices

The non-univocal relationship between h_P and the commonly used heterosis indices has two consequences. (i) For a given trait, comparing these indices in different crosses and/or environments and/or developmental stages is quite tricky: as soon as there is an effect of these factors on the scale of the trait and/or the difference between parental values (*i.e.* on z_m or z_b), it becomes impossible to compare the actual levels of heterosis between the conditions. (ii) When studying different traits, the problem is even more pronounced because each trait has its own scale of variation, making H_MP or H_BP (and even more H_mp or H_bp) useless for comparing their real levels of heterosis.

These pitfalls could easily be illustrated from our maize dataset. Fig. **2a** shows that classifying the traits for their degree of heterosis can give markedly different results depending on whether one uses the h_P index or one of the two indices H_MP and H_BP. For instance, in the cross F252×EP1 flowering time displays moderate heterosis according to H_MP and H_BP but it is actually the trait with the highest h_P value. Conversely, plant height is the second most heterotic trait regarding H_{MP} or H_{BP}, which is not the case if we consider h_{P}. Similarly, comparing heterosis of a given trait in different hybrids results in index-specific rankings: heterosis of ear height measured with h_{P} is maximum in hybrid B73×F252, while from H_{MP} and H_{BP} the highest values are in hybrid F252×EP1 (Fig. **2b**). Finally the effect of the environment on heterosis gives the same discrepancies between h_{P} on the one hand and H_{MP} or H_{BP} on the other hand (Fig. **2c**).

It is also informative to compare the variation of heterosis indices for a trait measured during development or growth. We fitted the percentage of flowering over time in the hybrids W117×F192 and W117×F252 and their parents, using Hill functions:

$$y = \frac{ax^n}{b + x^n}$$

where n is the Hill coefficient, then we computed the variation of heterosis for percentage of flowering estimated from the fitted curves (Fig. **3**). Again, h_{P} tells a specific story as compared to H_{MP} or H_{BP}. Both H_{MP} and H_{BP} decrease as flowering comes along because the coefficient of variation also decrease. This prevents to follow the variation of real heterosis.

The same type of result was observed in a simulation describing the increase of a population size that follows a logistic function, as observed for instance in yeast cultures. We used:

$$y = \frac{K}{1 + a\,\mathrm{e}^{-r\theta}}$$

where y is the size of the population, K the carrying capacity, a a constant, r the growth rate and θ the time. We assumed that the parents differed only for growth rate r and that there is additivity for this parameter. The result shows that H_{MP} and H_{BP} for population size follow over time variations clearly non congruent with that of h_{P} (Supporting information

Fig. S2).

Discussion

If H_{MP} and H_{BP} (and their non normalized forms H_{mp} and H_{bp}) do not give reliable information on non-additivity, why are they so commonly used? There are probably both historical and technical reasons: (i) The first scientists who quantified heterosis were plant breeders (Shull, 1908; East, 1936). In an economic perspective, the goal was and still is to develop hybrids "better" than the best- or mid-parent for desired agronomic traits, and not to know where is the hybrid value relative to the parental values. So the heterosis indices have been defined accordingly and the habit has remained; (ii) The indices giving the right non-additivity values, h_{P} ($= H_{\mathrm{PR}}$) for heterosis and D_{W} or D_{F} for dominance, can take high or very high values when the parents are close, due to the small differences $z_2 - z_1$ in the denominator of the fractions. This can produce extreme values that are not easy to represent and to manipulate for statistical treatments. Nevertheless such values are biological realities that convey precisely the inheritance of the traits under study, what H_{MP}, H_{BP}, H_{mp} and H_{bp} do not. In addition, from a practical point of view, a single index is sufficient to know the position of the hybrid relative to the mid- or the best-parent, whereas in a number of studies the authors compute and comment both H_{MP} and H_{BP} (or H_{mp} and H_{bp}). More important, as soon as it comes to compare amplitude of heterosis between traits, developmental stages, crosses or environmental conditions, there is no other choice but to use heterosis indices that are not affected by the scale of the parental values but account for the position of the hybrid in the parental range.

