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Quantitative effects of the abiotic factors temperature and day length on vernalization, flowering time and freezing tolerance of oilseed rape (*Brassica napus* L.).

Dissertation

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by

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1 QTL clusters in three genomic regions explain flowering time variation in a *Brassica napus* L. winter × spring-type DH population regarding day length and temperature

1.1 Abstract

Knowing the genetic basis of flowering time is of importance in breeding oilseed rape (*Brassica napus* L.) in times of changing winter and spring climate conditions. The vernalization requirement discriminates winter oilseed rape from spring-type rape. Once a genotype-specific vernalization requirement is satisfied, day length and temperature influence flowering time. However, the influences of day length and temperature have mostly been studied in spring-type rape, though they also influence flowering after vernalization in winter oilseed rape. In this study, a doubled haploid population of 194 lines derived from a cross between winter oilseed rape Express617 and spring-type rape DH4079 was examined for the effect of (1) 0, 4, and 8 weeks of vernalization and (2) low and high temperature (11°C and 22°C) in combination with long and short days (8/16 hours light) on flowering time. QTL analysis using a SNP-based map revealed major QTL for flowering time collocating in three genomic regions on chromosomes A02, A07, and C06. A major vernalization QTL V0a, located on A02, explained 56% of the phenotypic variance and contains the known candidate gene *FLOWERING LOCUS T*. Two homologous regions on chromosome C06 and A07 were newly discovered. On C06 spring-type alleles delayed flowering under short days and lower temperature, while on A07 winter-type alleles showed the same effect plus a minor vernalization QTL, both with candidate gene EARLY FLOWERING UNDER SHORT DAYS. We suggest the utilization of different flowering gene homologs in breeding *Brassica napus* L. to counter the environmental effects of climate change.

1.2 Introduction

Flowering time is regulated in a complex network with different pathways that interact with each other and are well studied in *Arabidopsis thaliana* (L.) Heynh. (Blümel et al. 2015). This encompasses internal signals in the autonomous and the gibberellin pathway, as well as external signals controlling vernalization, temperature, and day length pathways. Most of the environmental cues are sensed in the leaves and lead to the expression of *FLOWERING LOCUS T (FT)* through signaling cascades. The FT protein travels to the apical meristem and initiates the generative phase (Jaeger et al. 2013).

The vernalization pathway is well studied in *Brassica napus* L. (Ferreira et al. 1995; Raman et al. 2015). The need to go through a vernalization period to trigger flowering separates winter oilseed rape from spring-types but is also genotype specific and may vary quantitatively within and between winter, semi-winter, and spring-type genotypes (Richter and Möllers 2018). In crosses between spring-type and winter oilseed rape, one gene is often responsible for the split between the two types (Ferreira et al. 1995; Light et al. 2005). In winter annuals of *Arabidopsis thaliana* and winter oilseed rape (*Brassica napus* L.), the floral repressor FLOWERING LOCUS C (FLC) is a central regulator of the vernalization response (Ietswaart et al. 2012; Michaels and Amasino 1999; Tadege et al. 2001). In

amphidiploid oilseed rape flowering time regulation is much more complicated due to the presence of multiple orthologous and paralogous copies of genes affecting flowering time. In the reference genome Darmor-*bzh* up to nine copies of the *FLC* gene has been identified on different chromosomes of the A and C genome (Chalhoub et al. 2014; Zhu et al. 2012). Depending on the genotype different *FLC* copies may be active and hence contribute to the wide range of vernalization requirement found in spring, semi-winter and winter oilseed rape types (Schiessl et al. 2019). Raman et al. (2015) studied vernalization response in a diversity set that included spring-type and winter oilseed rape cultivars and found many candidate genes within the flowering pathway, from the vernalization specific *FLOWERING LOCUS C (FLC)* to flower initiator *TERMINAL FLOWER 1*. Schiessl et al. (2014) studied SNPs and copy number variation of several flowering time regulating genes in a *Brassica napus* L. diversity set and could link differences in *FLC* and *FT* to vernalization requirement and differences in *TEMPRANILLO1* to photoperiod. Schiessl et al. (2017) found 12 regions responsible for the split between spring and winter types with improved methods.

Once the genotype specific vernalization requirement is satisfied, primarily day length and temperature determine phenological development, provided sufficient water and nutrients are available, as well as substantial photosynthesis activity, since high sugar content and specific sugar signals are known to influence flowering positively (Cho et al. 2018). Like *Arabidopsis* (Amasino and Michaels 2010), oilseed rape is a long-day plant, for which longer day length and higher temperature generally lead to earlier flowering (Major 1980; Mendham and Salisbury 1995; Nelson et al. 2014). Studies in *Arabidopsis* show the complexity of the molecular mechanisms for the regulatory pathways of day length and temperature. They are known to interact with each other, as well as with the age and the gibberellin pathway, making this one of the most complex pathways for flowering (Blümel et al. 2015; Kim and Sung 2014; Song et al. 2013).

Experiments of Robertson et al. (2002) showed that vernalized seedlings of canola and Indian mustard responded immediately to the length of the photoperiod and that there was no photoperiod-insensitive phase. Testing the response to day length between 8 and 16 h in 5 *Brassica* species, Nanda et al. (1996) found that a change in photoperiod from 12 to 14 h reduced the time to flowering by 40%. Since only one genotype of four different *Brassica* species was tested this does not exclude genotypic differences in day length sensitivity. King and Kondra (1986) tested photoperiods between 12 and 20 h and found the highest response between 12 and 14 h and no further response beyond 18 h. Salisbury and Green (1991) reported interactions between temperature and day length on flowering time in spring genotypes of European, Canadian and Australian origin. Later flowering genotypes showed stronger responses to photoperiod than early flowering genotypes (King and Kondra 1986; Robertson et al. 2002).

So far QTL mapping studies identified chromosomes A02, A03, A10, C03, C04, C05 and C09 as carrying photoperiod sensitive genes (Axelsson et al. 2001; Cai et al. 2008; Luo et al. 2014; Rahman et al. 2018; Robert et al. 1998). However, most of the molecular markers used at that time do not allow identification of their physical position on current reference genomes (Chalhoub et al. 2014; Lee et al. 2020; Sun et al. 2017) Only few recent studies on

the effect of day length on flowering time had been performed in Brassica species. In a Canadian spring oilseed rape DH population Rahman et al. (2018) detected on C01 a number of QTL for flowering time at day lengths ranging from 10 to 18 hrs. In *Brassica rapa*, Xiao et al. (2019) mapped flowering time QTL for responses to ambient temperature and photoperiod.

In conclusion, all these studies have shown genotypic differences in response to day length and temperature. However, most research regarding flowering regulation through temperature and day length in *Brassica napus* was done with spring-types or in the context of how they influences vernalization, even though rising temperatures during winter and early spring caused by climate change make the reaction of winter oilseed rape to temperature and day length an important issue. Therefore, the objectives of the present work were (I) to characterize the doubled haploid (DH) population derived from a cross between spring-type DH4079 and winter oilseed rape Express617 for their vernalization requirement; (II) to test the impact of day length and temperature on flowering time in fully vernalized plants and study the connection with vernalization requirement; and (III) analyze the interaction between temperature and day length.

To achieve these objectives two experiments were performed: In the vernalization experiment the DH lines with no vernalization and four and eight weeks of vernalization treatment were scored for days to flowering. In the day length and temperature experiment, plants vernalized for nine weeks were grown under four different controlled conditions with combinations of short and long days (8 and 16 h) and at two temperature regimes (11 and 22°C) to determine days to flowering. A SNP-marker based linkage map was used to map QTL and identify candidate genes.

1.3 Material and Methods

1.3.1 Plant material

The inbred line 617 from the winter oilseed rape cultivar Express (Norddeutsche Pflanzenzucht Hans-Georg Lembke KG) and the doubled haploid line (Ferrie 2003) DH4079 from the Swedish spring-type cultivar Topas were crossed to generate F1 seeds. A DH population consisting of 194 lines was developed from clonally propagated F1-plants as described in Valdés et al. (2018).

1.3.2 Vernalization experiment

Vernalization requirement was determined by growing the plants in a randomized complete block design with 5 replications and three treatments: without vernalization (V0) and four (V4) and eight weeks of vernalization (V8) treatment. Each replication-treatment combination consisted of 194 DH lines with one plant per DH line. For parental genotypes and F1, two plants per replication were included and their mean value used for analysis. Plants were grown in 96 multi-pot trays (Quickpot 96, HerkuPlast Kubern GmbH, Ering) with a total size of 335 x 515 mm. Single pots had a size of 38 x 38 x 78 mm and were filled with soil (Fruhstorfer Erde type T25, HAWITA Gruppe GmbH, Vechta) and cultivated for three to four weeks in the greenhouse until the two to three leaf developmental stages (BBCH 12 to 13; Lancashire et al. 1991). Then, the multi-pot trays were transferred to a vernalization chamber

adjusted to 4–5°C and 8 h cool white light (Schuch Typ 164/12 L96C 82W) for the treatment specific time. Sowing and the beginning of vernalization treatment were performed in a staggered way to synchronize the end of the vernalization treatment. After the vernalization treatment, plants were transferred into larger pots (11 cm) filled with compost soil and cultivated under semi-controlled conditions in the greenhouse. Days to flowering (DTF) were recorded starting from the end of vernalization when plants were transferred to the greenhouse until the opening of the first flower. Plants that did not flower after 100 days but showed flower buds were recorded with a value of 115 DTF and those that did not show flower buds with 130 DTF.

1.3.3 Day length and temperature experiment

The effect of day length and temperature on flowering time of fully vernalized plants was determined in a split-split plot design with two factor levels in temperature (11 and 22°C) and two factor levels in day length (8 and 16 h) with 5 replications. Seeds of 188 DH lines, the parental genotypes, and the F1 were sown in two 96 multi-pot trays, grown in the greenhouse in four duplicates, and vernalized as described above for nine weeks. The Population was reduced to fit two multi-pot trays since space in the chamber was limited. After vernalization, the plants were transferred to two growth chambers with different temperatures, which were divided with sheets impervious to light to allow treatment with different day lengths. Therefore, the conditions consisted of four day length and temperature combinations of 8 h/11°C (SD11), 8 h/22°C (SD22), 16 h/11°C (LD11) and 16 h/22°C (LD22). For testing the effect of day lengths and temperatures, positions of the genotypes on the multi-pot trays were randomized in each replication and condition. Growth chambers were equipped with Philips MASTER Green Power CG T 400 Watt providing light intensities of 110–120 µmol*m^{-2}*s^{-1}. Plants were watered and fertilized on a regular basis and treated with fungicides and insecticides, when necessary. DTF was recorded starting from the day of transfer to the climate chamber. Replications were terminated at day 135. Genotypes that did not flower at day 135 but showed buds were recorded with a value of 150 DTF and if they did not show buds were recorded with a value of 165 DTF. The means over all replications of each condition were used to calculate differences in days to flowering. Differences between DTF under short and long days at the same temperature (SD-LD11 and SD-LD22) and between low and high temperature under the same day length (11-22LD and 11-22SD) were calculated. A full list of phenotypic data is available in Appendix A.

1.3.4 SNP marker analysis and linkage map development

A previously published full marker map consisting of 21,583 markers distributed over 19 linkage groups (Valdés et al. 2018) was used to develop a framework map consisting of 767 markers evenly distributed over the genome with R package ASMap (Taylor and Butler 2017). The length of total map was 2020.71 cM. Average distance of markers was 2.7 cM. Larger gaps between 11 cM and 19 cM were detected on linkage groups A09, C03, C04, C07 and C09. An overview over the whole genetic map is provided in Appendix B.

1.3.5 QTL analysis

Mean values over the five replications were used in QTL mapping for all traits. QTL mapping was performed with WinQTL Cartographer software version 2.5 (Wang et al. 2012), and composite interval mapping (CIM) algorithm was employed with following specifications: Independent LOD significance thresholds (α = 0.05) were estimated for each trait by 1000 permutation tests. Model 6 was employed, forward and backward stepwise regression method was used to set cofactors. The genome was scanned at 1 cM intervals, and the window size was set to 10 cM. The ninety-five percent confidence interval for each QTL was determined by one LOD drop from the peak position. Additive effects, as well as the percentage of phenotypic variance explained by a QTL, were determined. A positive additive effect of a QTL is an additive effect by the allele of winter oilseed rape parent Express617.

To test epistasis multiple interval mapping method was used. QTL found in CIM were used as input and BIC-M0 model with 1 cM walk speed and 10 cM window size. Additive × additive effects were significant with an LOD of 2.4.

SNP marker sequences of the framework map were provided by Isobel Parkin (AAFC, Saskatoon, Canada) and BLAT positions on reference genome of 'Damor-*bzh*' (Chalhoub et al. 2014) used to create a physical map. Figures of the maps were drawn with MapChart (Voorrips 2002).

1.3.6 Candidate genes

A list of important flowering candidate genes from *Arabidopsis thaliana* was adapted from Blümel et al. (2015; Appendix C). The whole genome sequence for every candidate gene was taken from the database TAIR (Berardini et al. 2015). Sequences were aligned using BLAT algorithm against the reference genome sequence of 'Damor-*bzh*' by use of the Genoscope database (Chalhoub et al. 2014). Results with BLAT scores below 350 were discarded.

1.3.7 Statistical analysis

PLABSTAT 3A software (Utz 2011) was used to calculate analysis of variance and heritabilities. The ANOVA for the vernalization experiment was performed using the model for randomized block design: $Y_{ijk} = \mu + r_i + v_j + g_k + r_i v_j + g_k r_i + g_k v_j + g_k v_j r_i$ is the trait value of the genotype k with the vernalization treatment j in replication i, μ is the general mean, r_i, g_k and v_j are effects of replication i, genotype k and vernalization treatment j, respectively, $r_i v_j$ is the interaction between ith replication and jth vernalization treatment, $g_k v_j$ and $g_k r_i$ are the interactions between the kth genotype with jth vernalization treatment and ith replication, respectively, while $g_k v_j r_i$ is the error term. Factors genotypes and replications were considered as random. Broad sense heritabilities were calculated with following formula: $H^2 = \sigma_g^2 \,/\, (\sigma_g^2 + \sigma_{ge}^2 \,/(R) + \sigma_{gev}^2 \,/(RV))$ with the factor levels R for replication and V for vernalization treatment.

ANOVA for day length and temperature experiment was performed using the model for a split-split plot design: $Y_{ijkl} = \mu + r_i + t_j + r_i t_j + d_k + t_j d_k + r_i t_j d_k + g_l + g_l t_j + g_l d_k + g_l t_j d_k + g_l t_j d_k r_i$ where Y_{ijkl} is the trait value of the genotype l in the day length condition k and the temperature condition j in replication i, μ is the general mean, t_j and r_i are effects of

temperature j and replication i, respectively, r_it_j is the interaction between ith replication and jth temperature, which is treated as the first stratum error. The effect of the kth day length is d_k and t_jd_k is the interaction between jth temperature and kth day length, $r_it_jd_k$ is the second stratum error (interactions between ith replication, jth temperature and kth day length); g_l is the effect of the lth genotype, g_lt_j, g_ld_k and $g_lt_jd_k$ are the interactions between the lth genotype with jth temperature and/or kth day length, while $g_lt_jd_kr_i$ is the third stratum error term. Factors genotypes and replications were taken as random. Broad sense heritabilities were calculated with following formula: $H^2 = \sigma_g^2 \,/\, (\sigma_g^2 + \sigma_{gtde}^2 /T)$ with coefficient T=20 as the product of all factor levels.

Other statistical analysis was performed in R (R. Core Team 2019). Means over replications were obtained and used to calculate Spearman Rank correlations. The median of the not vernalized DH lines (V0) was used to divide the DH population into 'spring' and 'winter' types (Appendix A). Differences between those groups were tested with a pairwise t-test for all traits. Figures of the descriptive statistics were done in R with the package ggplot2 (R. Core Team 2019; Wickham 2016). For the box plot (Fig. 1.2) a Tukey test was used to test significant differences (P≤0.01) between subgroups.

1.4 Results

1.4.1 Effect of vernalization treatment on flowering time

Flowering time of the DH population was greatly affected by the vernalization treatments of zero, four, and eight weeks (V0, V4, and V8, respectively). The analysis of variance showed significant effects for the genotype, vernalization treatment, and replication as well as for the two-fold interactions (Table 1.1). The variance component for the effect of vernalization was by far the largest, followed by the effects of the genotype and the vernalization × genotype interaction. Heritability was high with H^2 = 94%. Vernalization treatment reduced flowering time in the spring-type parent DH4079 from 41 days after V0 to 27 days after V8 (Table 1.2). After V0, the winter oilseed rape parent Express617 did not flower within the 100 days of the experiment, but already V4 was sufficient to induce flowering at 65 days. Even after V8, Express617 flowered 10 days later than DH4079. The flowering time of the F1-genotype was intermediate between the two parents for V4 and V8 and close to the median. In the DH lines the vernalization treatment reduced mean flowering time from 77 (V0) to 43 (V4) and 35 DTF (V8). The frequency distribution of flowering time (Fig. 1.1) showed a bimodal distribution for V0, which was separated at the median (71.7 days) in an early and late flowering half of the population, called 'spring' and 'winter' types, respectively. The 'spring' types were rather normally distributed and the 'winter' types were platykurtic after V0. After V4 and V8, the frequency distribution appeared unimodal with a decreasing positive skewness; however, the 'winter' types tended to flower later. Several DH lines took longer to flower after V4 and especially after V8 than winter oilseed rape parent Express617. Spearman Rank correlation coefficients for DTF between the three vernalization treatments ranged from 0.66 (V0:V8) and 0.82 (V4:V8) to 0.83 (V0:V4), which were all significant at the 0.01 probability level (data not shown).

Table 1.1 Components of variance, respective F-Test results from the analysis of variance and heritabilitiy for days to flowering in the DH population DH4079 × Express617 with three different vernalization treatments

Source	Degrees of freedom	Components of variance
Replication (R)	4	27.1 ***
Vernalization (V)	2	486.3 ***
Genotype (G)	193	140.9 ***
R × G	769	14.2 ***
V × G	386	138.9 ***
R × V	7	25.6 ***
R × V × G	1282	104.2
H2 (%)		94

*** P≤0.01

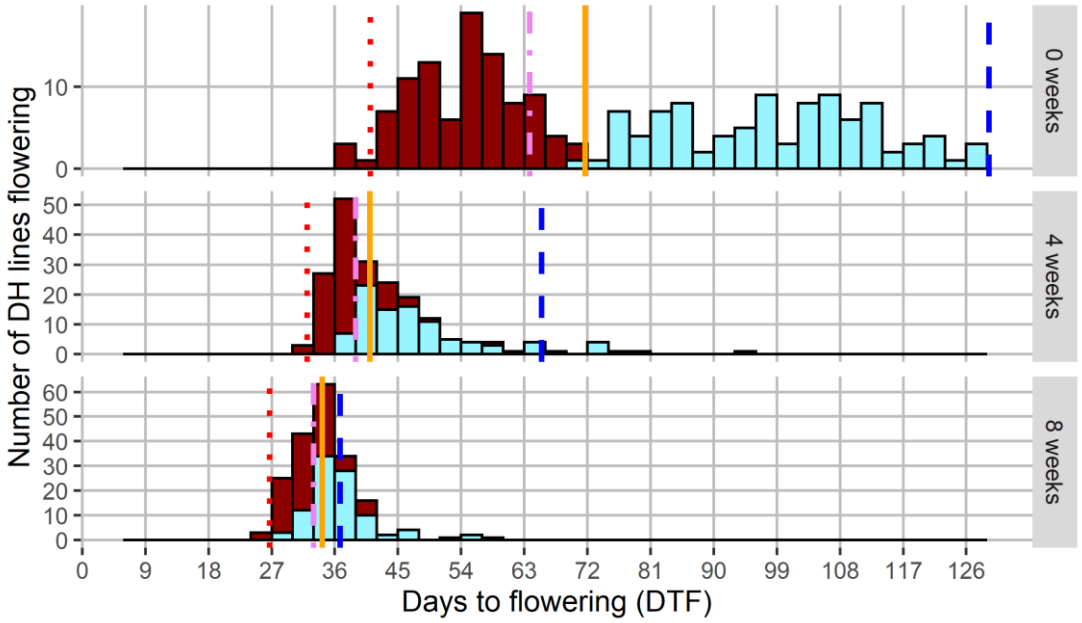

Fig. 1.1 Distribution of days to flowering (DTF) after different vernalization treatments of the DH population DH4079 × Express617. Spring-type parent DH4079 indicated with red dotted line, winter oilseed rape parent Express617 with dashed blue line, and F1 with dashed-dotted violet line. Orange solid line indicates the median of the DH population. The median of the not vernalized population (71.7 days to flowering at V0) was used to separate the population into 'spring' types (dark red) and 'winter' types (light blue)

Table 1.2 Descriptive statistics for days to flowering (DTF) with 0 (V0), 4 (V4), and 8 (V8) weeks of vernalization treatment, as well as across all vernalization treatments for the DH population DH4079 × Express617. Means of DTF for groups of 'spring' and 'winter' types in the population (with significance according to Student's t-Test) and means of DTF for F1 and parental genotypes

	DH lines											
					'spring'	t-	'winter'			Express		
treatment	min	max	median	mean	types	test	types	DH4079	F1	617	LSD 5%	H^2 [%]
V0	38	130	72	77	54	***	99	41	64	130	17.8	94
V4	30	96	41	43	38	***	49	32	39	65	12.9	78
V8	26	57	34	35	33	***	37	27	33	37	8.0	66
Across all treatments	26	130	41	52	42	***	62	33	45	77	8.7	94

LSD 5% = Least significant difference; * P≤0.10, ** P≤0.05, *** P≤0.01

1.4.2 Effect of day length and temperature on flowering time of fully vernalized plants

The analysis of variance showed that day length was the predominant effect influencing days to flowering compared to temperature, which was tested with two factor levels each: short days (SD)/long days (LD) and 11/22°C. The size of the variance components for the effect of day length was almost twenty times that of the temperature and more than two times that of the genotype (Table 1.3). The size of the variance components for the genotype × day length interaction was three times that of the interaction effects of genotype × temperature. Heritability of DTF was high at 95%. Short day conditions (SD, 8 h light) delayed the mean DTF in the DH population, as well as for the parents and F1, but also increased the range and some DH lines did not start to flower at all (Table 1.4). Under SD conditions, the means for DTF under the two temperature regimes were no longer significantly different (Table 1.4, Fig. 1.2).

