# Genetic Analysis of Biomass Heterosis in Rapeseed (*B. napus* L.)

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## Introduction

More than eighty years have passed since the phenomenon “Heterosis” was defined for the first time by Shull (1922). While with the production of hybrid varieties the practical application of heterosis in plant breeding is quite successful in many crop plants, the basic understanding of the phenomenon is not very advanced. To analyse the genetic basis of heterosis we have mapped QTL for early and late plant biomass in rapeseed using a doubled haploid population and its corresponding test crosses.

## Materials and Methods

### Plant Material

The plant material consists of a mapping population of 250 doubled haploid lines developed from a highly heterotic cross between an inbred line of the winter rapeseed cultivar ‘Express’ and a resynthesized rapeseed line ‘R53’. The doubled haploid lines were crossed with a male sterile line of ‘Express’ for the production of $F_1$ hybrids. The use of one of the parents as a tester for the hybrid production provides the opportunity for a straightforward determination of the effects of the mapped QTL. The doubled haploid lines and the corresponding hybrids were grown in a greenhouse and a field experiment following alpha lattice design. The greenhouse trial was focused on fresh biomass weight, measured four weeks after sowing. In the field experiment the plant height at maturity was measured and used as a proxy for late plant biomass. Midparent heterosis was estimated for each pair of doubled haploid line and corresponding hybrid.

### QTL mapping

Composite interval mapping was carried out with PLABQTL version 1.2. The phenotypic data from the doubled haploid lines and from the $F_1$ hybrids as well as the midparent heterosis of the doubled haploid lines and the corresponding hybrids were used separately as input for the QTL mapping. The data of the doubled haploid lines allowed an estimation of the additive effects of the QTL (**Fig. 1a**). The midparent heterosis (MPH) provided an estimate of the dominance effects (**Fig. 1b**). Using the data of the $F_1$ hybrids, QTL effects were derived which represent the sum or the difference of the additive and dominance effects of the respective QTL, depending on whether the donor allele (‘R53’) or the allele of the recurrent parent (‘Express’) is dominant (**Fig. 1b, 1c**).

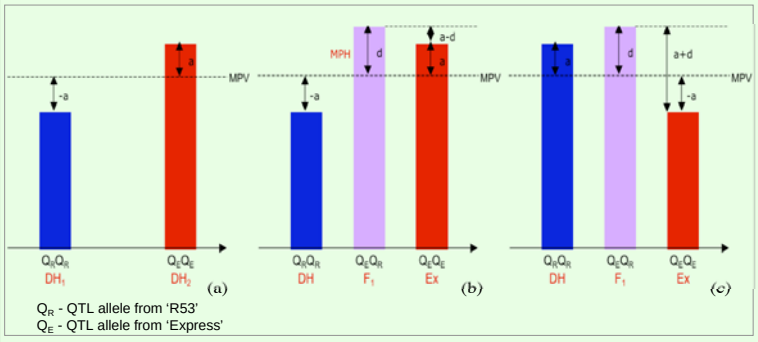


**Fig. 1** Genetic effects estimated from different input data for QTL mapping

## Results and Discussions

### A genetic linkage map of *B. napus*

A primary map was developed by mapping 230 SSR and 107 AFLP markers in 96 lines of the mapping population and a set of 182 of the most evenly distributed markers, covering all of the mapped genome, were also mapped in the rest of the lines for the construction of a framework map suitable for QTL mapping. (**Fig. 2**).

#### Mapping of QTL for plant biomass

The use of the three different data sets resulted in the detection of 7 QTL for early plant biomass located on 5 linkage groups (**Fig. 2**). Four QTL were mapped in the doubled haploid population and their additive effects were determined (**Tab. 1**). The confidence intervals of the two QTL mapped with the midparent heterosis data (**Tab. 1**) overlap very strongly with those of two of the QTL detected in the doubled haploid population indicating that most probably these are the same QTL.