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Author contributions

Conceptualization: DdV. Maize experiments: JBF. Data analyses and numerical applications: DdV and JBF. Writing article: DdV and JBF.

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Table 1. The dominance and heterosis indices. Light yellow background: the two dominance indices, Wright's (D_{W}) and Falconer's (D_{F}) ones. Light blue background: the five heterosis indices (see text). Subscripts: mp or MP, mid-parent; PR, potence ratio; bp or BP, best-parent. In the text, H_{PR} is also noted h_{P}. z_1 (resp. z_2): phenotypic value of parental homozygote 1 or of parent 1 (resp. 2). z_{12}: heterozygote or hybrid value. $\bar{z}$: mean parental value. By convention, $z_2 > z_1$.

Reference	Index	Index scales with their characteristic values
High homozygote	$D_{\mathrm{W}} = \frac{z_2 - z_{12}}{z_2 - z_1}$	$z_{12} = z_1$; $z_{12} = \bar{z}$; $z_{12} = z_2$ $+\infty$ — 1 — 0.5 — 0 — $-\infty$ Underdominance ; Recessivity ; Additivity ; Dominance ; Overdominance
Mean homozygote	$D_{\mathrm{F}} = \frac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$z_{12} = z_1$; $z_{12} = \bar{z}$; $z_{12} = z_2$ $-\infty$ — -1 — 0 — $+1$ — $+\infty$ Underdominance ; Recessivity ; Additivity ; Dominance ; Overdominance
Mid-parent	$H_{\mathrm{mp}} = z_{12} - \bar{z}$	$z_{12} = \bar{z}$ $-\infty$ — 0 — $+\infty$ Negative heterosis ; Additivity ; Mid- or best-parent heterosis
	$H_{\mathrm{MP}} = \frac{z_{12} - \bar{z}}{\bar{z}}$	$z_{12} = \bar{z}$ $-\infty$ — 0 — $+\infty$ Negative heterosis ; Additivity ; Mid- or best-parent heterosis
	$H_{\mathrm{PR}} = \frac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$z_{12} = z_1$; $z_{12} = \bar{z}$; $z_{12} = z_2$ $-\infty$ — -1 — 0 — $+1$ — $+\infty$ Worst-parent heterosis ; Negative mid-parent heterosis ; Additivity ; Positive mid-parent heterosis ; Best-parent heterosis
Best-parent	$H_{\mathrm{bp}} = z_{12} - z_2$	$z_{12} = z_2$ $-\infty$ — 0 — $+\infty$ Non-additivity or additivity ; Best-parent heterosis
	$H_{\mathrm{BP}} = \frac{z_{12} - z_2}{z_2}$	$z_{12} = z_2$ $-\infty$ — 0 — $+\infty$ Non-additivity or additivity ; Best-parent heterosis