Table 1.3 Components of variance and heritability for days to flowering (DTF) in the DH population DH4079 × Express617 at two different temperatures and under short and long day conditions after full vernalization treatment in the day length and temperature experiments

Source	Degrees of freedom	Components of variance
Replication (R)	4	36.1 *
Temperature (T)	1	34.9 **
Day length (D)	1	656.9 ***
Genotype (G)	183	244.9 ***
R × T	4	17.2 **
D × T	1	53.4 ***
R × D × T	14	9.3 ***
T × G	183	30.1 ***
D × G	183	91.2 ***
D × T × G	183	12.1 **
R × D × T × G	2641	236.8
H^2 (%)		95

* P≤0.10, ** P≤0.05, *** P≤0.01

Table 1.4 Descriptive statistics for days to flowering (DTF) of vernalized plants of the DH4079 × Express617 population cultured under low and high temperature (11 and 22°C) and under short day (SD) and long day (LD) conditions, as well as the effect of temperature and day length differences on DTF, as calculated for each genotype

	DH lines											
Condition	min	max	median	mean	'spring' types	t-test	'winter' types	DH4079	F1	Express 617	LSD 5%	H^2 [%]
LD 11	34	89	51	52	47	***	57	38	49	72	9.9	84
LD 22	17	105	31	35	28	***	42	17	30	58	13.4	87
SD 11	42	153	78	80	74	***	87	52	75	103	15.8	90
SD 22	28	165	74	78	69	***	87	33	63	118	29.8	86
Across all conditions	17	165	57	61	54	***	68	35	54	88	9.5	95
SD-LD11	-4	66	26	29	27	*	30	15	26	32		
SD-LD22	7	100	40	43	41		45	16	34	60		
11-22LD	-20	44	18	17	19	***	15	21	19	14		
11-22SD	-44	40	5	3	5	**	0	19	12	-15		

LSD 5% = Least significant difference; * P≤0.10, ** P≤0.05, *** P≤0.01

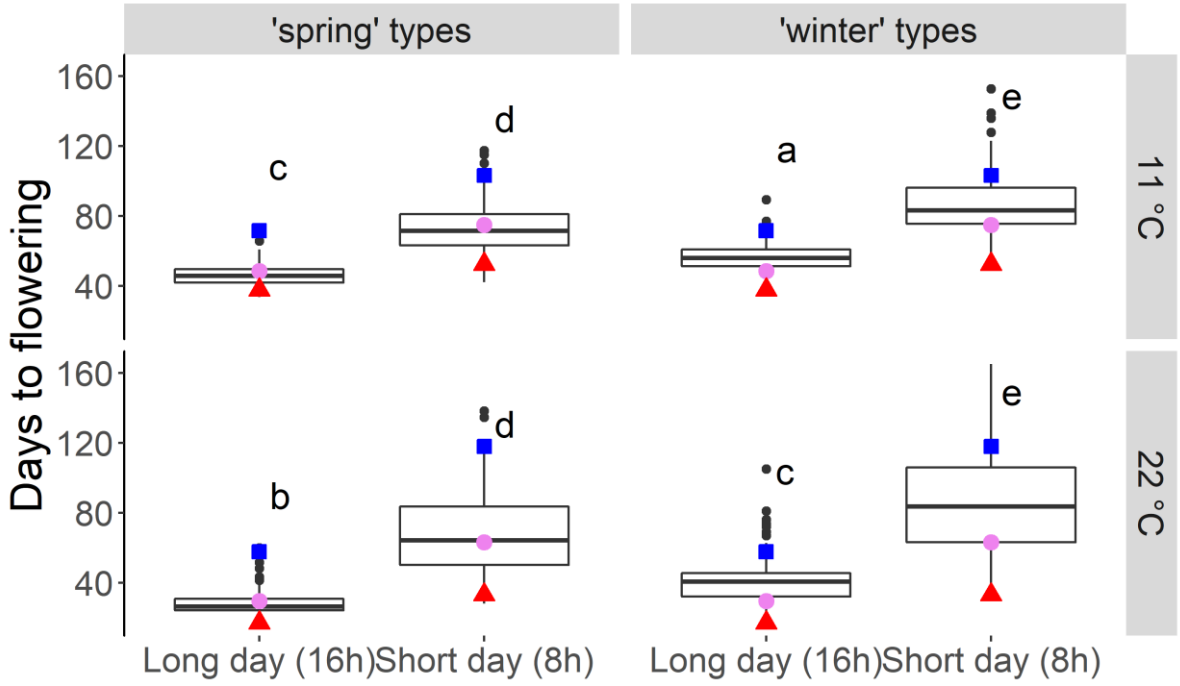

Fig. 1.2 Days to flowering of vernalized DH population divided into ‘spring’ types and ‘winter’ types (early and late flowering without vernalization, respectively) growing under different temperatures (11 and 22°C) and day length (short and long day) conditions. Letters indicate significantly different subgroups (P≤0.01) tested with Tukey test. Winter oilseed rape parent Express617 is indicated with blue square, spring-type parent DH4079 indicated with red triangle and F1 with violet circle

The mean of the DH lines showed an acceleration of flowering due to higher temperatures under long day conditions (LD, 16 h light) from 52 days at 11°C to 35 days at 22°C (Table 1.4). The range increased under warmer temperatures and especially under SD conditions (Fig. 1.2, Table 1.4). In all conditions winter oilseed rape parent Express617 flowered later than spring-type parent DH4079, and the F1 was intermediate but slightly closer to the spring-type parent (Fig. 1.2). A comparison of the DTF means between ‘spring’ and ‘winter’ types showed significant differences in all four conditions (Fig. 1.2, Table 1.4). The ‘spring’ types kept the tendency to flower earlier than the ‘winter’ types, especially under LD conditions.

The effect of day length differences on DTF, calculated by subtracting DTF under LD from DTF under SD, had a mean of 43 days in the DH population under 22°C (SD-LD22, Table 1.4) and only 29 days under 11°C (SD-LD11). However, under both temperatures the range was extensive from -4 up to 100 days. Values around zero indicated genotypes that were insensitive to day length. The mean of ‘spring’ and ‘winter’ types was not significantly different for SD-LD22 and was only significant at a significance level of P≤0.10 for SD-LD11. In the winter oilseed rape parent Express617, SD-LD11 was 32 days and SD-LD22 was 60 days, while spring-type parent DH4079 had lower and stable values at both temperatures (15 and 16 days, respectively).

The effect of temperature differences, calculated by subtracting DTF at 22°C from 11°C at the respective day lengths, showed a mean of 17 days under LD and 2.5 days under SD.

The values for this effect of temperature differences on the DH lines ranged between -20 and 44 days under the long day (11-22LD) and between -44 and 40 days under the short day condition (11-22SD). This huge range showed the ability of warm temperatures to either accelerate or delay DTF compared to cool temperatures, depending on the genotype, and in interaction with day length conditions. The means of 'spring' and 'winter' types were significantly different for 11-22SD and 11-22LD (see t-test in Table 1.4). Under LD conditions, the effect of temperature differences on spring-type parent DH4079 was 21 days, which is higher than that of Express617 with 14 days, and the F1 showed an intermediate phenotype, with an acceleration of flowering through warmer temperature. Under SD, the warmer temperature led to a delayed flowering time of -15 days in Express617, while still accelerating in the F1 (12 days) and DH4079 (19 days, Table 1.4). For DH4079, the effects of temperature differences showed the same stability with 21 and 19 days as the effects of day length differences (Table 1.4).

1.4.3 QTL mapping of days to flowering in vernalization experiment

QTL analysis for DTF in the vernalization experiment revealed six QTL after V0 that explained 73% of the phenotypic variance (TR^2), which decreased to 37% after V4 and 56% after V8, both with five QTL each (Table 1.5). The majority of QTL at the different treatments had positive additive effects, meaning that the alleles of the winter oilseed rape parent Express617 delayed DTF. However, minor QTL V0f on C03 and V8e on C06 had negative additive effects, where the alleles of the spring-type DH4079 delayed DTF. The major QTL V0a on chromosome A02 at 42 cM explained 56% of the phenotypic variance (Table 1.5, Fig. 1.3). The positive additive effect indicated that the Express617 allele delayed flowering time by 20 days. With a slightly shifted peak at 43 cM on A02, but overlapping confidence intervals, the largest QTL for DTF after V4 (V4a) and V8 (V8a) were detected, showing that the QTL is not completely vernalization dependent. The additive effect of the QTL decreased from 20 days in V0 to 4.2 days in V4 and 2.3 days in V8. The fraction of explained phenotypic variance of this QTL decreased dramatically from 56% to 14.2% and then slightly increased again to 19.7% between V0, V4, and V8, respectively; this pattern was also observed for the total explained variance described above (Table 1.5). The second largest QTL for V0 (V0e) mapped on chromosome C02 at 100 cM explaining 8.2% of the phenotypic variance and has an additive effect of 7.7 days. V0a and V0e showed an additive × additive epistatic effect of 2.6 (Table 1.6). On C02 at 109 cM, the second largest QTL of V4 (V4e) collocated with a QTL of V8 (V8d), with 9.4% and 9.6 % explained variance, respectively, and an additive effect of 3.2 and 1.6 days, respectively. QTL V4b, V4c, and V4d showed epistatic interactions with each other with an effect between 1.2 and 1.6 days; and V4b and V4e showed an epistatic effect of 2 days (Table 1.6). The second largest QTL for V8 was V8b located on A07 at 76 cM with an explained variance of 12.5% and an additive effect of 1.9 days.

Table 1.5 Quantitative trait loci mapped for days to flowering (DTF) with no vernalization (V0), with 4 (V4) and 8 (V8) weeks of vernalization in the DH4079 × Express617 population. A positive additive effect of a QTL is an increase of the trait by the allele of winter oilseed rape parent Express617.

QTL	Chr.	Position [cM]	CI [cM][a]	Markers flanking CI	LOD	Additive	R^2 [%][b]	TR^2 [%][c]
0 weeks vernalized plants (V0)								
V0a	A02	42	40.6 - 42.8	Bn-A02-p23491463 Bn-A02-p10227986	65.2	20.2	56.0	73.2
V0b	A02	84	79.3 - 89	Bn-A02-p25652516 Bn-A02-p27321599	4.6	3.7	1.9	
V0c	A03	73	70.8 - 76.9	Bn-A03-p8032849 Bn-A03-p6354338	5.3	4.0	2.1	
V0d	A07	102	96.5 - 103.1	Bn-A07-p21271213 Bn-scaff_24104_1-p344071	9.2	5.2	3.9	
V0e	C02	100	98.3 - 102.1	Bn-scaff_15714_1-p2481342 Bn-scaff_15714_1-p2989937	17.8	7.7	8.2	
V0f	C03	5	0.0 - 7.8	Bn-A03-p5357737 Bn-scaff_19111_1-p325137	3.1	-2.9	1.1	
4 weeks vernalized plants (V4)								
V4a	A02	43	39.8 - 45.3	Bn-A02-p23491463 Bn-A02-p11789023	10.2	4.2	14.2	37.0
V4b	A02	75	71.8 - 78.2	Bn-A02-p24844291 Bn-scaff_17177_1-p105819	2.7	2.1	3.5	
V4c	A03	90	87.9 - 91.7	Bn-A03-p3877500 Bn-scaff_18936_1-p358822	2.8	2.0	3.5	
V4d	A07	65	60.8 - 71.2	Bn-A07-p10755129 Bn-A07-p18187317	4.9	2.5	6.5	
V4e	C02	109	106.6 - 111.2	Bn-scaff_22970_1-p213807 Bn-A02-p1705187	7.0	3.2	9.4	
8 weeks vernalized plants (V8)								
V8a	A02	43	39.9 - 44.9	Bn-A02-p23491463 Bn-A02-p11789023	13.2	2.3	19.7	56.4
V8b	A07	76	73.1 - 77.8	Bn-A07-p18187317 Bn-A07-p19912379	8.9	1.9	12.5	
V8c	C02	29	25.1 - 33.2	Bn-scaff_17623_1-p714325 Bn-scaff_17109_4-p101748	3.8	1.1	5.0	
V8d	C02	109	106.8 - 110.6	Bn-scaff_22970_1-p213807 Bn-A02-p1705187	7.0	1.6	9.6	
V8e	C06	24	20.8 - 27.2	Bn-A07-p20251365 Bn-scaff_15763_1-p1492117	7.0	-1.7	9.6	

a= 95% confidence interval, b= explained phenotypic variance of the QTL, c = total explained phenotypic variance over all QTL found by analysis

Table 1.6 Epistatic effects in vernalization for QTL days to flowering (DTF) with no vernalization (V0), with 4 (V4) and 8 (V8) weeks of vernalization in the DH4079 × Express617 population.

1st QTL	Chr.	Pos. [cM]		2nd QTL	Chr.	Pos. [cM]	additive × additive effect
0 weeks vernalized plants (V0)							
V0a	A02	42	x	V0e	C02	100	2.6
4 weeks vernalized plants (V4)							
V4b	A02	75	x	V4c	A03	90	1.5
V4b	A02	75	x	V4d	A07	65	1.6
V4c	A03	90	x	V4d	A07	65	1.2
V4b	A02	75	x	V4e	C02	109	2.0

1.4.4 QTL mapping of days to flowering in day length and temperature experiment

QTL analysis for the day length and temperature experiment revealed that most QTL had positive effects, except for QTL on A05 (LD22c, SD22c) and C06 (LD22g, SD11e, SD22g), indicating that the delay of flowering was caused mainly by Express617 alleles of plants vernalized for nine weeks in all temperature or day length conditions (Table 1.7). For the DTF under cool LD conditions, three QTL were found that explained 35.7% of the total phenotypic variance (TR^2). For DTF under the other conditions, five to seven QTL were found that explained between 60 and 72% TR^2.

LD11a is the major QTL for DTF under cool LD conditions on A02 at 43 cM with an explained variance of 22% (Table 1.7), but a relatively low additive effect of 4.4 days. At the same position, the QTL LD22a was detected with a similar additive effect of 3.4 days but with a low explained variance of 3.6%. The biggest QTL under warm LD conditions, LD22d, was located on A07 at 88 cM, explaining 18% of the phenotypic variance and an additive effect of 6.1 days. The QTL LD22b on A02 had the second largest effect with 14.2% explained variance and an additive effect of 5.3 days (Table 1.7, Fig. 1.3).

The five QTL found for cool SD conditions have overlapping or close confident intervals with five of the seven QTL for warm SD conditions. Both SD conditions had their major QTL on A07; the QTL SD11b at 100 cM explained 24.8% of the variance with an additive effect of 10 days, and QTL SD22d at 96 cM explained 26.8% with an additive effect of 16 days (Table 1.7). The second largest QTL for cool SD conditions, SD11d, is on C02 at 108 cM (15%, 7 days), followed by SD11e on C06 at 7 cM (12%, -6.9 days). The second largest QTL for warm SD conditions, SD22g, is on C06 at 0.01 cM (15%, -13.1) followed by SD22f on C02 at 101 cM (11%, 10.4 days, Table 1.7).

For the effect of day length differences at 11°C (SD-LD11), six QTL were identified that together explained 73.3% of the phenotypic variance, but for SD-LD22 only three QTL were detected that explained 33.1% of the total phenotypic variance (Table 1.8). The biggest QTL for the effect of day length differences in 11°C, SD-LD11a, was located on A07 at 95 cM with an explained variance of 33.3% and an additive effect of 7.9 days. The second largest QTL, SD-LD11d on C06 at 7 cM, explained 19.5% of the phenotypic variance and the additive effect was -6.1 days. The effect of day length differences at 22°C had its major QTL SD-LD22c on C06 at 29 cM with 17.7% explained variance and an additive effect of -9.7 days; i.e. the DH4079 allele at this position increased DTF. The second largest QTL SD-LD22a was located on A07 at 77 cM (10.0% 8.6 days).

For the effect of temperature differences under LD (11-22LD) as well as SD (11-22SD), four QTL were mapped for each. They mapped at very similar positions and showed the same direction of the additive effects (Table 1.9). These QTL explained 40.3 and 45.1% of the total phenotypic variance, respectively. The largest QTL, 11-22LDb and 11-22SDb on A07, at 74 and 76 cM, respectively, explained 16.8 and 17.3% of the phenotypic variance, respectively. Their additive effects were negative (-3.5 and -7.2 days), meaning the Express617 allele made this effect smaller by either delaying DTF under 22°C or accelerating DTF under 11°C.

Table 1.7 Quantitative trait loci mapped for days to flowering (DTF) under different temperatures and day length conditions in the DH4079 × Express617 population. A positive additive effect of a QTL is an increase of the trait by the allele of winter oilseed rape parent Express617.

QTL	Chr.	Position [cM]	CI [cM][a]	Markers flanking CI	LOD	Additive	R^2 [%][b]	TR^2 [%][c]
Long day at 11 °C								
LD11a	A02	43	40.1 - 44.9	Bn-A02-p23491463 Bn-A02-p11789023	15.1	4.4	22.2	35.7
LD11b	C02	47	38.2 - 54.5	Bn-scaff_17109_4-p101748 Bn-scaff_20461_1-p322463	4.0	2.1	5.2	
LD11c	C02	108	105.1 - 109.7	Bn-scaff_15714_1-p2989937 Bn-A02-p1705187	6.6	2.8	8.4	
Long day at 22 °C								
LD22a	A02	43	39.6 - 45.6	Bn-A02-p23491463 Bn-A02-p12939509	3.2	3.4	3.6	68.0
LD22b	A02	63	60.1 - 68.5	Bn-A02-p22296426 Bn-scaff_17623_1-p472440	11.0	5.3	14.2	
LD22c	A05	88	78.8 - 93.3	Bn-A05-p2254100 Bn-A05-p529716	3.6	-2.7	4.0	
LD22d	A07	88	84.2 - 91	Bn-A07-p19912379 Bn-A07-p21271213	12.0	6.1	18.0	
LD22e	C02	38	34.2 - 47.4	Bn-scaff_17109_1-p1144887 Bn-scaff_20979_1-p153226	5.3	3.6	6.6	
LD22f	C02	100	98.6 - 105.1	Bn-scaff_15714_1-p2481342 Bn-scaff_22970_1-p213807	8.2	4.7	10.6	
LD22g	C06	15	11.3 - 19.1	Bn-scaff_17799_1-p1053450 Bn-A07-p20251365	7.8	-4.8	10.9	
Short day at 11 °C								
SD11a	A02	71	65.6 - 74.4	Bn-A02-p24378297 Bn-A02-p25218817	4.1	4.3	5.3	60.4
SD11b	A07	100	95 - 103.1	Bn-A07-p21271213 Bn-scaff_24104_1-p344071	17.0	10.2	24.8	
SD11c	C02	48	34.4 - 50.9	Bn-scaff_17109_4-p101748 Bn-scaff_16565_1-p767852	3.2	3.8	4.0	
SD11d	C02	108	106.1 - 110.7	Bn-scaff_15714_1-p2989937 Bn-A02-p1705187	11.0	7.4	15.0	
SD11e	C06	7	0.1 - 8.2	Bn-A07-p22140320 Bn-A07-p21354084	8.7	-6.9	12.0	
Short day at 22 °C								
SD22a	A02	44	39.5 – 50.0	Bn-A02-p23491463 Bn-A02-p15912199	3.4	5.8	3.8	72.2
SD22b	A02	72	64.5 - 77.5	Bn-A02-p23408870 Bn-A02-p25652516	2.6	5.0	2.9	
SD22c	A05	90	83.2 - 92.3	Bn-A05-p1554943 Bn-A05-p529716	4.3	-6.7	5.2	
SD22d	A07	96	93.8 - 97.7	Bn-A07-p21271213 Bn-scaff_17799_1-p393729	16	15.9	26.8	
SD22e	C02	38	33.2 - 41.2	Bn-scaff_17109_1-p1144887 Bn-scaff_15712_2-p104622	5.8	8.0	7.3	
SD22f	C02	101	98 - 104.7	Bn-scaff_15714_1-p2481342 Bn-scaff_15714_1-p2989937	8.4	10.4	11.0	
SD22g	C06	0.01	0 - 2.3	Bn-A07-p22140320 Bn-A07-p21587819	11.0	-13.1	15.0	

a= 95% confidence interval, b= explained phenotypic variance of the QTL, c = total explained phenotypic variance over all QTL found by analysis

Table 1.8 Quantitative trait loci for the effect of day length differences at two different temperatures in the DH4079 × Express617 population. A positive additive effect of a QTL is an increase of the trait by the allele of winter oilseed rape parent Express617.