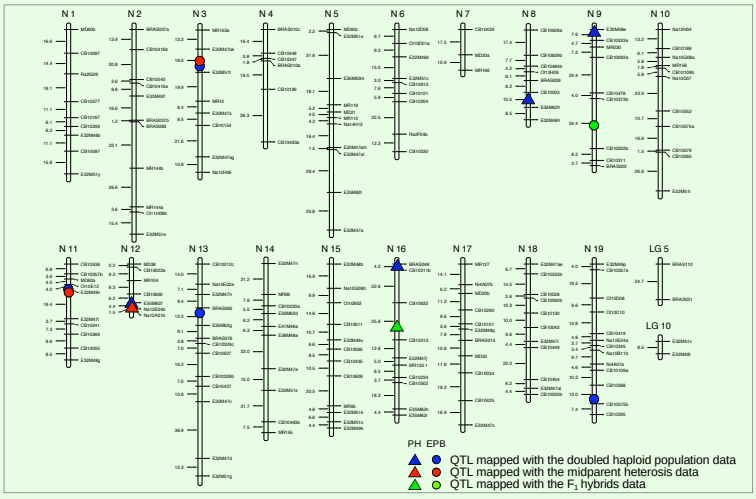


**Fig. 2** Genetic framework map of *B. napus* including QTL for early plant biomass (EPB) and plant height (PH)

**Table 1.** QTL for biomass mapped with the doubled haploid, midparent heterosis and test cross population data

| | | | DH-lines | | | MPH | | | Testcross population | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trait[a] | LG | Interval | LOD | Effect[b] | Vp[c] | LOD | Effect | Vp | LOD | Effect | Vp |
| EPB | N3 | E32M47ak-E32M51t | 4.07 | 0.700 | 6.7 | 6.56 | 1.210 | 7.7 | | | |
| EPB | N11 | OI10E12-E32M49n | 12.29 | 1.221 | 22.9 | 3.41 | 0.694 | 3.8 | | | |
| EPB | N13 | BRAS065-E35M62g | 7.45 | 0.850 | 12.3 | | | | | | |
| EPB | N19 | CB10288-CB10575b | 5.47 | 0.713 | 8.4 | | | | | | |
| EPB | N9 | CB10373b-CB10022b | | | | | | | 4.04 | 0.966 | 6.5 |
| PH | N8 | CB1003-E35M62h | 3.47 | -1.989 | 3.9 | | | | | | |
| PH | N9 | E32M48e-CB10533a | 3.48 | -1.653 | 3.0 | | | | | | |
| PH | N12 | E35M62f-Na12E04b | 3.24 | 1.766 | 3.0 | 4.32 | 2.796 | 5.5 | | | |
| PH | N16 | BRAS048-CB10211b | 6.19 | -2.733 | 7.7 | | | | | | |
| PH | N16 | CB10632-CB10213 | | | | | | | 6.21 | 3.336 | 9.8 |

[a] EPB: Early plant biomass; PH: Plant height [b] Effect for EPB [g/plant]; Effect for PH [cm]
[c] Vp: Explained phenotypic variance [%]

Based on this hypothesis the degree of dominance was estimated for the detected QTL. The QTL on linkage group N3 shows strong overdominance, while the QTL on N11 exhibits partial dominance. The QTL mapping with the F1 hybrid data resulted in the localization of one QTL whose effect most probably is the sum of the dominance and additive effect at that locus (**Tab. 1**).
Five QTL for plant height were detected by the use of the three different data sets (**Fig. 2**). Only additive effects were detected for 3 of them (QTL on N8, N9 and N16), while the QTL on N12 showed an additive effect of 1.77 cm (**Tab. 1**) and a dominance effect of 2.8 cm (**Tab 1**), meaning that the gene action at this locus is overdominance. Similar to the QTL for early plant biomass on linkage group N9, the QTL for plant height on N16 most probably represents the sum of the additive and dominance effect at this locus (**Tab. 1**).
The assessment of the degree of dominance for early and late biomass showed that the genetic effects responsible for heterosis in rapeseed include overdominance and partial dominance. At this stage of the analysis true overdominance at a single locus can not be distinguished from pseudooverdominance generated from the linkage in repulsion phase of genes with partial or full dominance. No significant correlation between early and late plant biomass of the hybrids and of the doubled haploid lines was observed. The correlation between the MPH of the two traits was significant at p = 1% but with a very low correlation coefficient of 0.2. This fact together with the lack of overlapping QTL for the two traits may indicate that different genes are responsible for biomass accumulation in the early and late stages of plant development.

## Acknowledgements

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