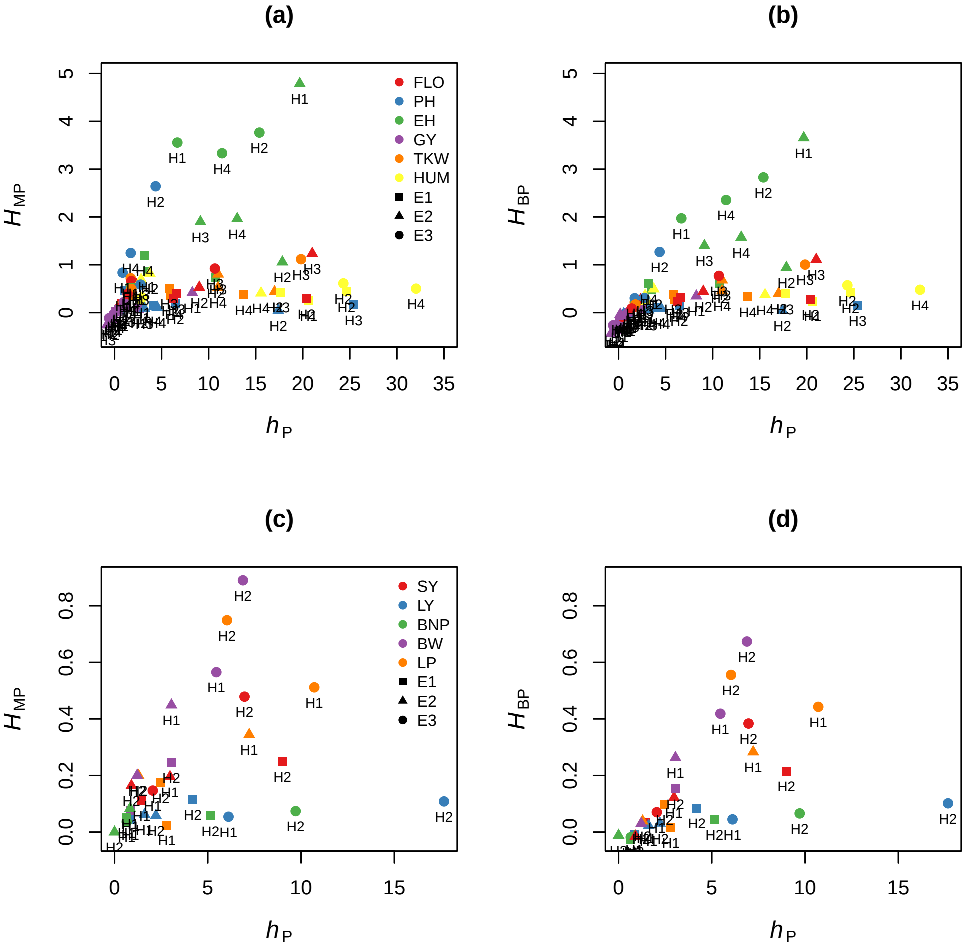
Figure legends

Figure 1 Relationship between the potence ratio h_P and the two heterosis indices H_{MP} and H_{BP}. (**a**), (**b**) Six traits have been measured in maize (FLO: flowering time [number of days between the day at 50% flowering and August, 12], PH: plant height, EH: ear height, GY: grain yield, TKW: thousand-kernel weight, KM: kernel moisture) in four crosses (H1: B73×F252, H2: F2×EP1, H3: F252×EP1, H4: F2×F252) and three environments in France (E1: Saint-Martin-de-Hinx, E2: Jargeau, E3: Rhodon). (**a**) Relationship between h_P and H_{MP}. (**b**) Relationship between h_P and H_{BP}. (For clarity, four out the 72 trait-cross-environment combinations are not represented because they have high h_P values.) (**c**), (**d**) Five traits have been measured in cotton (SY: seed yield, LY: lint yield, BNP: bolls per plant, BW: boll weight, LP: lint percent) in two crosses (H1: X1135×GX100-2 and H2: GX1135×VGX100-2) and three environments in China (E1: Handan, E2: Cangzhou, E3: Xiangyang). (**c**) Relationship between h_P and H_{MP}. (**d**) Relationship between h_P and H_{BP}. Data from Shang *et al.*, 2016.

Figure 2 Heterosis ranking according to the index. (**a**) Heterosis indices for six traits measured in the cross F252×EP1 grown in Saint-Martin-de-Hinx (France) in 2014. (**b**) Heterosis indices of ear height in four crosses grown in Saint-Martin-de-Hinx (France) in 2014. (**c**) Heterosis indices of plant height in the cross F2×F252 grown in the three environments. The six traits and the three environments are the same as in Fig. **1a**. The scales of the heterosis indices are normalized by the maximum value in the dataset considered (figures at the top right of the vertical lines).

Figure 3 Heterosis for flowering in two maize hybrids. (**a**) Percentage of flowering over time (number of days since January, 1st) for parents W117 and F192 and their hybrid, adjusted with a Hill function (see text) (**b**) Percentage of flowering over time for parents W117 and F252 and their hybrid. (**c**) Evolution of heterosis indices for the cross W117×F192. (**d**) Evolution of heterosis indices for the cross W117×F252.