QTL	Chr.	Position [cM]	CI [cM][a]	Markers flanking CI	LOD	Additive effect	R^2 [%][b]	TR^2 [%][c]
Effect of day length under 11°C (calculated difference between SD11 and LD 11)								
SD-LD11a	A07	95	93.4 - 97.3	Bn-A07-p21271213 Bn-A07-p21478337	20.0	7.9	33.3	73.3
SD-LD11b	C02	55	50.9 - 59.1	Bn-scaff_20979_1-p153226 Bn-scaff_15712_5-p941560	2.9	2.5	3.8	
SD-LD11c	C02	104	99.5 - 109.2	Bn-scaff_15714_1-p2481342 Bn-scaff_17752_1-p128342	7.1	4.1	9.8	
SD-LD11d	C06	7	4.5 - 10.6	Bn-A07-p22140320 Bn-A07-p20999615	13.0	-6.1	19.5	
SD-LD11e	C06	30	27.7 - 40.7	Bn-A07-p19515708 Bn-scaff_16510_1-p12919	2.6	-2.8	3.2	
SD-LD11f	C07	116	109.3 - 117.5	Bn-scaff_16110_1-p2412201 Bn-scaff_16110_1-p410525	3.1	2.4	3.8	
Effect of day length under 22°C (calculated difference between SD22 and LD22)								
SD-LD22a	A07	77	73 - 81.5	Bn-A07-p18187317 Bn-A07-p20662200	6.3	8.6	10.0	33.1
SD-LD22b	C02	101	94.3 - 110.3	Bn-scaff_15714_1-p1983642 Bn-A02-p1705187	3.5	5.1	5.3	
SD-LD22c	C06	29	25.8 - 32.2	Bn-A07-p19515708 Bn-scaff_18206_1-p435713	11.0	-9.7	17.7	

a= 95% confidence interval, b= explained phenotypic variance of the QTL, c = total explained phenotypic variance over all QTL found by analysis

For the effect of temperature difference under SD, the second largest QTL 11-22SDd on C06 at 28 cM explained 13.4% of the variance with a positive additive effect of 6.4 days. For the temperature effect under LD, second largest QTL, 11-22LDd, on C06 at 22 cM explained 12.3% of the phenotypic variance with an additive effect of 12.3.

Six epistatic effects were found between six of the seven QTL for DTF under warm LD. The strongest with an additive × additive effect of -2.5 was between LD22d on A07 and LD22g on C06. For DTF under warm SD, only one epistatic effect was recorded between SD22d on A07 and SD22g on C06 (a x a = -3.8). For three of the five QTL for DTF under cool SD, two epistatic effects were found. The stronger one between SD11b on A07 and SD11e on C06 with an effect of -4.9 is also the strongest epistatic effect in this study. For DTF under cool LD no epistatic effect was recorded (Table 1.10).

For the effect of day length in 11 °C, an epistatic effect between SD-LD11a on A07 and SD-LD11d on C06 of -3.8 days was found (Table 1.10). For the effect of day length in 22°C, an epistatic effect between SD-LD22a on A07 and SD-LD22c on C06 of -4.1 days was found. For the effect of temperature under long day, three QTL had three epistatic interactions. Between 11-22LDb on A07 and 11-22LDc on C02 the additive × additive effect was -2.1; between 11-22LDc on C02 and 11-22LDd on C06 the effect was 2.1; and between 11-22LDb on A07 and 11-22LDd on C06 the effect was 1.7. Two QTL for the effect of temperature under SD, 11-22SDa on A05 and 11-22SDd on C06, showed an epistatic effect of 2.4 (Table 1.10).

Table 1.9 Quantitative trait loci for the effect of temperature differences under short and long day conditions in the DH4079 × Express617 population. A positive additive effect of a QTL is an increase of the trait by the allele of winter oilseed rape parent Express617.

QTL	Chr.	Position [cM]	CI [cM][a]	Markers flanking CI	LOD	Additive effect	R^2 [%][b]	TR^2 [%][c]
Effect of temperature under long days (calculated difference between LD11 and LD22)								
11-22LDa	A05	82	79 - 88.7	Bn-A05-p2254100 Bn-A05-p1192706	3.5	2.0	6.3	40.3
11-22LDb	A07	74	70.2 - 76	Bn-scaff_15763_1-p1029560 Bn-A07-p19912379	8.8	-3.5	16.8	
11-22LDc	C02	38	33.9 - 47.2	Bn-scaff_17109_1-p1144887 Bn-scaff_20979_1-p153226	2.8	-1.8	4.9	
11-22LDd	C06	22	16.1 - 26.9	Bn-A07-p20999615 Bn-scaff_15763_1-p1492117	6.5	3.0	12.3	
Effect of temperature under short days (calculated difference between SD11 and SD22)								
11-22SDa	A05	88	85.8 - 92.1	Bn-A05-p1347246 Bn-A05-p529716	4.2	4.4	7.2	45.1
11-22SDb	A07	76	73.1 - 78.1	Bn-A07-p18187317 Bn-A07-p19912379	9.5	-7.2	17.3	
11-22SDc	C02	31	24.9 - 40.9	Bn-scaff_17623_1-p714325 Bn-scaff_15712_2-p104622	4.2	-4.6	7.3	
11-22SDd	C06	28	25.2 - 29.5	Bn-A07-p19515708 Bn-scaff_15763_1-p233149	7.6	6.4	13.4	

a= 95% confidence interval, b= explained phenotypic variance of the QTL, c = total explained phenotypic variance over all QTL found by analysis

Table 1.10 Epistatic effects for QTL for days to flowering (DTF) under different day length and temperature conditions, as well as for the effect of day length and temperature in the DH4079 × Express617 population.

1st QTL	Chr.	Pos. [cM]		2nd QTL	Chr.	Pos. [cM]	additive × additive effect
Long day at 22 °C							
LD22a	A02	43	x	LD22d	A07	88	1.5
LD22d	A07	88	x	LD22e	C02	38	2.3
LD22b	A02	63	x	LD22f	C02	100	1.7
LD22b	A02	63	x	LD22g	C06	15	-2.1
LD22d	A07	88	x	LD22g	C06	15	-2.5
LD22e	C02	38	x	LD22g	C06	15	-2.0
Short day at 11 °C							
SD11a	A02	71	x	SD11e	C06	7	-1.9
SD11b	A07	100	x	SD11e	C06	7	-4.9
Short day at 22 °C							
SD22d	A07	96	x	SD22g	C06	0.01	-3.8
Effect of day length under 11°C (calculated difference between SD11 and LD 11)							
SD-LD11a	A07	95	x	SD-LD11d	C06	7	-3.8
Effect of day length under 22°C (calculated difference between SD22 and LD22)							
SD-LD22a	A07	77	x	SD-LD22c	C06	29	-4.1
Effect of temperature under long days (calculated difference between LD11 and LD22)							
11-22LDb	A07	74	x	11-22LDc	C02	38	-2.1
11-22LDb	A07	74	x	11-22LDd	C06	22	1.7
11-22LDc	C02	38	x	11-22LDd	C06	22	2.1
Effect of temperature under short days (calculated difference between SD11 and SD22)							
11-22SDa	A05	88	x	11-22SDd	C06	28	2.4

1.4.5 Identification of three major genomic regions with clusters of collocating QTL

QTL analysis revealed that within and between the two experiments different flowering time QTL collocated or overlapped in three genomic regions on chromosomes A02, A07, and C06 (Table 1.5, Table 1.7 to 1.9). Therefore, these clusters were analyzed for candidate genes (Appendix C). On chromosome A02, the vernalization sensitive QTL V0a from the vernalization experiment had an overlapping confidence interval with QTL V4a and V8a (Table 1.5), as well as with QTL LD11a, LD22a, and SD22a from the temperature and day length experiment (Table 1.7, Fig. 1.3). LD11a was the major QTL for DTF under cool LD conditions on A02 at 43 cM with an explained variance of 22% (Table 1.7), but a relatively low additive effect of 4.4 days. At the same position, the QTL LD22a was detected with a similar additive effect of 3.4 days but with a low explained variance of 3.6%. At a very similar position at 44 cM, QTL SD22a was mapped at 22°C under the SD condition (3.8% explained variance and 5.8 days additive effect). All QTL showed overlapping confidence intervals (Fig. 1.3), but only LD11a was a major QTL. No QTL for the effect of day length or temperature differences were found in this cluster (Table 1.8 and 1.9). The winter oilseed rape

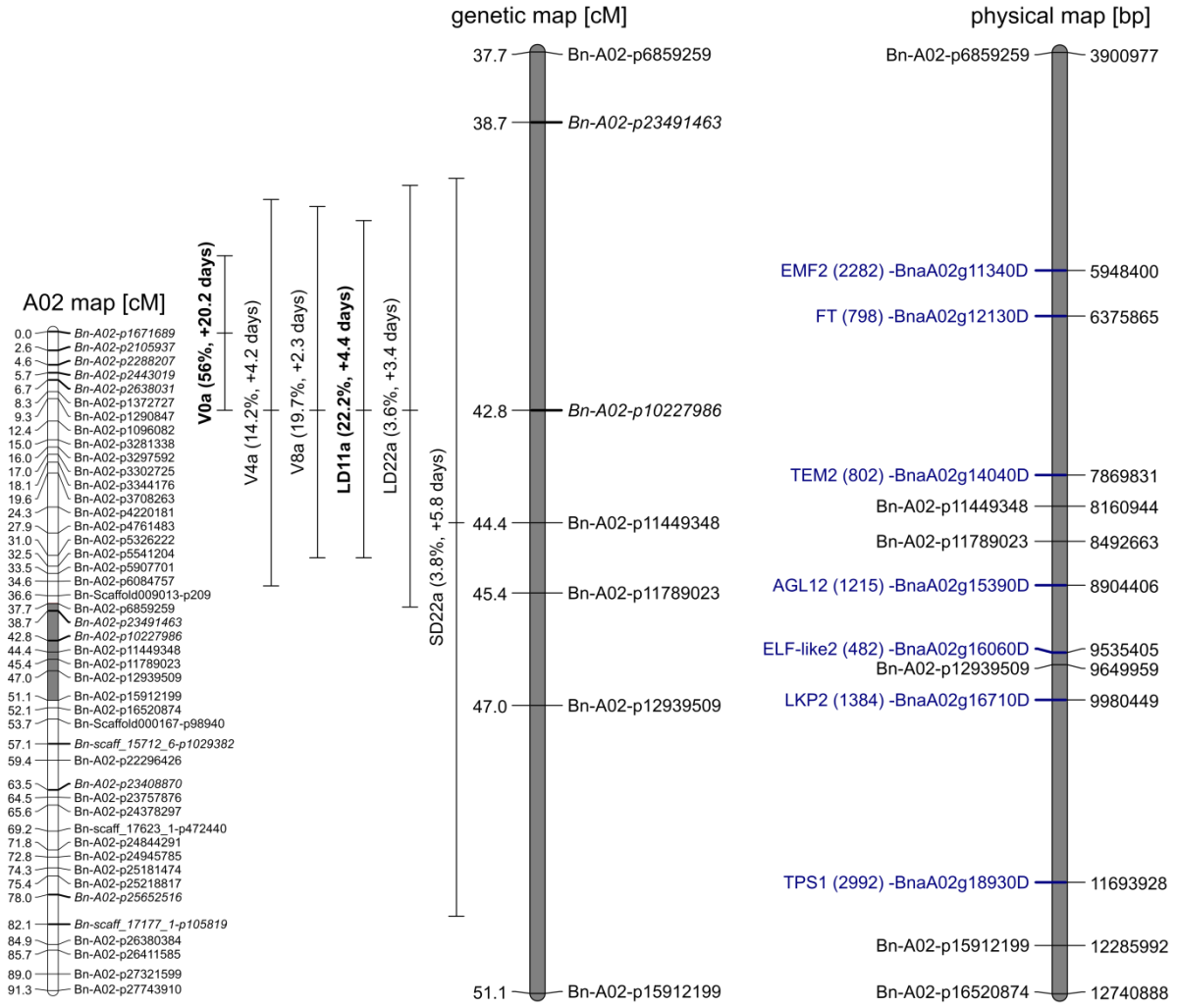

Fig. 1.3 Genetic (middle) and physical (right) map of the QTL cluster region on chromosome A02. Position of QTL cluster region marked grey in genetic map of A02 (right). QTL are given with peak and 95% confidence intervals. In brackets the variance explained in percent and additive effect in days for the respective QTL are given. Candidate genes with BLAT scores (blue) and the respective gene ID in the reference genome of 'Damor-bzh'

Express617 allele delayed flowering, especially in plants without vernalization and under cool long day conditions. Possible candidate genes for all QTL in this cluster were *FT* and *EMBRYONIC FLOWERING 2 (EMF2)* (Fig. 1.3; Appendix C).

On linkage group A07 two clusters were identified (Fig. 1.4). At the end of the genetic map between 93 and 103.1 cM major QTL for flowering time under SD conditions (SD11b, SD22d, and SD-LD11a) were mapped (Table 1.7 and 1.8, Fig. 1.4). They showed overlapping confidence intervals with the minor vernalization responsive QTL V0d at 102 cM with an additive effect of 5.2 explaining 3.9% of the total variance (Table 1.5). For those QTL, the Express617 allele delayed flowering. Two possible candidate genes were located in this genomic region: *EARLY FLOWERING IN SHORT DAYS* (*EFS*) for all QTL and *TREHALOSE-6-PHOSPHATE SYNTHASE 1* (*TPS1*) for SD11b and V0d (Fig. 1.4, Appendix C).

Between 70 and 82 cM on the same chromosome A07, a temperature dependent QTL cluster was observed. Major QTL 11-22LDb and 11-22SDb for the effects of temperature

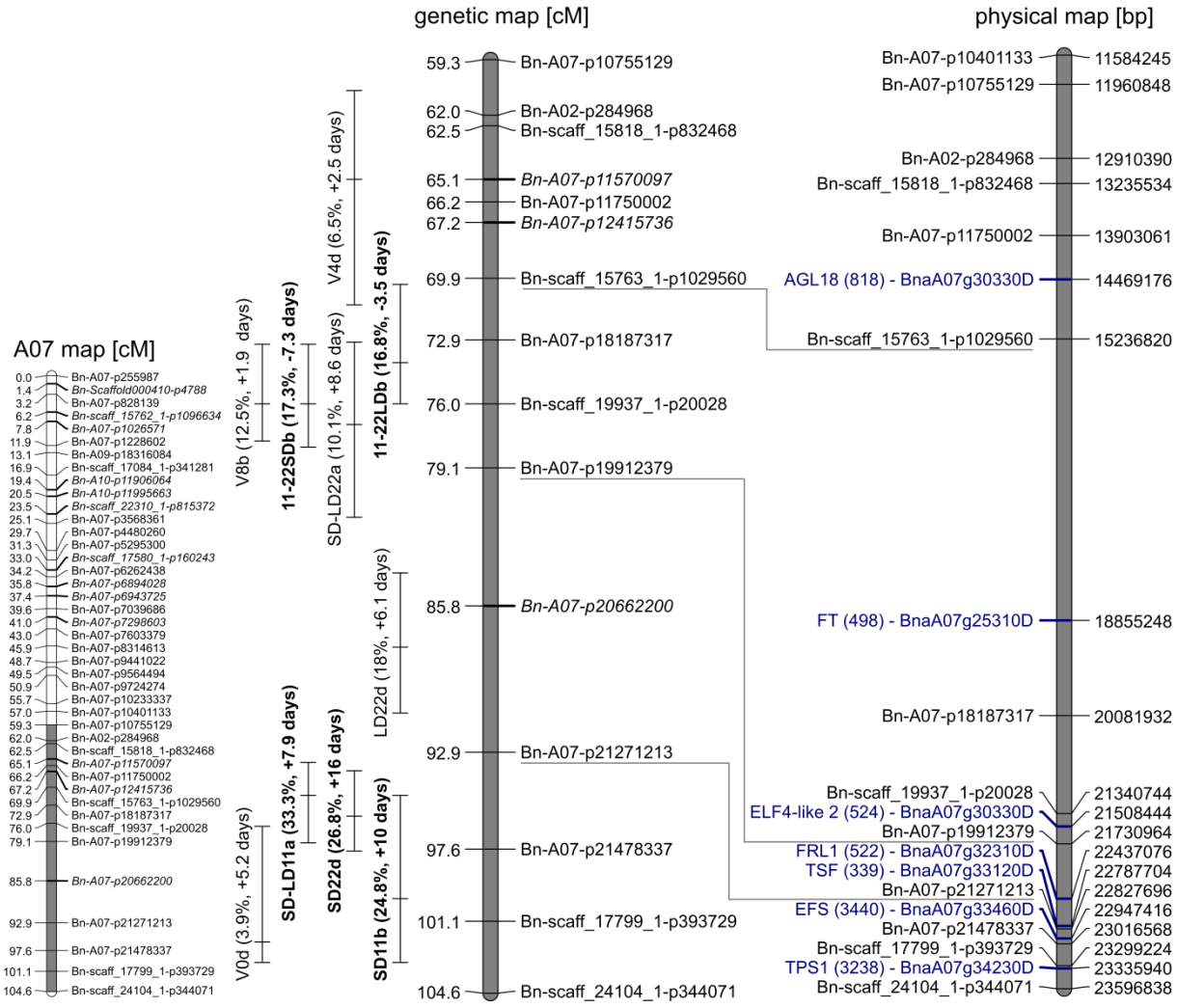

Fig. 1.4 Genetic (middle) and physical (right) map of the QTL clusters region on A07. Position of QTL cluster region marked grey in genetic map of A07 (right). QTL are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effect in days for the respective QTL are given. Candidate genes with BLAT scores (blue) and the respective gene ID in the reference genome of 'Damor-bzh'

differences (Table 1.9), QTL SD-LD22a for the effect of day length difference at 22°C (Table 1.8), and V8b from the vernalization experiment (Table 1.5) showed overlapping confidence intervals (Fig. 1.4). The Express617 allele delayed flowering in warm temperatures under both day length conditions, however, the effect seemed to be more pronounced under LD, since there was a QTL for the effect of day length differences under 22°C (SD-LD22a), as well as for V8 and warm LD conditions, indicating temperature and day length intersection. No candidate genes could be found in the genomic region between 73 and 76 cM where the confidence intervals of all those QTL overlapped. The confidence intervals of the four QTL 11-22SDb, SD-LD22a, and V8b covered a genomic region with an *EARLY FLOWERING4-like 2 (ELF4-like2)* homolog (Fig. 1.4, Appendix C). The confidence interval of QTL 11-22LDb was overlapping with QTL V4d for DTF after 4 weeks vernalization. They shared a copy of *FT* as a possible candidate gene (Fig. 1.4, Appendix B).