Key words: Flowering, growth rate, heterosis index, hybrid vigour, maize, non-additivity, yield.



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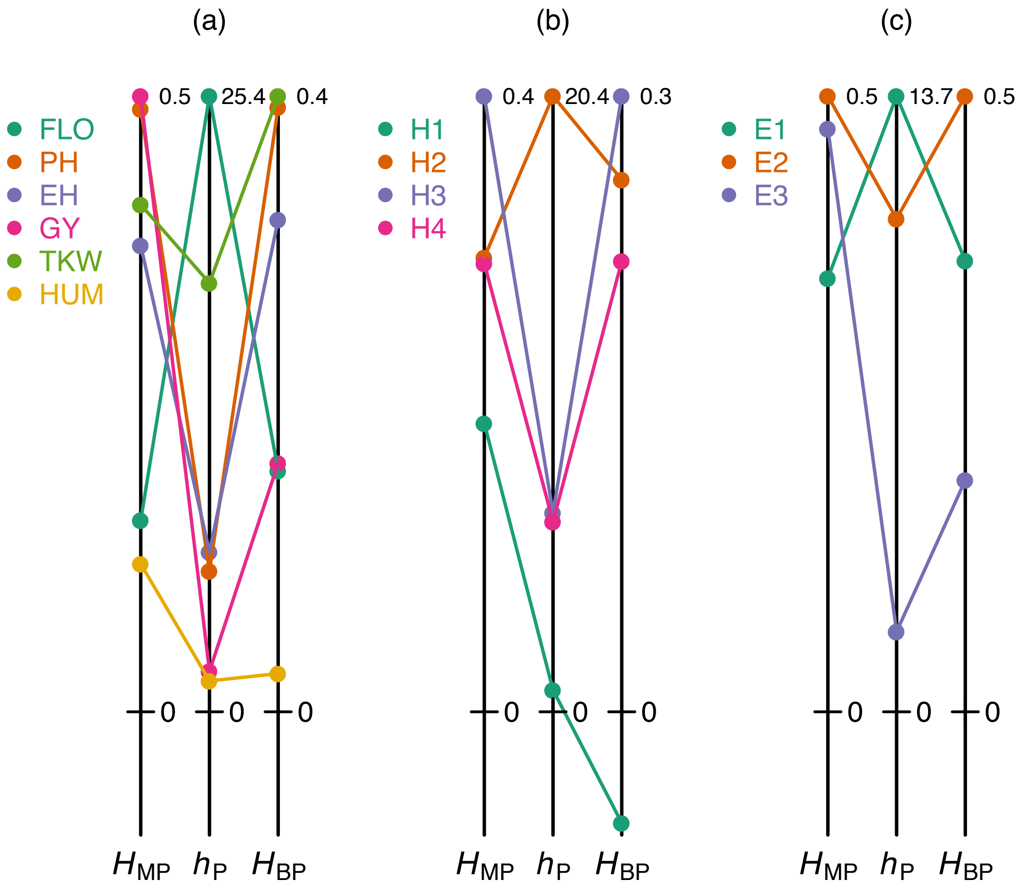
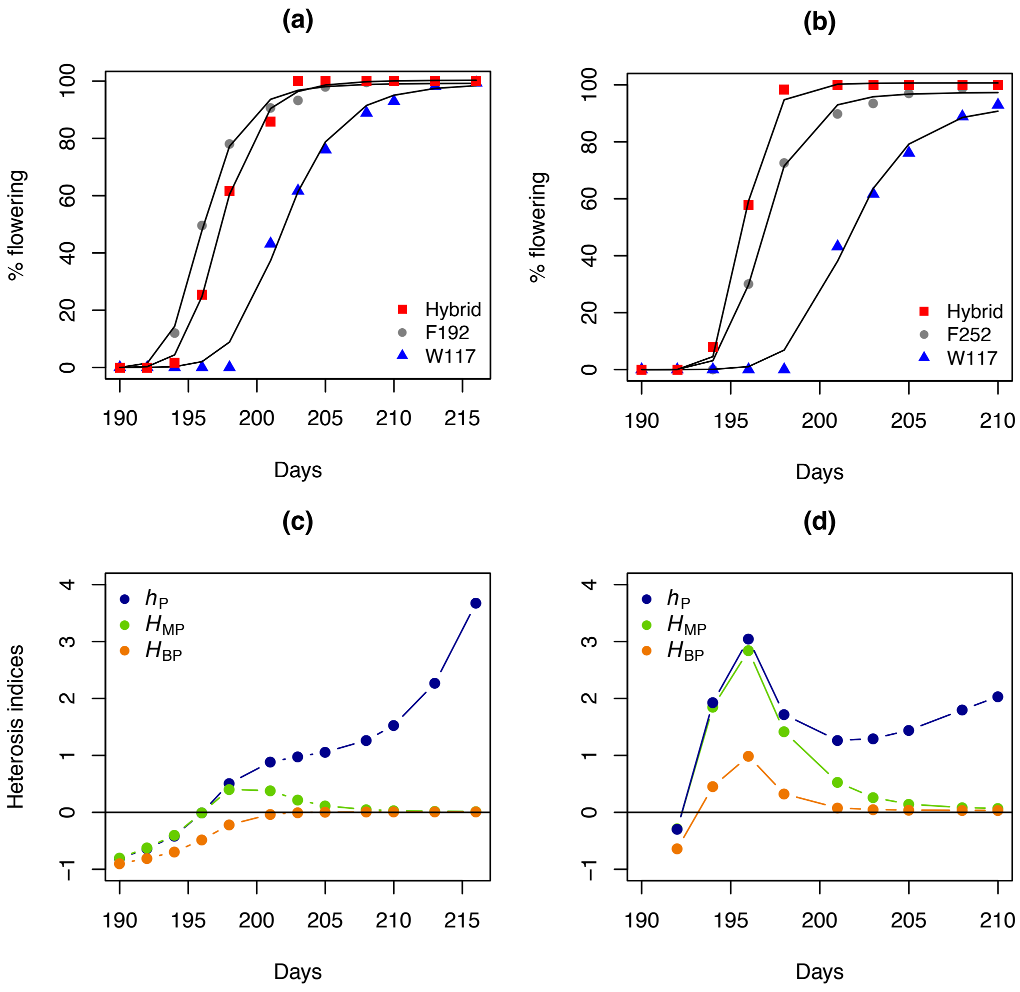


Figure 2. Heterosis ranking according to the index. (**a**) Heterosis indices for six traits measured in the cross F252×EP1 grown in Saint-Martin-de-Hinx (France) in 2014. (**b**) Heterosis indices of ear height in four crosses grown in Saint-Martin-de-Hinx (France) in 2014. (**c**) Heterosis indices of plant height in the cross F2×F252 grown in the three environments. The six traits and the three environments are the same as in Fig. **1a**. The scales of the heterosis indices are normalized by the maximum value in the dataset considered (figures at the top right of the vertical lines).



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Supporting information

Table S1 Heterosis indices expressed as functions of genetic effects. Subscripts: same as in Table 1. μ, mean of the multilocus homozygous genotypes; $\sum a$, sum of the additive effects; $\sum d$, sum of the dominance effects; $\sum e_{\text{dom}}$, sum of the dominance-by-dominance epistatic effects; $\sum e_{\text{add}}$, sum of the additive-by-additive epistatic effects; $\sum e_{\text{add even}}$, sum of the additive-by-additive epistatic effects involving an even number of genes; $\sum e_{\text{add odd}}$, sum of the additive-by-additive epistatic effects involving an odd number of genes (from Fiévet *et al.*, 2010).

Reference	Index	Index as function of genetic effects
Mid-parent	$H_{\text{mp}} = z_{12} - \bar{z}$	$\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}$
	$H_{\text{MP}} = \dfrac{z_{12} - \bar{z}}{\bar{z}}$	$\dfrac{\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}}{\mu + \sum e_{\text{add even}}}$
	$H_{\text{PR}} = \dfrac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$\dfrac{\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}}{\sum a + \sum e_{\text{add odd}}}$
Best-parent	$H_{\text{bp}} = z_{12} - z_2$	$\sum d + \sum e_{\text{dom}} - \sum a - \sum e_{\text{add}}$
	$H_{\text{BP}} = \dfrac{z_{12} - z_2}{z_2}$	$\dfrac{\sum d + \sum e_{\text{dom}} - \sum a - \sum e_{\text{add}}}{\mu + \sum a + \sum e_{\text{add}}}$