On the beginning of C06 from 0 to 11cM a QTL cluster for DTF under SD was located (Fig. 1.5). However, the confidence intervals did not overlap for all relevant QTL. Both SD conditions showed a QTL (SD22g and SD11e) with overlapping confidence intervals (Table

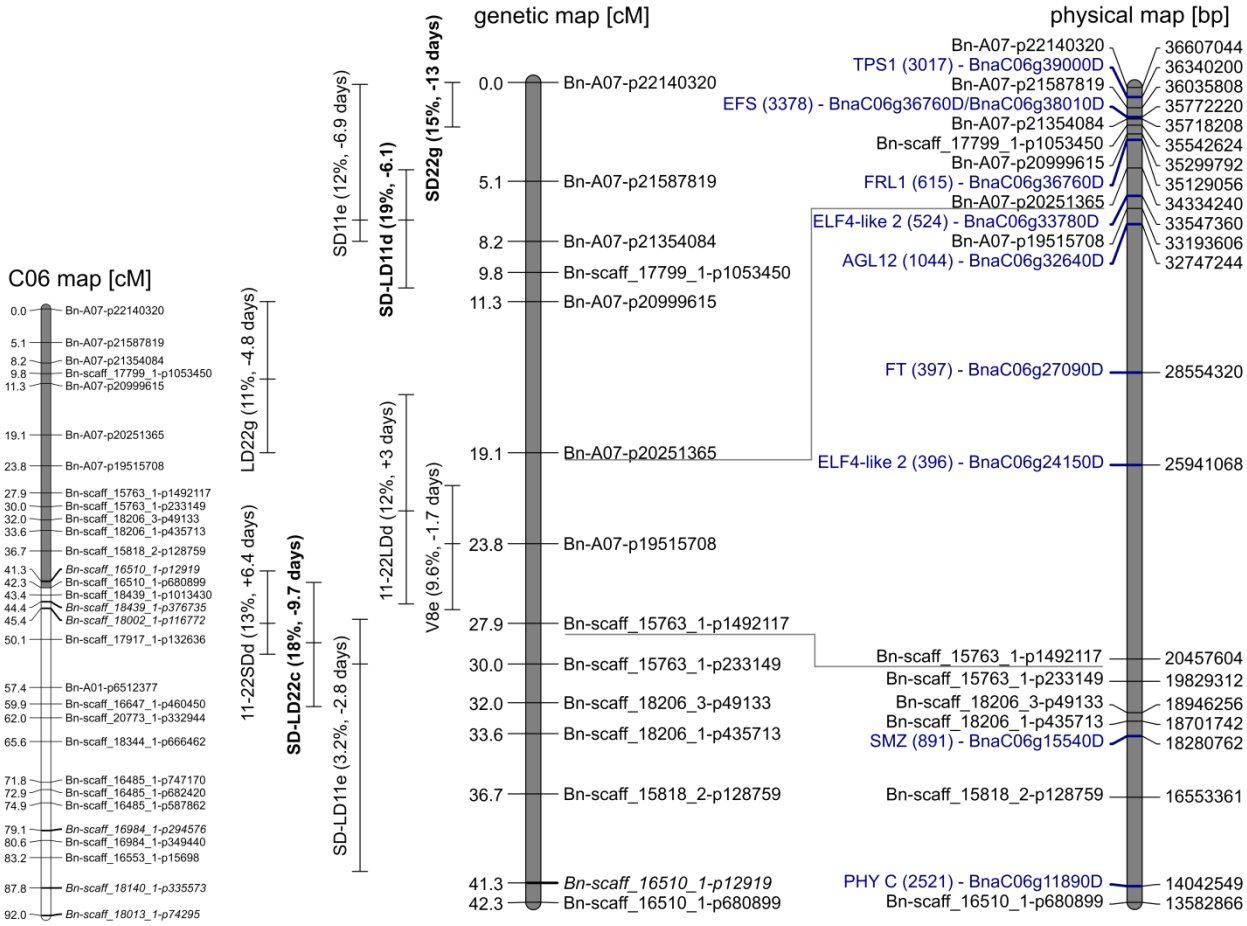

Fig. 1.5 Genetic (middle) and physical (right) map of the QTL clusters region on C06. Position of QTL cluster region marked grey in genetic map of C06 (right). QTL are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effect in days for the respective QTL are given. Candidate genes with BLAT scores (blue) and the respective gene ID in the reference genome of 'Damor-bzh'

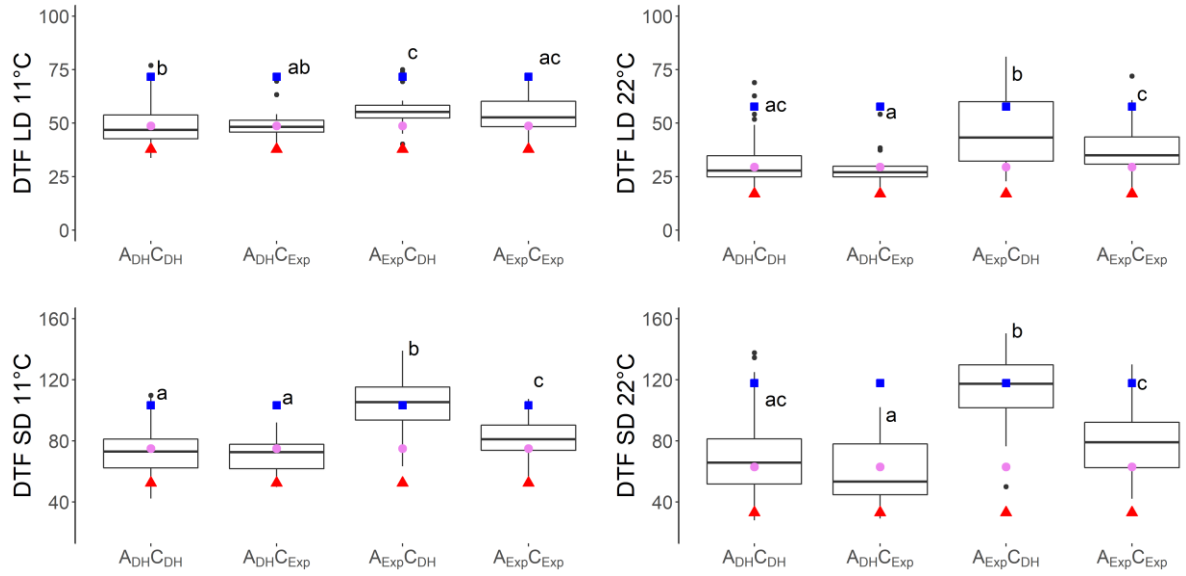

Fig. 1.6 Days to flowering (DTF) in different temperatures (11 and 22°C) and day length (short day SD and long day LD) conditions of vernalized DH population divided by alleles of two SNP markers: Bn-A07-p21478337 on A07 at 97.6 cM, indicated by A, and Bn-A07-p21354084 on C06 at 8.2 cM, indicated by C. Subscript 'DH' indicates DH4079 allele, subscript 'Exp' indicates Express617 allele. Letters indicate significantly different subgroups (P≤0.01) tested with Tukey test within conditions. Phenotypic value of Express617 (blue square), F1 (pink circle) and DH4079 (red triangle).

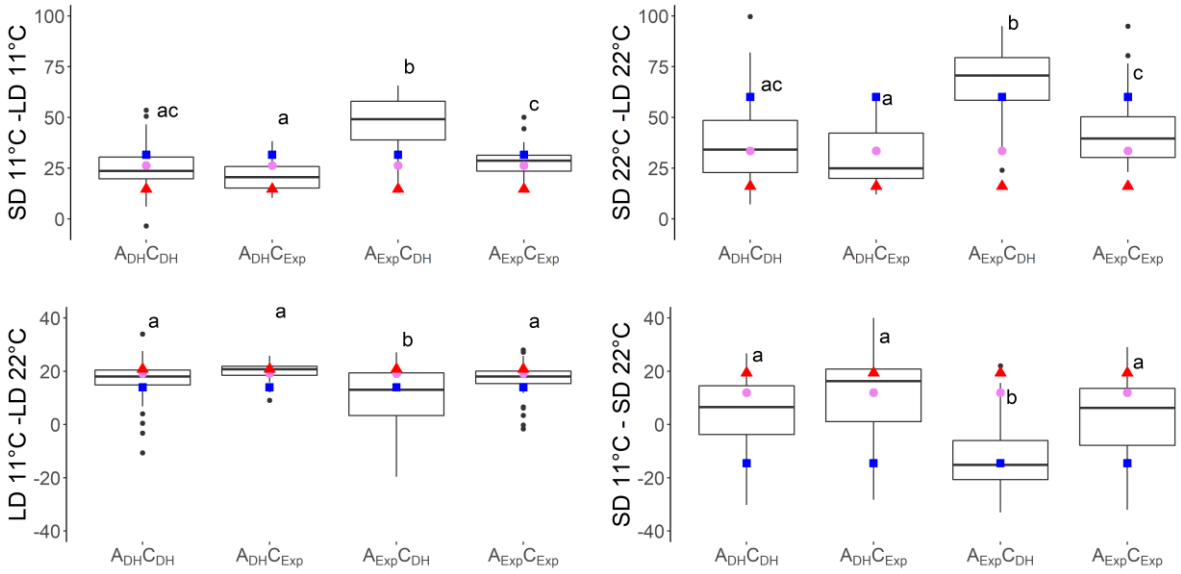

Fig. 1.7 Effects of temperature and day length calculated by subtracting Days to flowering (DTF) in different temperatures (11 minus 22°C) and day length (short day SD minus long day LD) conditions of vernalized DH population divided by alleles of two SNP markers: Bn-A07-p21478337 on A07 at 97.6 cM, indicated by A, and Bn-A07-p21354084 on C06 at 8.2 cM, indicated by C. Subscript 'DH' indicates DH4079 allele, subscript 'Exp' indicates Express617 allele. Letters indicate significantly different subgroups (P≤0.01) tested with Tukey test within conditions. Phenotypic value of Express617 (blue square), F1 (pink circle) and DH4079 (red triangle).

1.7, Fig. 1.5). A possible candidate gene is *TPS1* (Fig. 1.5, Appendix C). Major QTL SD-LD11d for the effect of day length difference under 11°C had an overlapping confidence interval QTL SD11e for cool SD. A possible candidate gene *EFS* was identified (Fig. 1.5, Appendix C). On the same chromosome C06 between 24 and 34 cM, a QTL cluster that reacted to day length and temperature can be found. The QTL SD-LD22c at 29 cM, SD-LD11e at 30 cM and 11-22SDd at 28 cM were overlapping with the confidence interval, but no candidate genes could be found for all three QTL. However, at the end of their confidence intervals, SD-LD22c and 11-22SDd were overlapping with the confidence interval of 11-22LDd and V8e, with possible candidate genes *ELF4-like2* and *FT*. Interestingly, the Express617 allele accelerated flowering under short days and/or warm temperatures in both clusters.

Many additive × additive epistatic effects were found between QTL on Chromosomes A07 and C06. The short day sensitive QTL clusters on A07 (93 to 103 cM) and C06 (0 to 11 cM) showed strong epistatic effects between QTL from both SD conditions as well as the effect of day length difference at 11 °C (Table 1.10). When grouping the DH population by the alleles of two markers, one on A07 (Bn-A07-p21478337, 97.6 cM) and one on C06 (Bn-A07-p21354084, 8.2 cM), the epistatic effect can be observed in the phenotype (Fig. 1.6 and Fig. 1.7). The Tukey test between the four haplotype groups showed no significant difference between the two groups that shared the DH4079 allele on A07 ($A_{DH}C_{DH}$ and $A_{DH}C_{Exp}$) under any condition. Therefore the DH allele on A07 masked the allelic effect on C06. Except for cool long day conditions in 11 °C the allele combination $A_{Exp}C_{DH}$ resulted in a significantly late flowering group of genotypes.

1.5 Discussion

1.5.1 A flowering time QTL cluster on linkage group A02 is responsible for the separation of ‘spring’ and ‘winter’ types

The DH population showed a bimodal distribution for days to flowering (DTF) with no vernalization (V0, Fig. 1.1) and therefore, the DH lines could be classified as either ‘spring’ or ‘winter’ types. The bimodal distribution led to the assumption that one major vernalization dependent QTL influences DTF, which was confirmed by QTL V0a, located on chromosome A02 at 42 cM explaining 56% of the phenotypic variance (Fig. 1.3, Table 1.5). Having one major flowering gene responsible for the difference in flowering in a cross between a spring and a winter type has been shown in earlier studies (Ferreira et al. 1995; Light et al. 2005).

In addition to the vernalization dependent effect of this QTL, there is a general effect on flowering time independent of the environmental conditions. This general difference in flowering between ‘spring’ and ‘winter’ types after vernalization, could be observed in both phenotyping and QTL analysis as follows. In the phenotypic analysis, a few ‘winter’ DH lines still showed delayed flowering after being vernalized for 8 weeks (V8) in comparison to the rest of the population, as well as winter oilseed rape parent Express617, and the general tendency of ‘winter’ types to flower later than ‘spring’ types could be observed in all vernalization treatments (Fig. 1.1). From the experimental setting it cannot be concluded whether a longer vernalization treatment would result in a further reduced DTF. Even though in the day length and temperature experiment the plants were vernalized for nine weeks to

avoid incomplete vernalization, the general difference between ‘spring’ and ‘winter’ types in flowering time was still observed in the day length and temperature experiment (Table 1.4).
In the QTL analysis, the major vernalization QTL V0a had an overlapping confidence interval with QTL LD11a, LD22a, V8a, V4a, and SD22a. In all these treatments, vernalization was applied, and the additive effects of the QTL were similar, ranging from +2.3 (V8a) to +5.8 days (SD22a). Furthermore, no QTL for the effect of temperature or day length differences were mapped in this cluster. Since these effects were calculated as the difference between two conditions, the general influence present in both conditions would be removed. In conclusion, the major vernalization QTL V0a was also or was collocating with an environmentally independent flowering time QTL, which was the cause of the general difference in phenotype between ‘spring’ and ‘winter’ types.
Candidate genes located in the genomic region of this cluster on linkage group A02 were well-known genes from the vernalization pathway *EMF2* and *FT* (Fig. 1.3). One might have expected FLC as a candidate gene; however, the FLC copy on A02 was located at 135'303 bp (Appendix C). In *Arabidopsis thaliana* EMF2 is part of the POLYCOMB REPRESSIVE COMPLEX 2, which is responsible for the repression of several flowering genes in the vegetative phase, including *FLC, MADS AFFECTING FLOWERING 4* and *5*, *FT* and *AGAMOUS-LIKE 19* (Blümel et al. 2015). Jiang et al. (2008) showed that *emf* mutants tend to flower earlier, since *FT* is not suppressed, despite FLC being active. Stronger *FT* suppression through a functional *EMF2* allele of Express617 could have caused the general delay in flowering, as well as a stronger vernalization requirement. FT is known as part of the florigen signal traveling from the leaves to the shoot apical meristem and triggering the generative phase (Blümel et al. 2015; Turck et al. 2008). Wang et al. (2009) detected six different *FT* homologs in a *Brassica napus* winter × semi-winter DH population, three on each sub genome. They found that in winter oilseed rape cultivar Tapidor two of the six *FT* homologs, *BnA2.FT* and *BnC2.FT*, had a disrupted CArG box, which would prevent regulation through binding of FLC. In an association analysis, they showed the two *BnA2.FT* alleles significantly segregated spring and winter oilseed rape types in a diversity set. Raman et al. (2015) identified *BnA02.FT* as a candidate gene for vernalization response in a GWAS study. Schiessl et al. (2014) linked differences in copy number variation and SNPs for *FT* to differences in vernalization requirement. Even in a DH population from the cross of the two winter rapeseed genotypes L16 × Express617, Ghanbari et al. (2020) mapped a major QTL for the beginning of flowering in autumn sown field trials on A02, which collocated with candidate gene *BnA02.FT*, with the Express617 allele delaying flowering time. After a winter period in the field, vernalization requirement was already satisfied, supporting a general flowering time QTL like observed in our population.
A possible explanation for the major vernalization QTL on A02 also being a general flowering time QTL, is a FLC dependent *FT* homolog from Express617 and a FLC independent *FT* homolog from DH4079 as proposed in Wang et al. (2009). These two homologs could very well have a different function than the original *FT* in *Arabidopsis*. Guo et al. (2014) tested the expression of different *FT* homologs in Express617 in different developmental stages. *BnA2.FT* was only found to be expressed after floral transition, which indicates a different regulation mechanism. However, this would contradict our conclusion that *FT* is a likely

candidate gene. *FT* would explain the general difference between 'spring' and 'winter' types as observed in the present population. The high BLAT score (which indicates how well the *Arabidopsis* gene aligns with the reference genome, see above) indicates that *EMF2* is a conserved gene between *Arabidopsis thaliana* and *Brassica napus,* and most mutations in *EMF2* have a severe impact on the phenotype of the plant (Chanvivattana et al. 2004), which makes different alleles in the population unlikely. If both, *FT* and *EMF2,* genes have different alleles, linkage would prevent a difference to be seen in the phenotypic data.

The second largest vernalization dependent QTL V0e is located on C02 (Table 1.5, Appendix B). In this genomic region, a copy of *FLC* is located (Appendix C). *FLC* is a well-known MADS-Box-transcription factor repressing *FT* expression without vernalization (Raman et al. 2013; Tadege et al. 2001) and different copies had been identified to determine the phenotypic difference between spring and winter oilseed rape (Ghanbari et al. 2020; Sheldon et al. 2000; Zou et al. 2012). The QTL V0e showed epistatic interaction with the major vernalization QTL V0a (Table 1.6). As mentioned earlier FLC is a well-known repressor for *FT*, and *FLC* is repressed by a complex containing EMF2 (Jiang et al. 2008). Ergo, both candidate genes for QTL V0a are known to interact with the candidate gene for V0e. It can be concluded that the winter oilseed rape parent Express617 has a functioning *FLC* on C02, which is a transcription factor essential for the suppression of flowering before vernalization. But a bigger role played the *FT* gene, which is vernalization insensitive in the spring-type rape, maybe with a broken CArG box as discovered in Wang et al. (2009). Since *FT* is central to flowering time regulation and not just included in the vernalization pathway like *FLC* (Blümel et al. 2015), the different alleles cause a general, environmentally independent difference between DH lines with the respective alleles even after vernalization.

1.5.2 Flowering under short days is regulated by homologous regions on chromosomes A07 and C06

The day length and temperature experiment showed the strong delay of DTF under short day conditions to the point where some genotypes did not even start flowering at the end of the experiment (Fig. 1.2). The delay of flowering under short days was also observed in both parents (Table 1.4).

QTL analysis showed two important genomic regions, where several QTL for DTF under SD conditions and the effects of day length differences collocated. The first cluster was located on chromosome A07 between 93 and 103 cM, where QTL for short day traits (SD22d, SD-LD11a and SD11b) collocated with minor vernalization QTL V0d (Fig. 1.4). The second cluster was located at the beginning of the genetic map of C06 between 0 and 11 cM, where the confidence interval of QTL SD11e overlapped with those of QTL SD22g and SD-LD11d (Fig. 1.5). The QTL clusters were positioned in regions on linkage groups A07 and C06, which are in synteny to each other according to Chalhoub et al. (2014). However, the direction of the additive effect was different in the clusters on A07 and C06. It was positive for the QTL on A07, meaning the winter oilseed rape Express617 allele delayed flowering under short day conditions and in non-vernalized plants. In contrast to that, the additive effect was negative for the QTL on C06, with the spring-type DH4079 allele delaying flowering under short days but showing no response to vernalization. Additionally, epistatic effects were

recorded between the respective QTL (Table 1.10). The DH alleles on A07 masked the allelic effect on C06, as the group with the $A_{DH}C_{DH}$ haplotype and the group with the $A_{DH}C_{Exp}$ haplotype showed no significant difference in their mean according to the Tukey-Test (Fig.1.6 and Fig.1.7). The allele combination $A_{Exp}C_{DH}$ was resulting in the largest delay in flowering under short days and also warm long day conditions (Fig.1.6), as can be seen especially in the effect of day length differences, where this allele combination was always significantly different from the others (Fig.1.7). In both homologous genomic regions, copies of the flowering time candidate genes *EFS a*nd *TPS1* were located. In *Arabidopsis thaliana,* TPS1 is the protein responsible for the synthesis of Trehalose-6-phosphate (T6P), a sugar signal. TPS1 is necessary for the expression of *FT* and other flowering inducing genes. This prevents flowering of weak plants with not enough photosynthesis levels to support the sugar demand during flowering (Wahl et al. 2013). However, there is no current knowledge about an influence of TPS1 on flowering through the day length or vernalization pathways. EFS is known in *Arabidopsis* as a *FLC* activator (recruited by the *PAF1*-like complex), meaning its activity delays flowering. Kim et al. (2005) showed that a mutation in *EFS* accelerates flowering time under short days more than *fri* or *flc* mutations with an active *EFS*. Thus, there is an FLC independent effect of *EFS* on flowering time under short days, whose mechanism is not yet known.

An explanation for the opposing effects of the QTL clusters is for winter oilseed rape Express617 to have an active *EFS* homolog on chromosome A07 that has the same function as in *Arabidopsis* and delays flowering under short days by activating *FLC* in the vernalization pathway, as well as in the *FLC* independent pathway (Kim et al. 2005). The spring-type DH4079, however, would contribute an *EFS* homolog on C06 with the FLC independent effect repressing flowering under short days but without the function in the vernalization pathway. A homolog like this would at the very least not be a disadvantage in breeding for a spring-type, as such a variety does not need vernalization but might still delay flowering to avoid late frost.

Furthermore, DH4079 contributed an allele on A07, which masked the effect of the C06 alleles (Table 1.10, Fig. 1.6). The C06 DH4079 allele could only delay flowering in the absence of the A07 DH4079 allele (Fig.1.6). This would point to an unregulated activator, but the candidate genes are repressors. It can be speculated, that the lack of delay in flowering from the A07 DH4079 allele might stem from some epigenetic, post-transcriptional regulation. Further research is needed to reveal the complexity of flowering time regulation found in these two homolog regions.

The results of QTL mapping studies finding photosensitive genes on chromosomes A02, A03, A10, C03, C04, C05 and C09 could not be confirmed (Axelsson et al. 2001; Cai et al. 2008; Luo et al. 2014; Rahman et al. 2018; Robert et al. 1998) in the DH4079 × Express617 population.

1.5.3 Temperature × day length interactions lead to genotype specific delay or acceleration of DTF under warm short days

Fully vernalized plants grown under long days and 11°C showed the least phenotypic variance in days to flowering of all four conditions (Fig. 1.2). Furthermore, only 35.7% of the

phenotypic variance could be explained by the genotypic analysis and no QTL were found on the QTL cluster on A07 and C06 (Table 1.7). It can be concluded that long days and 11°C is a good neutral condition for day length and temperature experiment.

The effect of temperature on DTF was much smaller than that of the effect of day length and even smaller than that of the interaction between temperature and day length (Table 1.3). Surprisingly, higher temperatures can either delay or accelerate flowering, depending on the genotype (Table 1.4). A long-term study of wild plants in England showed that, while most plant species reacted with earlier flowering to higher temperatures due to climate change, some delayed their flowering (Fitter and Fitter 2002). QTL analysis showed that the homoeologous regions on linkage groups A07 and C06 had similar clusters for temperature and day length (Table 1.5 – 1.9, Fig. 1.4 and 1.5). The cluster on A07 between 70.2 and 81.5 cM was comprised of QTL 11-22LDb, 11-22SDb, SD-LD22a, and V8b (Fig.1.4). The cluster on C06 between 16.1 and 40.7 cM was comprised of QTL 11-22LDd, 11-22SDd, SD-LD22c, SD-LD11e and V8e (Fig.1.5). On A07 it was the Express617 allele and on C06 the DH4079 allele, which delayed DTF under 22°C and/ or short days. The two clusters showed epistatic effects between QTL 11-22LDb and 11-22LDd (a × a =1.7) and SD-LD22a and SD-LD22c (a × a = -4.1). The QTL 11-22SDb and 11-22SDd as well as V8b and V8e showed no epistasis.

In each of those genomic regions, homologous copies of the flowering regulator genes *ELF4-LIKE 2* and *FT* were located. No details about the function of *ELF4-LIKE 2* are known. In *Arabidopsis, ELF4-LIKE 2* could not rescue *elf4* mutants (Lin et al. 2019), which does not exclude another function in flowering time regulation. Teper-Bamnolker and Samach (2005) studied the effect of *FT* overexpression on flowering in *Arabidopsis thaliana*. The overexpression caused early flowering and an increase in downstream transcripts. However, when studying the difference between 23°C and 12°C, downstream transcripts were downregulated in the latter condition, raising the question of a temperature dependent activity of *FT*. Ghanbari (2016) found *FT* on C06 as the candidate gene for a flowering time QTL in an autumn sown field trial of the DH population of Sansibar × Oase, two winter oilseed rape genotypes, thus influencing flowering time in spring after full vernalization.

In the phenotypic analysis, DH4079 as a Swedish spring-type showed a reaction to temperature that was independent of day length and vice-versa (Table 1.4), so when sown in spring, the cultivar can react to warm temperatures without a negative interaction with day length. In contrast, German winter oilseed rape Express617 reacted differently to warmer temperature depending on the day length. Under long days, DTF were accelerated, like in DH4079, but delayed under short days. It should be noted, that in this experiment the temperatures were constant and did not change between night and day. Other conditions might have led to different results.

It can be concluded, that there is genotype specific interaction between temperature and day length. When sown in the field in autumn, winter oilseed rape should not induce flowering in warm winter days, while spring-types may induce flowering earlier if warm temperatures permit it. *FT* is again a viable candidate gene, since Teper-Bamnolker and Samach (2005) found evidence of temperature dependence in *FT*.

1.5.4 Conclusions and perspectives

Vernalization response is well studied in *Brassica napus* L. and we confirmed a flowering time QTL on linkage group A02 in the genomic region of the *FT* gene which separates spring-type from winter oilseed rape. New photoperiod related QTL were located on chromosomes A07, C06, as well as C02 and C07. The gene *EFS*, which represses flowering under short days, was identified as a viable candidate gene for QTL on A07 and C06. The influence of temperature × day length interactions on flowering time after vernalization is less studied for rapeseed, although with pending climate change, this might become an issue when warm spring temperatures shift to earlier months when the days are shorter. We found that the effects for temperature and day length interactions are greater than just the temperature effect, and suggest that these two important abiotic factors should not be studied independently. The effect of temperature under short days is also genotype-specific and the combination of higher temperatures and short day conditions can either delay or accelerate flowering time.

Both parental genotypes had alleles, which suppressed flowering under short days and warm temperatures, but on different loci. On C06, the alleles derived from spring-type parent DH4079 were responsible for the effect of the QTL, while on A07, the alleles from winter-type parent Express617 were responsible. The Express617 allele on A07 also responded to vernalization. In the presence of the DH4079 allele on A07, the effects of the alleles on C06 were masked and the delay in flowering time through short day conditions was not expressed. The QTL on C06 and A07 were located in homoeologous regions and resulted consequently in the same candidate genes. This genetic diversity is a valuable basis for breeding *Brassica napus* to counter the environmental effects of climate change.

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2 Freezing tolerance in *Brassica napus* L.

2.1 Abstract

Cold response is the adaptation of a plants biochemistry and morphology to cold climate and prepares the plant for frost events to increase survival. Especially in winter crops freezing tolerance is an important trait. In this study cold hardened rapeseed from a DH population derived from a cross DH4079 × Express617 of spring and winter oilseed rape, was tested in a climate chamber at -14°C for freezing tolerance. Traits of the plants morphology after hardening, as well as freezing damage after the frost treatment and traits for regrowth and survival 11 days after end of frost treatment were recorded. A SNP based marker map was used for a QTL analysis. Freezing damage of the leaves and the stem was recorded separately and the results showed that freezing tolerance is partly specific to organ and genotype. Stem elongation, regardless of hypocotyl or epicotyl, increases susceptibility to freezing. However in QTL analysis no connection between stem elongation and freezing tolerance was found.

2.2 Introduction

2.2.1 What is freezing tolerance

Freezing tolerance as the ability of a plant to survive subzero temperatures without tissue damage is an important trait for all winter crops. A distinction is made between the inert freezing tolerance and the tolerance achieved by cold acclimation (Teutonico et al. 1995). Cold acclimation can already start as soon as the temperature is below 14°C (Bond et al. 2011).

2.2.2 Gene networks in cold response

The acclimation to cold, also called cold hardening, is a process that involves the perception of low temperatures with a signaling cascade, the physiological changes in the plant transcriptome, proteome and metabolome which also highly influences phenotype and morphology, as well as the response to cold as an abiotic stress.

The number of genes responding to cold in *Arabidopsis thaliana* amounts to 10%-15% of all genes, a percentage also found for *Brassica napus* (Ke et al. 2020; Lee et al. 2005; Park et al. 2015). These so-called cold-regulated (COR) genes are regulated by a variety of pathways. The most studied are the CBF dependent pathways. C-REPEAT/DRE BINDING FACTORs (CBFs) are transcription factors responsible for transcribing COR genes (Park et al. 2015) and are regulated by factors from several pathways, like INDUCER OF CBF EXPRESSION 1 (ICE1), which activates CBFs transcription or 14-3-3s proteins which promote CBF degradation (Guo et al. 2018). However, CBFs are not the only regulators of COR genes, and often the same pathway can act CBF dependent and independent (Eremina et al. 2016; Guo et al. 2018). The calcium signal cascade, which is signaling cold from the plasma membrane via a mitogen-activated protein kinases (MAPK) cascade, is well understood and studied (Guo et al. 2018).

Eremina et al. (2016) reviewed the known effect of phytohormones on freezing tolerance: The abiotic stress hormone abscisic acid (ABA) is well studied as a positive freezing tolerance regulator, where ABA application on plants increases freezing tolerance, and

functions both CBF dependent and independent. Gibberellic acid (GA) promotes plant growth by regulating the elongation and the division of cells. Under cold conditions the GA metabolism is inhibited. Several GA-regulated proteins such as DELLA are responsible for the cold response including CBF expression. This complex molecular regulation is not yet completely understood in its entirety. Jasmonic acid (JA) is involved in many abiotic and biotic stress responses, and has been shown to increase freezing tolerance through CBF and inhibits growth. JA signaling is known to be connected to GA signaling. Auxin and cytokinins, which control plant growth in cross-talk, may also have an influence on freezing tolerance, but studies on those two are not yet conclusive. Similarly Ethylene, important for growth and development as well as in the response to stress, has been shown to increase and decrease freezing tolerance, which makes its role unclear. Brassinosteroids (BR) have a similar function as GA on growth, but are reported to increase freezing tolerance (Eremina et al. 2016; Lv and Li 2020; Ye et al. 2019). They are known stress signals in response to pathogens, heat, cold, drought, and shade (Lv and Li 2020). The key regulator is BRASSINOSTEROID-INSENSITIVE2 (BIN2), which is inhibited through brassinosteroid and other signals (Lv and Li 2020) and decreases in the beginning of cold stress and therefore ICE and CBFs are active, leading to expression of COR genes (Ye et al. 2019). Active BIN2 is responsible for the phosphorylation and therefore degradation of ICE1 (Ye et al. 2019) and CESTA as well as BRASSINAZOLE-RESISTANT 1 (BZR1), two COR gene activators.

In summary, phytohormones for general stress responses are involved in cold acclimation, but also many phytohormones involved in growth regulation, like GA, BR and Auxin, are found to be part of the cold response and cold acclimation, providing a connection between growth and cold acclimation.

He et al. (2019) showed in a transcriptome analysis in two semi-winter rapeseed genotypes that genes in the ABA and JA plant hormone signaling pathways are differentially expressed, confirming for *Brassica napus* the use of plant hormone signals in cold acclimation (4°C) and freezing stress (-4°C). In the transcriptome analysis of Wei et al. (2021) *Brassica napus* leaves from two cultivars were harvested at -4°C. The majority of up-regulated transcription factors were in the ethylene pathway, but also genes from other phytohormone signaling pathways and the calcium signal cascade were upregulated in response to cold. However, many transcription factors, which were present in the transcriptome, could not be found in the proteome. Ke et al. (2020) found differentially expressed genes (DEGs) in environmental stress, energy production, processes in the photosynthesis and chromatin organization. In the comparison between a winter and a semi-winter type, they found 40% of the DEGs to be genotype-specific.

2.2.3 Freezing tolerance and winter hardiness

While winter crops including winter oilseed rape often have to survive several frost events with temperatures of -20°C (Rapacz and Chilmonik 2000), spring-type rape has to survive later but usually milder frost spells in spring (Wrucke et al. 2019). The ability to survive harsh winter conditions is called winter hardiness.

Freezing tolerance is one aspect of winter hardiness and correlation between freezing tolerance predicted by labatory methods (see 2.2.4) and plant survival in the field is often

weak (Rapacz et al. 2015). Rapacz and Markowski (1999) observed a strong correlation between winter hardiness and freezing tolerance determined in a freezing chamber (r=0.8) within a diversity set of cultivars that were released within 20 years, which included low erucic acid high glucosinolate (0+) cultivars and early low erucic acid low glucosinolate (double low or 00) cultivars released in the 1990, when the paper was published.

2.2.4 How freezing tolerance is measured

Since the term cold tolerance includes a wide spectrum from winter hardiness to freezing tolerance, experimental design for phenotyping can differ widely. Rapacz et al. (2015) compared several methods in wheat; first, simple winter survival in field using scores from 1 to 9 based on appearances, second, plants hardened under field conditions receiving frost treatment in a climate chamber, and third, plants receiving a very short cold acclimation (24 h) and were tested in a climate chamber. In the climate chamber methods the trait expression was measured in % of plant survival. As expected, the winter survival in the field was very dependent on the year.

When it is possible to test for freezing tolerance in different temperatures, the 50% lethal temperature (LT_{50}) can be calculated (Rapacz and Markowski 1999; Waalen et al. 2011). Instead of scoring frost damage or survival, regrowth of the plant after frost can be used to assess freezing tolerance (Rapacz et al. 2001; Rapacz and Markowski 1999; Waalen et al. 2011).

Two methods have been frequently used to estimate freezing tolerance without a frost chamber. Electrolyte leakage and chlorophyll fluorescence are two laboratory methods to estimate the freezing damage on leaves in regard to the plasma or thylakoid membranes, respectively (Rapacz et al. 2015). Waalen et al. 2011 found that the results of electrolyte leakage and actual plant survival did not correspond. Rapacz et al. (2015) found the correlation between chlorophyll fluorescence and freezing tolerance as well as winter survival to be highly varying.

Not only correlation between methods estimating freezing tolerance, like electrolyte leakage, and phenotyped frost damage is often underwhelming, but also genomic analyses often lack significant results connecting those two types of traits. Kole et al. (2002) tested both freezing tolerance by electrolyte leakage and winter hardiness in a *Brassica rapa* and a *Brassica napus* population and found only one instance of an overlap of a freezing tolerance QTL and a winter hardiness QTL in the *Brassica rapa*, and none in the *Brassica napus* population. Huang et al. (2018) could only find QTL for estimated freezing tolerance, but not for observed frost damage.

2.2.5 Transcriptomics and GWAS studies on freezing tolerance

With the advent of transcriptomics, it is now possible to have direct insight in the vast number of cold regulated genes and their role in cold response (He et al. 2019; Ke et al. 2020; Wei et al. 2021). Tissue samples for RNA analysis can either be taken during cold acclimation condition or during freezing stress (He et al. 2019). Before, many GWAS studies in freezing tolerance resulted in a high number of significant SNPs distributed over the whole genome, often with a surprisingly low significance threshold (Fiebelkorn et al. 2018; Wrucke et al.

2019; Wrucke et al. 2020). This might be explained, since it was found that 10% of the transcriptome is influenced by cold (Ke et al. 2020).

2.2.6 The connection of freezing tolerance with plant growth and development

After germination, *Brassica napus* exhibits a rosette form, where the internodia are not elongated (Lancashire et al. 1991). The elongation of the internodia is assumed to indicate, one, the transition to the generative phase, and two, a sign of increased susceptibility to freezing damage. An important factor for winter and semi-winter oilseed rape to enter the generative phase is vernalization, and consequently the prevailing hypothesis is that vernalization requirement is an important factor for freezing tolerance.

Rapacz and Markowski (1999) could show a high correlation between vernalization requirement and frost tolerance in a sample set of *Brassica napus* cultivars released in the 1970, which mainly comprised low erucic acid high glucosinolate (0+) cultivars. In double low cultivars from the 1990, they found no longer a correlation between these traits. Rapacz and Chilmonik (2000) observed six spring types and two winter types grown in an open-air vegetation room over one winter (1995/96) and measured chlorophyll fluorescence as well as electrolyte leakage, and scored frost damage after each frost period. They observed increased frost damage of spring types already in January, while winter types started to lose their frost tolerance later by end of February and April. All spring types had a survival rate of 0% by April. When freezing sensitivity increased in the spring types, the authors noticed the elongation of the stems. In their conclusion stem elongation decreases freezing tolerance, and high vernalization requirement is not a requisite for the ability of cold acclimation, but for maintaining freezing tolerance or winter hardiness though the winter by preventing growth and development. Rapacz et al. (2001) studied two *Brassica napus* cultivars, spring type 'Star' and winter oilseed rape 'Górczanski', not only for freezing tolerance by electrolyte leakage, by LT50, and by plant regrowth, but also for growth traits, photosynthetic ability, soluble sugar content, and water content in leaves and shoot. Between four and eight weeks of growing under cold acclimation conditions the spring type started to severely loose freezing tolerance, while winter type was able to maintain its freezing tolerance on one level until the end of their experiment at 10 weeks of cold acclimation. Flowering time was also influenced by the duration of cold acclimation; non acclimated spring rape flowered after 17 days. After four weeks cold acclimation and subsequent transfer to warm conditions, the plants flowered after 14 days. After 6 weeks of cold acclimation and subsequent transfer to warm conditions, plants reduced the time until flowering to nine days. Between four and eight weeks of cold acclimation the spring type showed morphological changes by elongating the epicotyl and petioles, and increasing leaf size. The reduction of freezing tolerance corresponded to a reduction of soluble sugars and increased water content. Kole et al. (2002) and Teutonico and Osborn (1995) found a genomic region with collocating QTL for winter hardiness and internode length in *Brassica rapa*. Hurry et al. (1995) showed that growth, sugar accumulation and photosynthesis rates decreased in spring type rape cv. ‘Paroll’ compared to winter oilseed rape cv. ‘Tor’ under cold hardening conditions.

It is still unclear how growth, vernalization, and plant development are intertwined with freezing tolerance and winter survival.

2.2.7 Research questions

A doubled haploid (DH) population derived from a cross between spring-type DH4079 and winter oilseed rape Express617 was previously studied for flowering time in dependence of vernalization, day length and temperature. The objective of this work is to study the quantitative variation and inheritance of freezing tolerance in the same DH population. We want to test the hypothesis that an elongated stem makes the plant more susceptible to freezing damage. The above ground parts of a plant are leaves, epicotyl and hypocotyl. These organs were examined separate from each other to determine if (a) they differ in their freezing tolerances, (b) if freezing damage on these parts has different effects on regrowth and (c) if we find the same QTL for freezing tolerance of the different parts of the plant. We critically examine the traits used, to see differences in phenotyping frost damage in different plant organs as well as at different time points. A QTL analysis with a SNP-marker based linkage map was used to find candidate genes.

2.3 Material and Methods

2.3.1 Plant material

The inbred line 617 of the winter oilseed rape cultivar Express (Norddeutsche Pflanzenzucht Hans-Georg Lembke KG) and the doubled haploid line DH4079 (Ferrie 2003) of the Swedish spring-type cultivar Topas were crossed to generate F1 seeds. From clonally propagated F1-plants a DH population initially consisting of 200 DH lines was developed as described in Valdés et al. (2018); a reduced number of 187 DH lines were used in this experiment. Unfortunately, six DH lines were later discovered to be three pairs of genetic duplicates, therefore only 184 DH lines are used for analysis. This DH population was already described for flowering time regulation through vernalization, day length and temperature in the first chapter. There it was shown that the DH population showed a bimodal segregation for days to flowering without vernalization, and therefore for vernalization requirement. Accordingly, the population was halved into two groups referred to as ‘spring’ and ‘winter’ types (see chapter 1.4.1, Appendix A).

2.3.2 Experimental design and characterization of the DH Population for freezing tolerance

One plant of each of the 184 DH lines from the DH population, five plants of each parent and three plants of the F1 hybrid from which the DH population was derived made up one set of 200 plants tested in the following simple rectangular lattice design generated with PLABPLAN (Utz 1998). Each set comprised 20 incomplete blocks with 10 individual plants, ergo 200 plants. Two sets are one lattice and were sown, grown, cold-acclimated, treated with frost, and regrown simultaneously as one repetition. The analysis of the freezing tolerance experiment consisted of nine repetitions.

Seeds were sown in Styrofoam boxes to simulate more natural freezing of the soil from its surface. A 1:1 mixture of Fruhstorfer Erde type T25 (HAWITA Gruppe GmbH, Vechta) and local compost soil was used. The dimensions of one Styrofoam box were 38 × 38 × 78 mm. Each box contained two incomplete blocks á 20 plants. Plants were cultivated for three weeks in the greenhouse until the two to three leaf developmental stages (BBCH 12 to 13;

Lancashire et al. 1991). For cold-hardening, the plant material was transferred to a climate chamber adjusted to 4 to 5 °C and 8 h cool white light (Schuch Typ 164/12 L96C 82W). The plants were hardened for seven weeks and afterwards scored the first time (after Hardening, Table 2.1). Then they were moved to the climate chamber (Vötsch VB4018 (4qm)) where they received one additional night at 4 to 6°C followed by two consecutive 16h frost nights with 2h at 0°C, a transition period of six hours to a minimum temperature of -14°C, holding the temperature 4 h and another transition period for 4 h to 0°C. Days lasted 8 hours at 4 to 6°C. Afterwards plants were moved to a frost free greenhouse with mild conditions, but no exact temperature control, were they were scored two times; four days after the end of the frost treatment (after Frost), and 11 days after the end of the frost treatment after a regrowth period (after Regrowth, Table 2.1). A full list of phenotypic data is available in Appendix D.