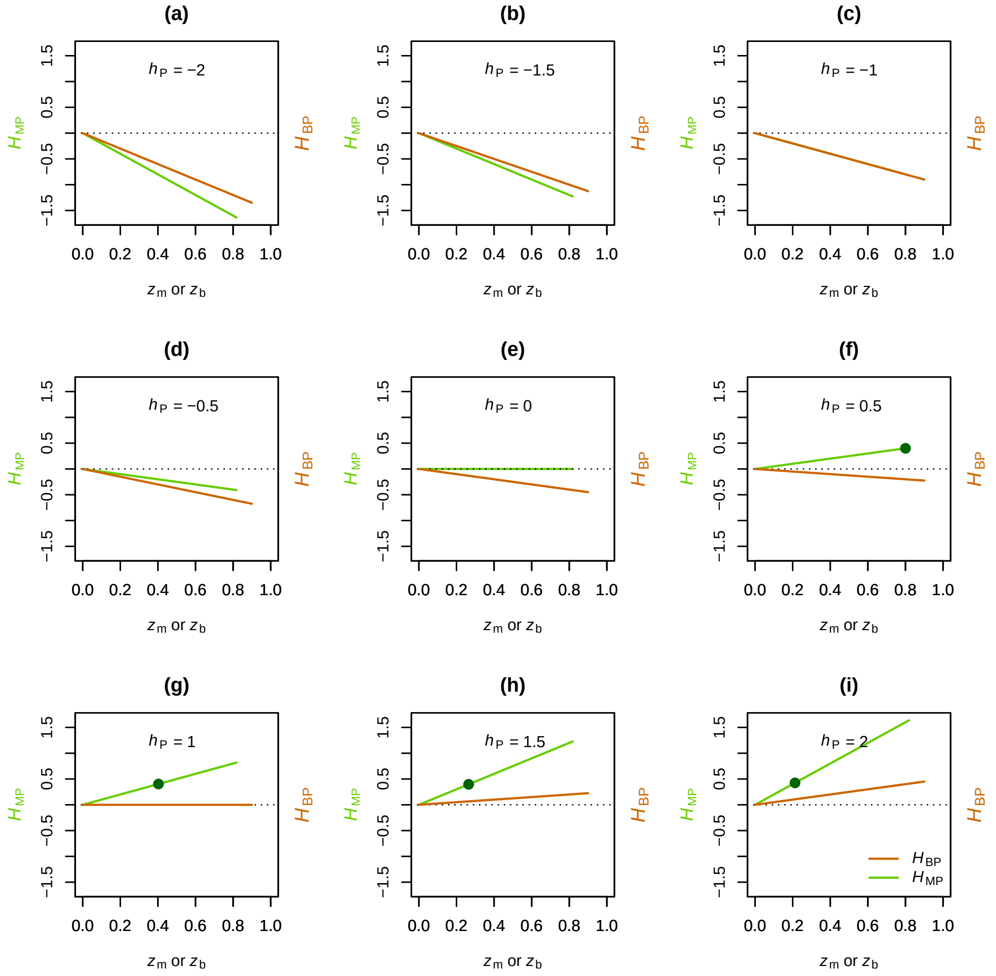

Fig. S1 Influence of the scale of the parental values on H_{MP} and H_{BP} for different values of the potence ratio h_{P}. (**a**) to (**i**) h_{P} values from -2 to 2. $z_{\mathrm{m}} = \frac{z_2-z_1}{z_1+z_2}$ and $z_{\mathrm{b}} = \frac{z_2-x_1}{z_2}$, with $z_1 = 1$ and z_2 varying from 1 to 10 (see equations 1 and 2 in the text). Green line: relationship between z and H_{MP}. Orange line: relationship between z_{b} and H_{BP}. Dotted line: H_{MP} or $H_{\mathrm{BP}} = 