Table 2.1 Name and description of the traits scored in the freezing tolerance experiment.

Trait	Description
After Hardening	
Number of Leaves	Number of all unfolded leaves
Vigor	Score 1 – 9; from 1 – underdeveloped to 9 – very vigorous; leaf size and stem thickness was taken into account
Hypocotyl Length	Above the soil in [cm]
Epicotyl Length	Measured in [cm]
Stem Length	Sum of Epicotyl and Hypocotyl Length in [cm]
After Frost	
Number of Viable Leaves	Number of leaves with no or low amount of freezing damage
Leaf Survival Rate	Ratio of Number of Viable Leaves after Frost / Number of Leaves after Hardening
Leaf Damage Score	Score 1 – 9; from 1 – no damage, 5 – half of the leaves frostbitten, to 9 – all leaves frostbitten
Stem Damage Score	Score 1 – 9; from 1 – no damage to 9 – stem completely frostbitten
After Regrowth	
Number of Leaves	Number of all viable leaves
Death Rate	From 0 to 1; Single plants scored binary with 0 – plant survived frost treatment or 1 – plant lethally damaged
Number of Regrown Leaves	Difference of Number of Leaves after Regrowth subtracted by Number of Viable Leaves

2.3.3 Statistical analysis

PLABSTAT 3A software (Utz 2011) was used to calculate adjusted means for each repetition from the two sets in the lattice design. With the adjusted means an analysis of variance (ANOVA) and heritabilities H^2 were calculated in PLABSTAT. The ANOVA for was performed using the model for a randomized complete block design $Y_{jk} = \mu + r_j + g_k + g_k r_j$. In this model, Y_{jk} is the trait value of the genotype k in repetition j, μ is the general mean, r_j is the effect of repetition j, g_k is the effect of genotype k and $g_k r_j$ is the interactions between the kth genotype with jth repetition and includes the error term. Factors genotypes and repetitions were considered as random. Broad sense heritabilities were calculated with following formula: $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{gr}^2 / J)$ with J=9 indicating the factor levels for repetition.

Other statistical analyses were performed in R (R. Core Team 2019). Since parental genotypes and F1 had more than one plant in the experimental design, first the mean over

one repetition was calculated. A pairwise t-test ("stats" package, R. Core Team 2019) was used to test differences among both parents, and F1, p-values were adjusted according to Bonferroni. A t-test was used to test differences between extreme genotypes (DH line with minimum or maximum values for each trait) and the respective parent (depending which parent had the lower or higher value in the respective trait) to test for transgression (Appendix E).

Means over nine repetitions were obtained and used for further statistical analyses. Student's t-test was used to test differences between the two groups 'spring' and 'winter' types, which contained an equal number of DH lines. Correlations were calculated with Spearman method (r_S) and a t-test without adjusted p-values was performed to test for the significance of the correlation using package "psych" (Revelle 2019). Figures of the descriptive statistics were generated in R with the package "ggplot2" (R. Core Team 2019; Wickham 2016)). For boxplots the whiskers represent the default with maximum 1.5 IQR (Interquartile range).

2.3.4 SNP marker analysis and linkage map development

A previously published full marker map consisting of 21,583 markers distributed across 19 linkage groups (Valdés et al. 2018) was used to develop a framework map consisting of 767 markers evenly distributed over the genome (see chapter 1, Appendix B).

2.3.5 QTL analysis

Mean values over the nine repetitions were used for all traits in QTL mapping. QTL mapping was performed with WinQTL Cartographer software version 2.5 (Wang et al. 2012), and composite interval mapping (CIM) algorithm was employed with following specifications: Independent LOD significance thresholds ($\alpha = 0.05$) were estimated for each trait by 1000 permutation tests. The so-called Model 6 was employed, forward and backward stepwise regression method was used to set cofactors. The linkage groups were scanned at 1 cM intervals, and the window size was set to 10 cM. The ninety-five percent confidence interval for each QTL was determined by one LOD drop from the peak position. Additive effects, as well as the percentage of phenotypic variance explained by a QTL, were determined.

SNP marker sequences of the framework map were provided by Isobel Parkin (AAFC, Saskatoon, Canada) and BLAT positions on reference genome of 'Damor-*bzh*' (Chalhoub et al. 2014) used to create a physical map. A positive additive effect is to be interpreted as an increase of a trait value caused by the allele of winter oilseed rape parent Express617. Figures of the maps were drawn with MapChart (Voorrips 2002).

To test epistasis multiple interval mapping method was used. QTL found in CIM were used as input and BIC-M0 model with 1 cM walk speed and 10 cM window size. Additive × additive effects were significant with an LOD of 2.4.

2.3.6 Candidate gene analysis

A list of important freezing tolerance candidate genes from *Arabidopsis thaliana* L. was adapted from several reviews on the regulation of freezing tolerance and cold response (Chen et al. 2011; Eremina et al. 2016; Guo et al. 2018; Liu et al. 2019; Zheng et al. 2018). The whole genome sequence for every candidate gene was taken from the database TAIR (Berardini et al. 2015) and aligned using BLAT algorithm against the reference genome

sequence of 'Damor-*bzh*' by use of the Genoscope database (Chalhoub et al. 2014). Results with BLAT scores below 350 were discarded. The list can be viewed in Appendix F.

2.4 Results

2.4.1 ANOVA

The ANOVA (Table 2.2) showed strong significant effects for genotype and repetition in all traits. The heritabilities were high with 91% for Hypocotyl Length after Hardening as a maximum, but dropped for traits scored after the frost treatment and regrowth, e.g. the Number of Regrown Leaves had the lowest heritability with 50%. This is to be expected, since these traits were scored at a later time point in the experiment, after the plants went through different environments varying environmental conditions, which is likely to increase their phenotypic variance by adding further experimental error between the entries. Regarding Hypocotyl Length and the related trait Stem Length, the genotype explained a larger proportion of the observed variation than the repetition. For all other traits, the variation explained by the genotype was the smallest.

Table 2.2 Components of variance, respective F-Test results indicated with asterisks, and heritabilities (H^2) from the analysis of variance for traits from the freezing tolerance experiment. The adjusted means from the lattice design of 184 lines of the DH population DH4079 × Express617 were tested in nine repetitions.

Trait	**Repetition (R)**	**Genotype (G)**	**R×G**	**H^2 [%]**
Degrees of Freedom	8	183	1438	
After Hardening				
Number of Leaves	0.42 ***	0.14 ***	0.28	82
Vigor	0.52 ***	0.10 ***	0.32	74
Hypocotyl Length	0.07 ***	0.16 ***	0.13	92
Epicotyl Length	0.26 ***	0.18 ***	0.22	88
Stem Length	0.43 ***	0.46 ***	0.40	91
After Frost				
Number of Viable Leaves	0.52 ***	0.15 ***	0.57	70
Leaf Survival Rate	0.02 ***	0.01 ***	0.02	68
Leaf Damage Score	1.01 ***	0.33 ***	1.41	68
Stem Damage Score	2.61 ***	0.74 ***	2.35	74
After Regrowth				
Number of Leaves	1.78 ***	0.54 ***	2.08	70
Death Rate	0.07 ***	0.01 ***	0.08	62
Number of Regrown Leaves	0.89 ***	0.17 ***	1.49	50

* P≤0.10, ** P≤0.05, *** P≤0.01

2.4.2 Descriptive statistics

In chapter 1, the population was divided into 'spring' and 'winter' types based on their flowering time without vernalization. A t-test showed that the means of 'spring' and 'winter' types were significantly different, except for the Number of Leaves after Hardening (Table 2.3). However, the difference between the two groups was not large, especially when compared to the differences exhibited by the parental genotypes.

Table 2.3 Descriptive statistics for traits of the freezing tolerance experiment. Values of the extreme genotypes in the DH population DH4079 × Express617 as min and max values including significance to the next parental genotype, as well as the DH population mean. Means for groups of 'spring' and 'winter' types in the population (with significance according to Student's t-Test). Means for parental genotypes and F1 with significance according Student's t-tests.

	DH population								F1 and parental genotypes					
Trait	min	t-test min[a]	max	t-test max[a]	mean	'spring' types	t-test[b]	'winter' types	DH4079 (P1)	P1-F1 t-test[c]	F1	P2-F1 t-test[c]	Express 617 (P2)	P1-P2 t-test[c]
After Hardening														
Number of Leaves	3.2	**	6.1	***	4.9	4.9	*ns*	4.8	4.6	*ns*	4.9	*ns*	5.3	*ns*
Vigor	4.4	**	6.5	***	5.4	5.4	***	5.3	5.4	*ns*	5.9	*ns*	6.2	*
Hypocotyl Length	1.5	**	3.9	***	2.6	2.7	***	2.5	2.9	*ns*	3.0	***	2.1	***
Epicotyl Length	0.3	***	2.5	*ns*	1.2	1.3	***	1.1	1.7	*ns*	1.2	*ns*	1.1	*
Stem Length	2.0	**	6.2	***	3.8	4.0	***	3.5	4.7	*ns*	4.1	**	3.2	***
After Frost														
Number of Viable Leaves	0.8	*ns*	3.7	**	2.2	2.1	***	2.4	1.8	*ns*	2.4	*ns*	3.0	**
Leaf Survival Rate	0.18	*ns*	0.67	***	0.45	0.43	***	0.48	0.37	*ns*	0.51	*ns*	0.57	**
Leaf Damage Score	3.9	*ns*	7.7	*ns*	5.8	6.0	***	5.5	6.6	*ns*	5.5	*ns*	4.6	***
Stem Damage Score	1.6	*ns*	7.5	*	4.1	4.3	***	3.8	5.0	*ns*	3.4	*ns*	2.6	**
After Regrowth														
Number of Leaves	1.1	**	5.6	***	3.4	3.2	***	3.7	2.6	*	4.3	*ns*	5.1	**
Death Rate	0.07	*ns*	0.87	**	0.39	0.43	***	0.35	0.49	*ns*	0.25	*ns*	0.22	*
Number of Regrown Leaves	-0.3	*	2.7	**	1.2	1.1	**	1.3	0.8	*ns*	1.9	*ns*	2.1	*ns*

* P≤0.10, ** P≤0.05, *** P≤0.01, *ns* – not significant, a) Student's t-test to test for significant differences between means over nine repetitions between DH line with minimum or maximum values against parental genotype with minimum or maximum values, respectively. c) Pairwise t-test to test for significant differences between means over nine repetitions between the F1, spring-type parent DH4079 and winter rape parent Express617. b) Student's t-test to test for significant differences between the means of two groups from mean values from the DH lines.

For the Number of Leaves after Hardening the DH population had a range between 3.2 to 6.1 leaves with a mean of 4.9 (Table 2.3). The mean of the parents and the F1 were not significantly different from each other and showed values around the population mean (4.6 – 5.3), and similarly ‘spring’ and ‘winter’ types (4.9 and 4.8, respectively). However, the extreme genotypes were significantly different from the parents. For Vigor after Hardening, the DH population received lower scores than expected, since the mean and median were equal to the Vigor of the lower performing parent DH4079 (Table 2.3, Fig. 2.1). Even though the genotype with the lowest Vigor was only one point lower than DH4079 and the genotype with highest Vigor was only 0.3 points better than Express617, those differences were significant. Winter oilseed parent Express617 had a significantly shorter Stem Length and developed more Vigor than spring-type parent DH4079 (Table 2.3). The genotypes classified as ‘spring’ types had a slightly higher Vigor and a longer Stem Length than the ‘winter’ types, contrary to the parents (Table 2.3, Fig. 2.1). The F1 was showing an intermediate phenotype in most traits with two exceptions. First exception was Hypocotyl Length, where the F1 showed with 3.0 cm a mean phenotype closer to DH4079 (2.9 cm) than to Express617 (2.1 cm). Second exception was Epicotyl Length, where the phenotype of the F1 was with a mean of 1.2 cm closer to Express617 (1.1 cm) than to DH4079 (1.7 cm, Table 2.3). However, only the difference between F1 and Express617 for Hypocotyl and Stem length (F1 was 0.9cm larger) were significant. For Epicotyl Length, the difference between the parents was only significant at P≤0.10. The extreme genotypes showed statistically significant transgression for all traits after Hardening with the exception of Epicotyl Length, where the maximum

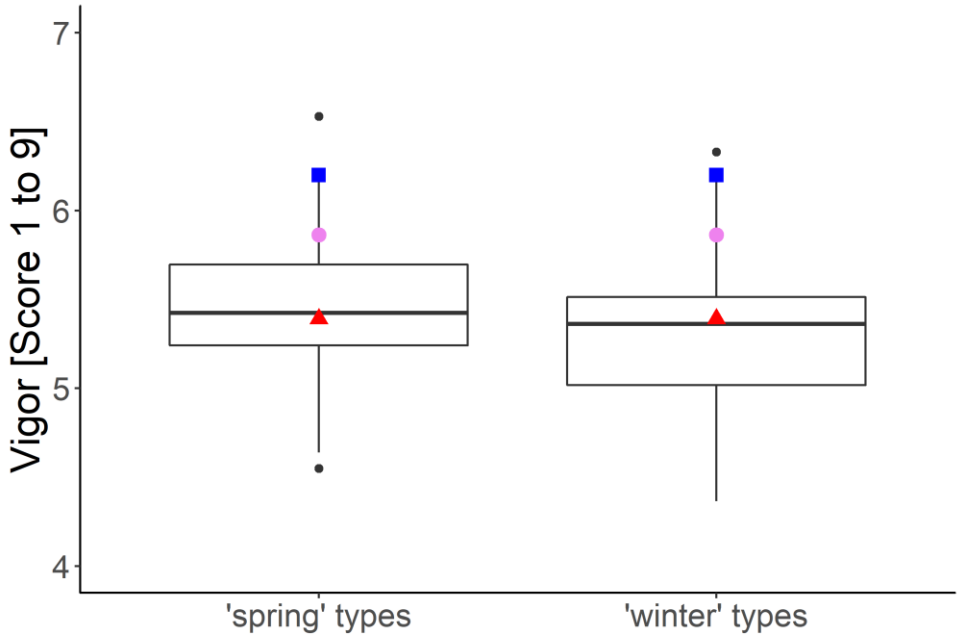

Fig. 2.1 Boxplot for trait Vigor after Hardening. Vigor was scored from 1 (least vigorous) to 9 (very vigorous) in DH population derived from a cross between DH4079 × Express617 divided into ‘spring’ types and ‘winter’ types according to vernalization requirement. Winter oilseed rape parent Express617 is indicated with blue square, spring-type parent DH4079 indicated with red triangle and F1 with violet circle.

genotype and DH4079 showed no significant difference. In general, the Hypocotyl Length was nearly double the Epicotyl Length.

As expected, winter oilseed rape Express617 exhibited a significantly higher freezing tolerance than spring-type DH4079. Express617 showed a significantly larger Leaf Survival Rate as more than half (0.57) of the leaves were viable after Frost while for DH4079 it was a third (0.37). The Leaf Damage Score of Express617 was 4.6 and significantly lower than the score of DH4079 (6.6). A similar pattern was observed for Stem Damage Score (2.6 vs 5.0). The extreme freezing tolerant genotypes had Leaf Damage Scores as low as 3.9 and Stem Damage Scores as low as 1.6, however they were not significantly different from freezing tolerant parent Express617. The extreme susceptible genotype with Leaf Damage Score of 7.7 was not significantly different from susceptible parent DH4079, while the genotype with the highest Stem Damage Score of 7.5 was significantly different with a p-value smaller than 0.1 (Table 2.3). However, more than half of the population showed an intermediate phenotype for both traits (Fig. 2.2).

The traits assessed after Regrowth (Table 2.3) showed that winter oilseed rape parent Express617 recovered better after frost treatment than spring-type parent DH4079. The F1 showed an intermediate phenotype, but skewed towards Express617. The Number of Leaves after Regrowth, for example, was 2.6 for DH4079, 4.3 for F1 and 5.1 for Express.

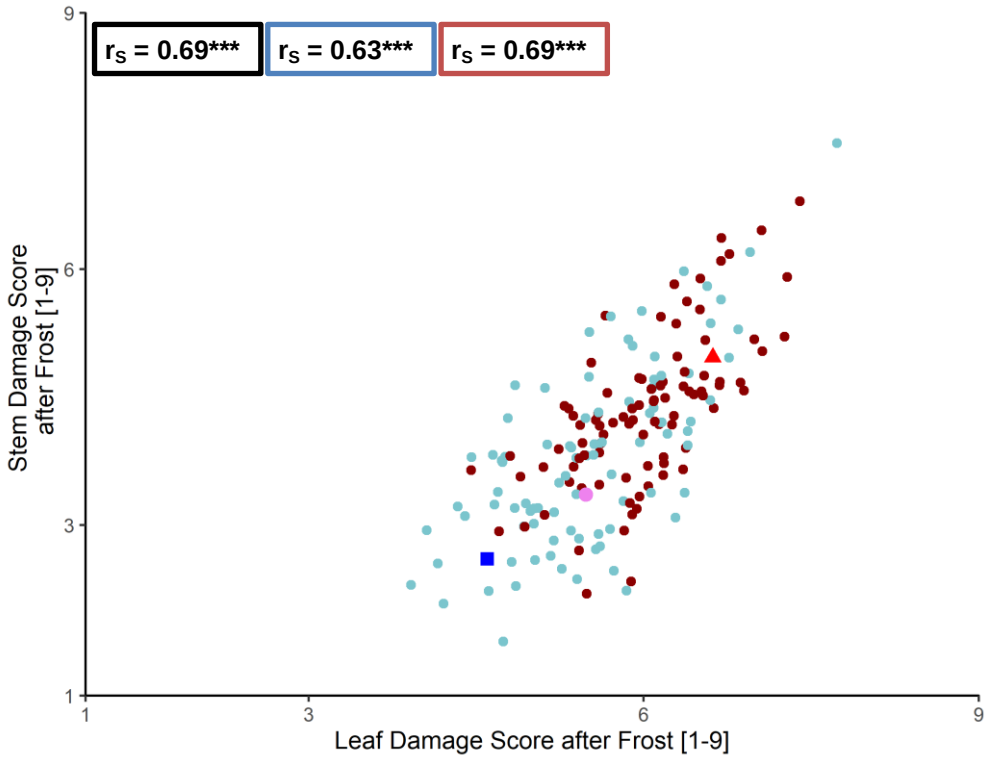

Fig. 2.2 Scatterplot for the traits Leaf Damage Score after Frost and Stem Damage Score after Frost, which were scored from 1 (no damage) to 9 (completely frostbitten), in DH population derived from a cross between DH4079 × Express617. The population was divided in ‘winter‘ (blue) and ‘spring‘ types (red). Winter oilseed rape parent Express617 is indicated with blue square, spring-type parent DH4079 indicated with red triangle and F1 with violet circle.

This difference of 1.7 between DH4079 and F1 was significant; the difference between F1 and Express617 of 0.8 was not significant. Also, the extreme genotypes showed significant differences to the respective parents with 1.1 as minimum and 5.6 as maximum. The Number of Regrown Leaves had a mean of 0.8 for spring-type DH4079, but 1.9 and 2.1 for the F1 and Express617, respectively (Table 2.3), but here the t-test showed these means to be not significantly different. Number of Regrown Leaves and Number of Leaves after Regrowth were the only traits after Frost and after Regrowth where extreme genotypes with both minimum and maximum values showed significant transgression. The Death Rate of winter oilseed parent Express617 was 0.22, while spring-type DH4079 was significantly different with a Death Rate of 0.49. The F1 was again closer to Express617 with 0.25, but not significantly different to either parent. The DH population mean was 0.39. The genotype with the lowest Death Rate of 0.07 was not significantly different from Express617, while the genotype with the highest Death Rate of 0.87 was significantly different from the freezing susceptible parent line DH4079.

2.4.3 Correlation

Number of Leaves and Vigor after Hardening had seemingly no impact on freezing tolerance, since the Number of Leaves after Hardening were only significantly correlated with Vigor (0.41) and the Number of Viable Leaves after Frost (0.24), and with Number of Leaves after Regrowth (0.22) and Number of Regrown Leaves (0.16), but not with Leaf Survival Rate (-0.11, Table 2.4). A higher Number of Leaves after Hardening naturally results in higher values for traits, which also involve counting number of leaves, recorded over the duration of the experiment. Because of this dependence, the significant correlations observed between these traits could be expected. Leaf Survival Rate was calculated to remove this dependence, and the lack of significant correlation with Number of Leaves after Hardening confirmed the rightfulness of this approach. Vigor after Hardening was only moderately correlated with other traits recorded after Hardening, and had low correlations with Number of Viable Leaves after Frost (0.13) and no significant correlation with all other traits after Frost or after Regrowth. Only in ‘spring’ types, Vigor after Hardening had significant ($P > 0.10$), but very low correlation coefficients with Number of Leaves after Regrowth (0.19) and Death Rate after Regrowth (-0.19, Table 2.5).