0$. The dark green points show that a given H_{MP} value (≈ 0.4) can be observed for quite different h_{P} values, and the same is true for H_{BP}.

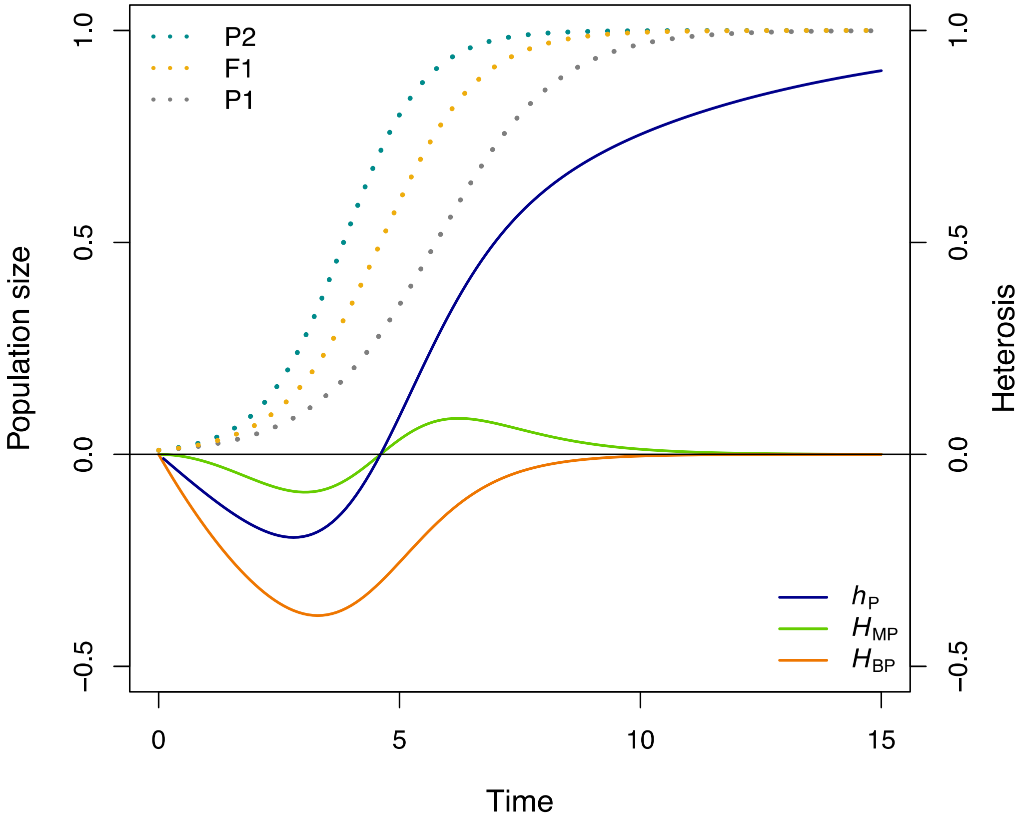

Fig. S2 Heterosis of population size (simulations). The population sizes (dotted curves) follows over time a logistic function with $K = 1$ and $a = 100$ (see text). Parents P1 and P2 and hybrid F1 have respectively the growth rates $r = 0.8$, $r = 1.2$ and $r = 1$. Solid curves (right scale): profiles of heterosis indices.