The three traits describing the shoot length after Hardening (Hypocotyl Length, Epicotyl Length, and Stem Length, the latter being the sum of the two former, see Table 2.1) were correlated with freezing tolerance. In the analysis of the whole DH population, Hypocotyl Length had a correlation of 0.33 with Epicotyl Length (Table 2.4). The three stem length traits were all significantly, but only weakly to moderately correlate with all traits after Frost and Regrowth. The highest correlation of the three was observed between Stem Length and Stem Damage Score with 0.45. The correlations of Stem Damage Score after Frost with Epicotyl Length and Hypocotyl Length after Hardening were very similar with 0.37 and 0.36, respectively (Table 2.4, Fig. 2.3). When examining in the analyses of ‘spring’ and ‘winter’ types, which contain only half of the number of genotypes, the correlations between Epicotyl Length and after Frost traits regarding leaves (Number of Viable Leaves, Leaf Survival Rate and Leaf Damage Score) were no longer significant (Table 2.5, Table 2.6). In the ‘winter’

types also Hypocotyl Length and Stem Length after Hardening had less or no significant correlations with these traits. But the correlation with Stem Damage Score was still moderately strong and strongly significant in both groups (Table 2.5, Table 2.6, Fig. 2.3).

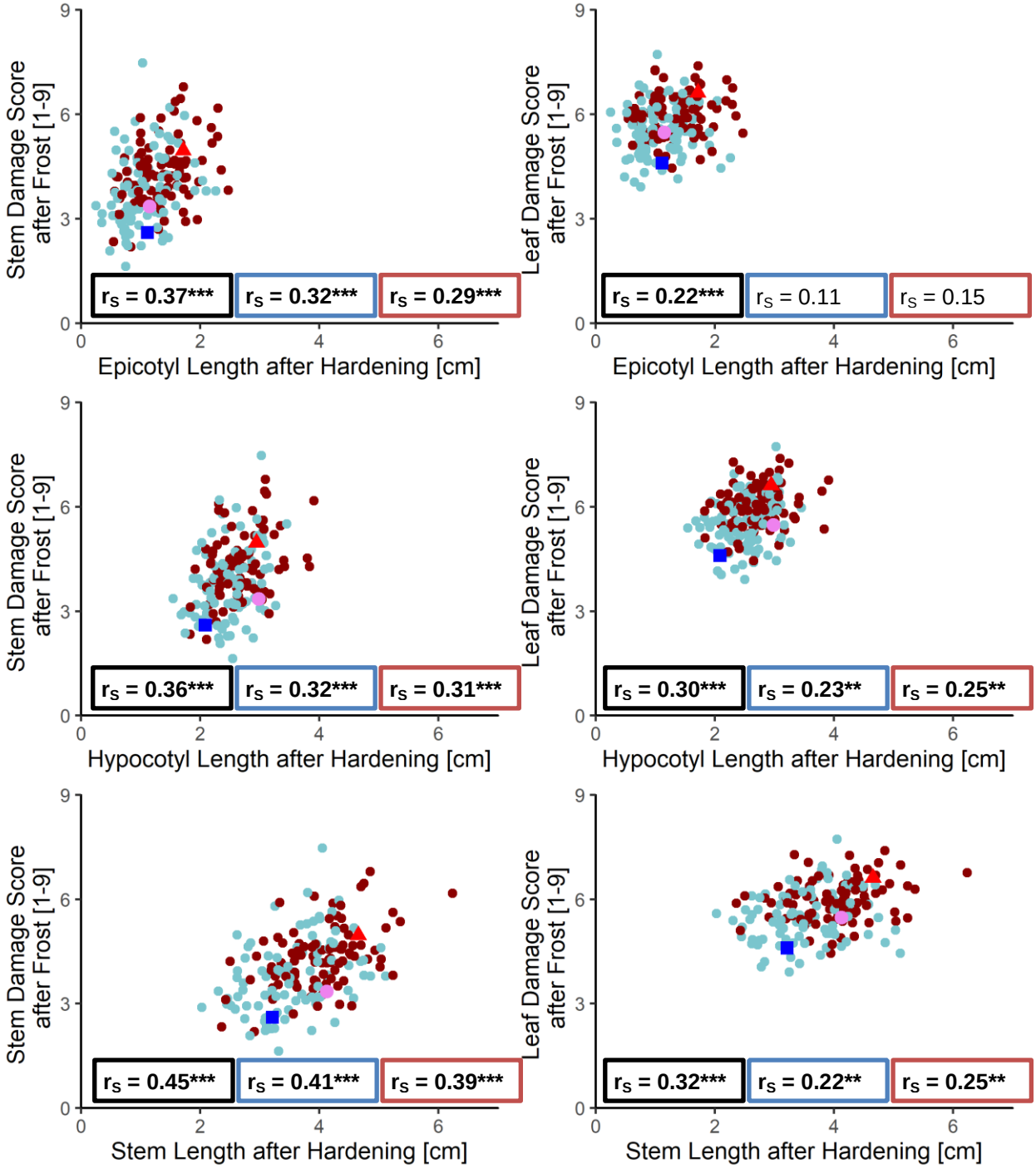

Fig. 2.3 Scatterplots for traits Epicotyl, Hypocotyl and Stem Length after Hardening plotted against Stem Damage Score after Frost (left) and Leaf Damage Score after Frost (right) in the DH population derived from a cross between DH4079 × Express617. Population was divided by vernalization requirement in two groups: 'spring' types indicated in red and 'winter' types indicated in blue. Spearman rank correlation r_S for the whole DH population (black), 'spring' (red), and 'winter' types (blue). Winter oilseed rape parent Express617 is indicated with blue square, spring-type parent DH4079 indicated with red triangle and F1 with violet circle.

Table 2.4 Spearman rank correlations between all traits from the frost tolerance experiment in the DH population DH4079 × Express617.

	After Hardening					After Frost				After Regrowth	
Trait	Number of Leaves	Vigor	Hypocotyl Length	Epicotyl Length	Stem Length	Number of Viable Leaves	Leaf Survival Rate	Leaf Damage Score	Stem Damage score	Number of Leaves	Death Rate
After Hardening											
Number of Leaves	-										
Vigor	0.41 ***	-									
Hypocotyl Length	-0.11	0.16 **	-								
Epicotyl Length	-0.00	0.30 ***	0.33 ***	-							
Stem Length	-0.07	0.28 ***	0.78 ***	0.82 ***	-						
After Frost											
Number of Viable Leaves	0.24 ***	0.13 *	-0.29 ***	-0.16 **	-0.27 ***	-					
Leaf Survival Rate	-0.11	-0.02	-0.27 ***	-0.17 **	-0.26 ***	0.90 ***	-				
Leaf Damage Score	-0.05	-0.04	0.30 ***	0.22 ***	0.32 ***	-0.91 ***	-0.92 ***	-			
Stem Damage Score	-0.03	-0.05	0.36 ***	0.37 ***	0.45 ***	-0.61 ***	-0.62 ***	0.69 ***	-		
After Regrowth											
Number of Leaves	0.22 ***	0.11	-0.29 ***	-0.25 ***	-0.34 ***	0.78 ***	0.71 ***	-0.76 ***	-0.76 ***	-	
Death Rate	-0.09	-0.09	0.35 ***	0.24 ***	0.36 ***	-0.61 ***	-0.59 ***	0.66 ***	0.84 ***	-0.81 ***	-
Number of Regrown Leaves	0.16 **	0.08	-0.23 ***	-0.25 ***	-0.31 ***	0.43 ***	0.40 ***	-0.45 ***	-0.67 ***	0.88 ***	-0.75 ***

* P≤0.10, ** P≤0.05, *** P≤0.01

Table 2.5 Spearman rank correlations between all traits from the frost tolerance experiments in the 'spring' type half of the DH population DH4079 × Express617.

	After Hardening					After Frost				After Regrowth	
Trait (only from 'spring' types)	Number of Leaves	Vigor	Hypocotyl Length	Epicotyl Length	Stem Length	Number of Viable Leaves	Leaf Survival Rate	Leaf Damage Score	Stem damage score	Number of Leaves	Death Rate
After Hardening											
Number of Leaves	-										
Vigor	0.38 ***	-									
Hypocotyl Length	-0.12	0.16	-								
Epicotyl Length	-0.04	0.23 **	0.18 *	-							
Stem Length	-0.06	0.24 **	0.73 ***	0.75 ***	-						
After Frost											
Number of Viable Leaves	0.29 ***	0.18 *	-0.28 ***	-0.10	-0.23 **	-					
Leaf Survival Rate	-0.03	0.05	-0.29 ***	-0.12	-0.27 ***	0.92 ***	-				
Leaf Damage Score	-0.13	-0.14	0.25 **	0.15	0.25 **	-0.91 ***	-0.90 ***	-			
Stem Damage Score	-0.04	-0.05	0.31 ***	0.29 ***	0.39 ***	-0.60 ***	-0.63 ***	0.69 ***	-		
After Regrowth											
Number of Leaves	0.27 ***	0.19 *	-0.34 ***	-0.24 **	-0.38 ***	0.80 ***	0.77 ***	-0.81 ***	-0.77 ***	-	
Death Rate	-0.11	-0.19 *	0.31 ***	0.14	0.29 ***	-0.61 ***	-0.61 ***	0.66 ***	0.78 ***	-0.79 ***	-
Number of Regrown Leaves	0.19 *	0.15	-0.35 ***	-0.26 **	-0.41 ***	0.44 ***	0.45 ***	-0.51 ***	-0.68 ***	0.87 ***	-0.73 ***

* P≤0.10, ** P≤0.05, *** P≤0.01

Table 2.6 Spearman rank correlations between all traits from the frost tolerance experiments in the 'winter' type half of the DH population DH4079 × Express617.

	After Hardening					After Frost				After Regrowth	
Trait (only from ‚winter' types)	Number of Leaves	Vigor	Hypocotyl Length	Epicotyl Length	Stem Length	Number of Viable Leaves	Leaf Survival Rate	Leaf Damage Score	Stem damage score	Number of Leaves	Death Rate
After Hardening											
Number of Leaves	-										
Vigor	0.45 ***	-									
Hypocotyl Length	-0.12	0.11	-								
Epicotyl Length	0.03	0.27 ***	0.38 ***	-							
Stem Length	-0.10	0.19 *	0.84 ***	0.80 ***	-						
After Frost											
Number of Viable Leaves	0.24 **	0.24 **	-0.20 *	-0.01	-0.14	-					
Leaf Survival Rate	-0.17	0.06	-0.17	-0.08	-0.13	0.87 ***	-				
Leaf Damage Score	-0.03	-0.12	0.23 **	0.11	0.22 **	-0.89 ***	-0.90 ***	-			
Stem Damage Score	-0.06	-0.16	0.32 ***	0.32 ***	0.41 ***	-0.58 ***	-0.55 ***	0.63 ***	-		
After Regrowth											
Number of Leaves	0.24 **	0.16	-0.18 *	-0.12	-0.21 **	0.72 ***	0.59 ***	-0.67 ***	-0.74 ***	-	
Death Rate	-0.14	-0.12	0.31 ***	0.19 *	0.32 ***	-0.54 ***	-0.48 ***	0.58 ***	0.85 ***	-0.80 ***	-
Number of Regrown Leaves	0.15	0.09	-0.10	-0.17	-0.18 *	0.37 ***	0.29 ***	-0.36 ***	-0.64 ***	0.89 ***	-0.77 ***

* P≤0.10, ** P≤0.05, *** P≤0.01

All traits after Frost were strongly correlated with each other, e.g. Leaf and Stem Damage Score were correlated with 0.69 (Table 2.4, Fig. 2.2). They were also strongly correlated with traits after Regrowth (Table 2.4 to Table 2.6). The Number of Regrown Leaves was negatively correlated with Leaf Damage Score with -0.45 and Stem Damage Score with -0.67 (Table 2.4). The traits Death Rate and Number of Regrown Leaves had higher correlation coefficients with Leaf Damage Sore in 'spring' types (Table 2.5) than in 'winter' types (Table 2.6). The correlation coefficients with Stem Damage Score, however, were lower in 'spring' than in 'winter' types. The traits after Regrowth showed very high correlations with each other (Table 2.4 to Table 2.6).

2.4.4 QTL Analysis

The QTL analysis could detect DNA-markers with significant associations with the variation of all assessed traits, hence putative QTL for all traits were identified. The total variance explained (TR^2) by the significant markers showed a wide range between the traits, ranging from 12.28% for Vigor after Hardening to 65.99% for Epicotyl Length after Hardening (Table 2.7). For four traits epistatic effects were detected (Table 2.8).

For the trait Number of Leaves after Hardening, five minor QTL were found explaining a total variance of 32.49%. Here, the largest QTL Leaves_H_2 was found on A09 at 26.11 cM explaining 11.25% of the phenotypic variance, and an additive effect of 0.14. For the trait Vigor only one minor QTL, Vigor_H, on A05 was found. For Hypocotyl Length six minor QTL with an explained phenotypic variance ranging from 4.20% to 9.30% were found, explaining a total of 44.18% of the phenotypic variance observed. The trait Epicotyl Length showed four minor and a major QTL explaining 65.99% of the variance. The major QTL, EpiL_H_2, was found on A07 at 101.11 cM explaining 53.01% of the phenotypic variance and had an additive effect of -0.34 cm. The negative additive effect indicates that the allele from spring-type parent DH4079 caused an increase in Epicotyl Length. Interestingly, the QTL of Hypocotyl and Epicotyl Length were not collocating. For Epicotyl Length after Hardening, two epistatic effects were detected, one between the major QTL EpiL_H_2 on A07 and the minor QTL EpiL_H_5 on C03 with an additive × additive effect of -0.05, the other between two minor QTL (EpiL_H_3 and EpiL_H_4) with an additive × additive effect of 0.05 (Table 2.8). Stem Length showed five QTL (Table 2.7). The largest, StemL_H_3, on A07 at 101.11 cM, explained 37.59% of the phenotypic variation with an additive effect of -0.45. StemL_H_3 collocated with the major QTL for Epicotyl Length, EpiL_H_2, but had a lower explained variance and a higher additive effect. The higher additive effect was caused by an underlying not significant QTL for Hypocotyl Length, which probably added to the higher phenotypic expression of Stem Length in comparison to Epicotyl Length. Two minor QTL for Stem Length collocated with two QTL for Hypocotyl Length on A01 and C05, and another on C07 at 18.4 cM was found on same linkage group as HypL_H6 at 6.7 cM. QTL StemL_H_2 on A02 did not appear in either Epi- or Hypocotyl Length. Stem Length after Hardening had an epistatic effect between minor QTL StemL_H_1 on A01 and major QTL StemL_H_2 on A02 with an additive × additive effect of 0.09 (Table 2.8).

For the traits scored after Frost, the Number of Viable Leaves showed five minor QTL and the moderate QTL Leaves_F_5 on C06 at 25.81 cM explaining 19.24% of the phenotypic

variance, which had an additive effect of 0.20 (Table 2.7). Number of Viable Leaves after Frost had two epistatic effects, one between two minor QTL, Leaves_F_1 and Leaves_F_4, with an additive × additive effect of -0.09, and between major QTL Leaves_F_5 on C06 and minor QTL Leaves_F_6 on C09 with an additive × additive effect of -0.06 (Table 2.8). The Leaf Survival Rate (Table 2.7) had a moderate QTL LSurR_F_5 on C06 at 27.91 cM explaining 26.33% of the phenotypic variance with and additive effect of 0.05, which was collocating with Leaves_F_5. Additionally, the trait showed five minor QTL, which were not collocating with the minor QTL for the Number of Viable Leaves after Frost, although some found on the same linkage group. Both traits had positive and negative effects. For Leaf Damage Score after Frost, five QTL were found which all had a negative effect, indicating that all alleles for freezing tolerance were inherited through winter oilseed rape parent Express617. The QTL Leaf_Dam_F_4 on C06 at 8.11 cM had the highest value for phenotype explained with 11.8 %. Interestingly, the three leaf traits after Frost had some collocating or close together mapping QTL on A01, A02, and C06, but showed unique QTL, too. The QTL for Leaf Damage Score could explain the least amount of the total variance with 34.87%. Stem Damage Score after Frost showed only two QTL explaining together 36.39% of the phenotypic variance, and both with negative additive effects. The major QTL, Stem_Dam_F_2, was located on C06 at 8.21 cM with an explained phenotypic variance of 27.71% and an additive effect of -0.56, collocating with QTL Leaf_Dam_F_4. Stem Damage Score after Frost had an epistatic effect between both QTL with an additive × additive effect of 0.03 (Table 2.8).

For the traits after Regrowth, Number of Leaves mapped with three minor and a major QTL, Leaves_R_2, on C06 at 13.31 cM with an explained variance of 22.92% and an additive effect of 0.43 (Table 2.7). Death Rate after Regrowth had three minor and one major QTL, DeathRate_R_2, on C06 at 8.21 cM with an explained variance of 25.12% and an additive effect of -0.08. Number of Regrown Leaves had four QTL with a total explained variance of 32.48%. The biggest QTL was NewLeaves_R_3 on C06 at 5.01 cM explaining 16.65% of the variance and having an additive effect of 0.24.

All traits after Frost and after Regrowth had their biggest QTL on linkage group C06. However, the explained variance could not explain more than 26.33%. The additive effects were therefore quite small.

Table 2.7 Quantitative trait loci mapped in the frost experiments after Hardening (for 7 weeks), after Frost (treatment for two nights at -14°C), and after Regrowth (11 days) in the DH4079 × Express617 population. A positive additive effect of a QTL is an additive effect by the allele of winter oilseed rape parent Express617.

QTLname	Chr.	Pos. [cM]	Confidence interval[a]	flanking markers of confidence interval	LOD	add. effect	R^2 [%][b]	TR^2 [%][c]
After Hardening								
Number of Leaves								
Leaves_H_1	A05	57.31	53.3 - 63.0	Bn-A05-p5770114 \ Bn-A05-p3021668	3.12	-0.10	6.12	32.49
Leaves_H_2	A09	26.11	19.4 - 33.3	Bn-A09-p1929245 \ Bn-A09-p4384911	5.83	0.14	11.25	
Leaves_H_3	C01	0.01	0.0 - 3.1	Bn-scaff_20809_1-p163800 \ Bn-scaff_15838_1-p628547	4.00	0.11	7.28	
Leaves_H_4	C03	49.61	46.8 - 53.9	Bn-scaff_22067_1-p111337 \ Bn-scaff_17298_1-p202774	4.26	0.11	7.84	
Vigor								
Vigor_H	A05	52.71	50.1 - 57.6	Bn-A05-p6739093 \ Bn-A05-p3988218	5.98	0.13	12.28	12.28
Hypocotyl Length								
HypL_H_1	A01	70.61	65.4 - 75.5	Bn-A01-p2882270 \ Bn-A01-p1966955	5.37	-0.13	8.69	44.18
HypL_H_2	A03	113.81	110.6 - 119.7	Bn-A03-p1514927 \ Bn-A03-p565187	2.97	-0.09	4.20	
HypL_H_3	A09	0.01	0 - 4.1	Bn-A09-p941202 \ Bn-A01-p26969210	3.55	0.10	5.40	
HypL_H_4	C05	45.81	43.7 - 48.8	Bn-scaff_21369_1-p380883 \ Bn-scaff_18826_1-p1037969	5.80	0.13	9.30	
HypL_H_5	C06	11.31	8.4 - 15.1	Bn-A07-p21354084 \ Bn-A07-p20251365	4.89	-0.12	7.56	
HypL_H_6	C07	6.71	3.7 - 10.7	Bn-scaff_27609_1-p6012 \ Bn-scaff_16200_1-p340573	5.77	-0.13	9.04	
Epicotyl Length								
EpiL_H_1	A05	60.51	55.1 - 65.7	Bn-A05-p5252542 \ Bn-A05-p2925195	2.83	0.07	2.18	65.99
EpiL_H_2	A07	101.11	99.5 - 102.5	Bn-A07-p21478337 \ Bn-scaff_24104_1-p344071	40.63	-0.34	53.01	
EpiL_H_3	A09	33.91	25.1 - 40	Bn-A09-p3029767 \ Bn-A09-p4447029	3.44	-0.07	2.66	
EpiL_H_4	C02	74.11	71.2 - 78.5	Bn-scaff_16269_1-p529343 \ Bn-scaff_15714_1-p118511	6.73	-0.11	5.54	
EpiL_H_5	C03	54.81	48.5 - 59.4	Bn-scaff_17521_1-p1052808 \ Bn-scaff_17298_1-p909103	3.36	0.07	2.59	
Stem Length								
StemL_H_1	A01	69.61	65.1 - 75	Bn-A01-p2882270 \ Bn-A01-p2148059	4.77	-0.17	5.43	56.65
StemL_H_2	A02	53.71	52.2 - 59.1	Bn-A02-p16520874 \ Bn-A02-p22296426	3.15	-0.14	3.49	
StemL_H_3	A07	101.11	99 - 102.9	Bn-A07-p21478337 \ Bn-scaff_24104_1-p344071	25.21	-0.45	37.59	
StemL_H_4	C05	46.31	44.8 - 48.4	Bn-scaff_15609_1-p5345 \ Bn-scaff_18826_1-p1037969	4.05	0.15	4.53	

QTLname	Chr.	Pos. [cM]	Confidence interval[a]	flanking markers of confidence interval	LOD	add. effect	R^2 [%][b]	TR^2 [%][c]
StemL_H_5	C07	18.41	18.3 - 27	Bn-scaff_15626_1-p692196 \ Bn-scaff_18202_1-p1468929	4.65	-0.17	5.62	
After Frost								
Number of Viable Leaves								
Leaves_F_1	A01	74.51	67.8 - 75.2	Bn-A01-p2569303 \ Bn-A01-p2148059	3.62	0.11	5.77	46.31
Leaves_F_2	A01	89.81	86.5 - 92.9	Bn-A01-p1453156 \ Bn-A01-p923356	2.79	0.10	4.10	
Leaves_F_3	A02	32.51	29.2 - 39.7	Bn-A02-p4761483 \ Bn-A02-p10227986	4.48	0.12	6.58	
Leaves_F_4	A09	25.11	21.1 - 29.6	Bn-A09-p1829952 \ Bn-A09-p3347911	3.82	0.11	5.56	
Leaves_F_5	C06	25.81	19.9 - 29.3	Bn-A07-p20251365 \ Bn-scaff_15763_1-p233149	11.67	0.20	19.24	
Leaves_F_6	C09	75.91	72.8 - 77.5	Bn-scaff_18100_1-p271298 \ Bn-scaff_22835_1-p327368	3.50	-0.11	5.07	
Leaf Survival Rate								
LSurR_F_1	A01	80.31	75.0 - 82.5	Bn-A01-p2291940 \ Bn-A01-p1606312	2.98	-0.02	4.30	48.93
LSurR_F_2	A02	49.01	45.4 - 52	Bn-A02-p11449348 \ Bn-A02-p16520874	4.60	-0.02	6.56	
LSurR_F_3	A07	65.11	58.6 - 67.2	Bn-A07-p10401133 \ Bn-A07-p12415736	3.19	0.02	4.30	
LSurR_F_4	C03	7.81	6.7 - 13.7	Bn-scaff_18322_1-p818265 \ Bn-scaff_19111_1-p325137	2.79	0.02	3.48	
LSurR_F_5	C06	27.91	25.3 - 29.3	Bn-A07-p19515708 \ Bn-scaff_15763_1-p233149	16.38	0.05	26.33	
LSurR_F_6	C08	96.11	94.3 - 100.2	Bn-scaff_20947_1-p127456 \ Bn-scaff_16021_1-p585766	2.94	-0.02	3.94	
Leaf Damage Score								
Leaf_Dam_F_1	A01	79.31	75.2 - 84	Bn-A01-p2291940 \ Bn-A01-p1606312	4.08	-0.16	4.96	34.87
Leaf_Dam_F_2	A02	36.61	34.8 - 37.7	Bn-A02-p6084757 \ Bn-A02-p23491463	6.68	-0.20	8.09	
Leaf_Dam_F_3	A03	34.09	29.1 – 46.4	Bn-A03-p21075664 \ Bn-A03-p15708192	4.67	-0.17	5.49	
Leaf_Dam_F_4	C06	8.11	5.1 - 9.4	Bn-A07-p22140320 \ Bn-scaff_17799_1-p1053450	9.41	-0.27	11.81	
Leaf_Dam_F_5	C06	41.31	36.7 - 42.4	Bn-scaff_15818_2-p128759 \ Bn-scaff_18439_1-p1013430	3.88	-0.17	4.52	
Stem Damage Score								
Stem_Dam_F_1	C02	100.41	98 - 103.2	Bn-scaff_15714_1-p2481342 \ Bn-scaff_15714_1-p2989937	6.17	-0.32	8.68	36.39
Stem_Dam_F_2	C06	8.21	4.3 - 9.3	Bn-A07-p22140320 \ Bn-scaff_17799_1-p1053450	17.05	-0.56	27.71	

QTLname	Chr.	Pos. [cM]	Confidence interval[a]	flanking markers of confidence interval	LOD	add. effect	R^2 [%][b]	TR^2 [%][c]
After Regrowth								
Number of Leaves								
Leaves_R_1	C02	51.91	50 - 58.2	Bn-scaff_21705_1-p375849 \ Bn-scaff_20461_1-p322463	3.92	0.23	6.12	37.83
Leaves_R_2	C06	13.31	13.1 - 18.3	Bn-A07-p20999615 \ Bn-A07-p20251365	11.89	0.43	22.92	
Leaves_R_3	C06	26.81	20.7 - 36.7	Bn-A07-p20251365 \ Bn-scaff_16510_1-p12919	2.63	0.21	4.25	
Leaves_R_4	C09	83.71	81.1 - 97.1	Bn-scaff_19436_1-p236134 \ Bn-scaff_17526_1-p860459	2.94	-0.19	4.54	
Death Rate								
DeathRate_R_1	C02	100.41	97.8 - 103.1	Bn-scaff_15714_1-p2481342 \ Bn-scaff_15714_1-p2989937	4.80	-0.05	7.59	42.71
DeathRate_R_2	C06	8.21	1.7 - 9.5	Bn-A07-p22140320 \ Bn-scaff_17799_1-p1053450	14.06	-0.08	25.12	
DeathRate_R_3	C09	81.11	76.6 - 87.8	Bn-scaff_20836_1-p261578 \ Bn-scaff_17190_1-p1119408	3.29	0.04	5.08	
DeathRate_R_4	C09	98.81	87.8 - 101.1	Bn-scaff_17487_1-p235174 \ Bn-scaff_17526_1-p860459	2.99	0.04	4.92	
Number of Regrown Leaves								
NewLeaves_R_1	C02	75.71	65.1 - 81.3	Bn-scaff_18514_1-p28001 \ Bn-scaff_15714_1-p328756	2.69	0.13	4.60	32.49
NewLeaves_R_2	C03	53.11	44.1 - 62.3	Bn-scaff_22067_1-p111337 \ Bn-scaff_17298_1-p1370828	3.27	-0.14	5.80	
NewLeaves_R_3	C06	5.01	1.3 - 9.6	Bn-A07-p22140320 \ Bn-scaff_17799_1-p1053450	8.93	0.24	16.65	
NewLeaves_R_4	C07	79.71	72.8 - 87.2	Bn-scaff_15705_1-p577327 \ Bn-scaff_16069_1-p4484876	3.16	-0.14	5.44	

a= 95% confidence interval, b= explained phenotypic variance of the QTL, c = total explained phenotypic variance over all QTL found by analysis

Table 2.8 Epistatic effects for QTL mapped in the freezing tolerance experiment for the DH4079 × Express617 population.

Trait	1st QTL	Chr.	pos. [cM]		2nd QTL	Chr.	pos. [cM]	additive × additive effect
after Hardening								
Epicotyl Length	EpiL_H_2	A07	101.1	×	EpiL_H_5	C03	54.81	-0.05
	EpiL_H_3	A09	33.91	×	EpiL_H_4	C02	74.11	0.05
Stem Length	StemL_H_1	A01	69.61	×	StemL_H_2	A02	53.71	0.09
after Frost								
Number of Viable Leaves	Leaves_F_1	A01	74.51	×	Leaves_F_4	A09	25.11	-0.09
	Leaves_F_5	C06	25.81	×	Leaves_F_6	C09	75.91	-0.06
Stem Damage Score	Stem_Dam_F_1	C02	100.41	×	Stem_Dam_F_2	C06	8.21	0.03

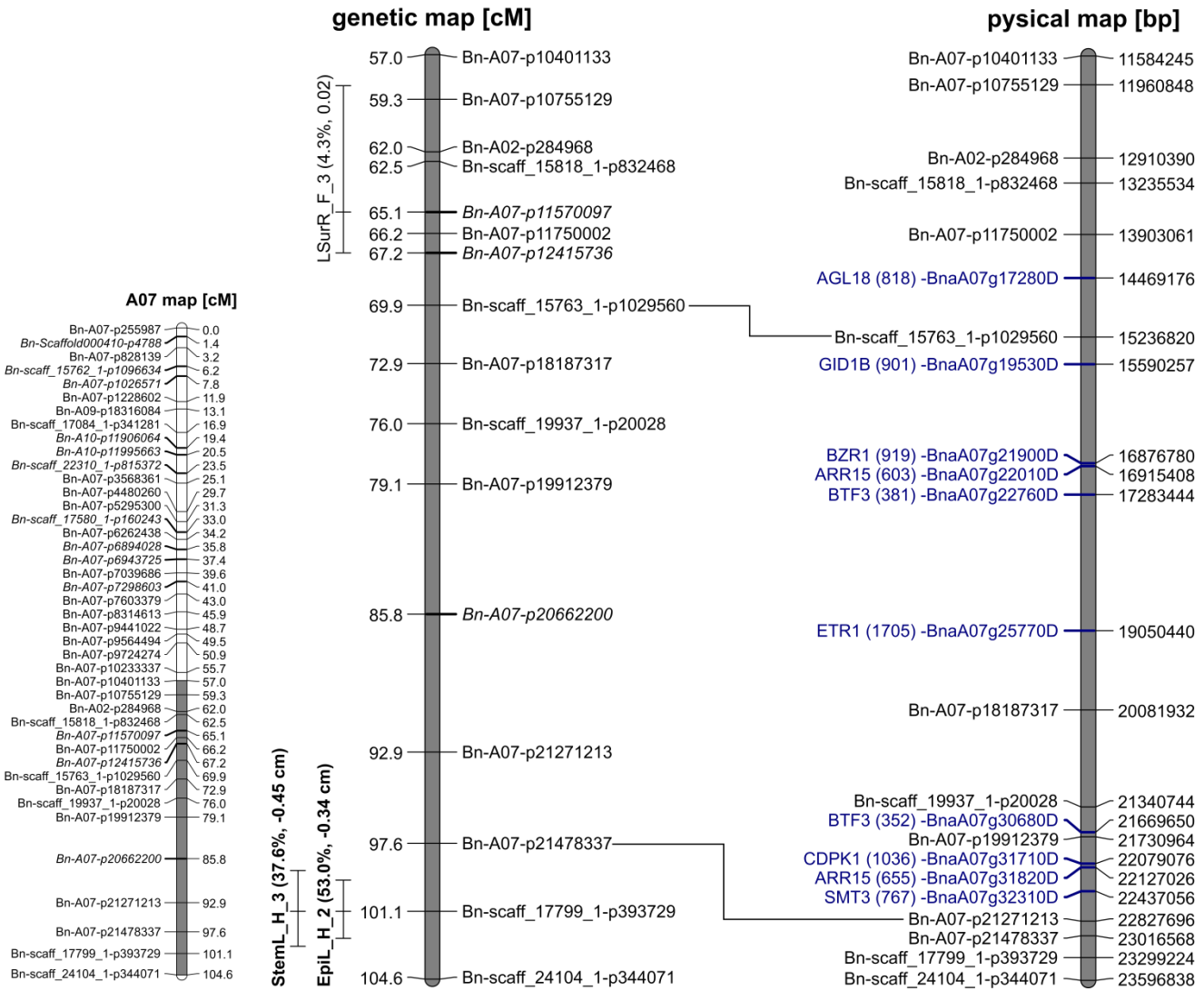

Fig. 2.4 Genetic (middle) and physical (right) maps of the QTL clusters region on A07, which marked grey in genetic map of A07 (right). QTL are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effect in days for the respective QTL are given. Candidate genes with BLAT scores (blue) and the respective gene ID in the reference genome of 'Damor-*bzh*'

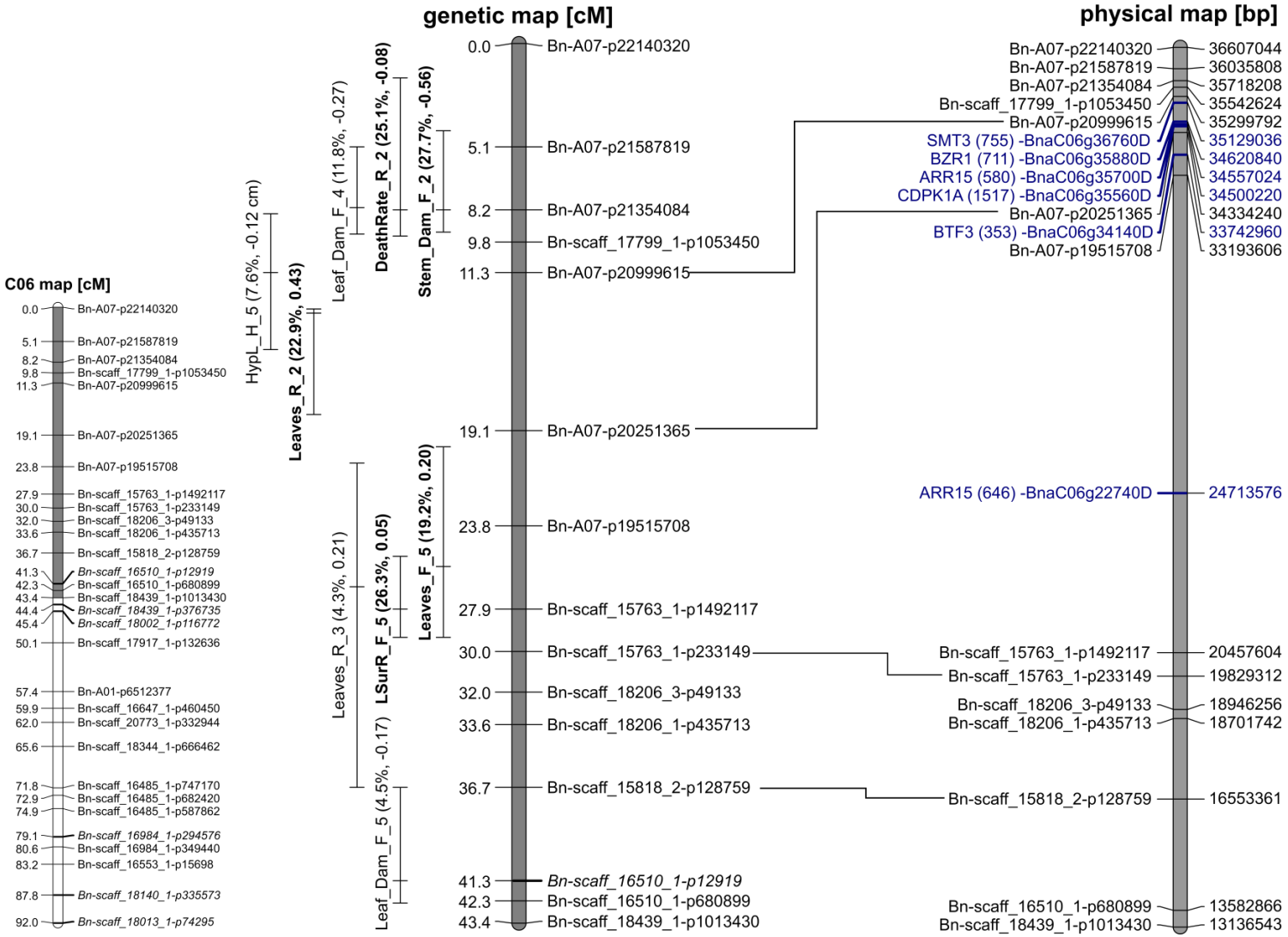

Fig. 2.5 Genetic (middle) and physical (right) map of the QTL clusters region on C06. Position of QTL cluster region marked grey in genetic map of C06 (right). QTL are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effect in days for the respective QTL are given. Candidate genes with BLAT scores (blue) and the respective gene ID in the reference genome of 'Damor-*bzh*'

2.4.5 Identification of genomic regions with clusters of collocating QTL

In two genomic regions on chromosome A07 and C06, QTL for several different traits were collocating or had overlapping confidence intervals. These QTL cluster were examined for candidate genes.

On chromosome A07, two major QTL, EpiL_H_2 for Epicotyl Length and StemL_H_3 for Stem Length, were collocating (Table 2.7). No Candidate genes known for freezing tolerance were found (Appendix F, Fig. 2.4). No traits scored after Frost or after Regrowth had QTL located on A07, except a minor QTL for the Leaf Survival Rate, which was located 35 cM apart from this cluster (Fig. 2.4).

On chromosome C06, nine QTL were mapped in the region between 1.7 and 42.4 cM. All traits scored after Frost and after Regrowth had the QTL explaining the largest part of their phenotypic variance mapped in this region (Table 2.7, Fig. 2.5). Between 1.7 and 9.5 cM on C06 the QTL Stem_Dam_F_2 and Leaf_Dam_F_4, both traits that score freezing damage after Frost, as well as DeathRate_R2 for Death Rate after Regrowth mapped. No Candidate genes from our candidate gene list for freezing tolerance were found (Appendix F, Fig. 2.5). Those three QTL had an overlapping confidence interval with minor QTL HypL_H_5 for Hypocotyl Length. HypL_H_5 had an overlapping confidence interval with the major QTL Leaves_R_2 for Number of Leaves after Regrowth. These two QTL had the candidate genes *STEROL METHYLTRANSFERASE 3* (*SMT3*), *BRASSINAZOLE-RESISTANT 1* (*BZR1*), *ARABIDOPSIS THALIANA RESPONSE REGULATOR 15* (*ARR15*) and *CALCIUM-DEPENDEND PROTEIN KINASE 1A* (*CDPK1A*) (Appendix F, Fig. 2.5).

Between 19.9 and 36.7 cM on chromosome C06 the minor QTL Leaves_R_3 for Number of Leaves after Regrowth, which is a trait that includes the Number of Viable Leaves after Frost, unless some died of other causes like wilting. This QTL had a huge confidence interval, which overlapped with the two major QTL, Leaves_F_5 for Number of Viable Leaves after Frost and LSurR_F_5 for Ratio of Frozen Leaves after Frost. All three QTL share the candidate gene *ARR15*. Leaves_F_5 and Leaves_R_3 also share *BASIC TRANSCRIPTION FACTOR 3* (*BTF3*) as a candidate gene (Appendix F, Fig. 2.5).

2.5 Discussion

2.5.1 How to best phenotype freezing tolerance

Freezing tolerance is a highly complex trait, and researchers try to find adequate and efficient approaches and techniques to score or quantify it (Fiebelkorn and Rahman 2016; Rapacz et al. 2015; Waalen et al. 2011). The traits used in this study were critically examined for their methodology in the following paragraph.

The leaves were counted in every stage of the freezing tolerance experiment in an attempt to have a quantifiable trait instead of a score. Since a higher number of leaves before Frost will influence the absolute number of surviving leaves, the Number of Viable Leaves after Frost and the Number of Leaves after Regrowth were used to calculate the relative traits Leaf Survival Rate and Number of Regrown Leaves, respectively (Table 2.1). Since the two absolute traits and the two relative traits showed differences in their correlations (Table 2.4) and their detected QTL (Table 2.7), all traits were included in the analysis.

Leaf Survival Rate and Leaf Damage Score are the two traits that exclusively focus on freezing tolerance of the leaves. In contrast to Leaf Survival Rate, Leaf Damage Score was an estimate for the relative number of leaves which survived frost, scored on a scale from 1 to 9 (Table 2.1), which is a faster procedure than counting leaves, but results in an estimate. They both showed a heritability of 68% (Table 2.2). Leaf Damage Score had slightly higher correlations with the other traits than Leaf Survival Rate (Table 2.4). In the QTL analysis, the trait Leaf Survival Rate showed six QTL with a total explained variance of 48.9 %, while Leaf Damage Score only showed five QTL explaining 34.87% of the variance (Table 2.7). The two traits showed only one pair of collocating QTL on A01 and two other, which were located in close vicinity in the QTL analysis on A02 and C06 (Table 2.7, Appendix B), but upon further investigations, the traits had non-significant QTL collocating on chromosomes A03, A07, A09, C02, C03 and C09 (data not shown). While the QTL analysis was more successful for Leaf Survival Rate, the qualitative trait Leaf Damage Score showed higher correlations. These traits gave different results, although they should have been very similar, since they both examined the relative number of loss in leaves (Table 2.1).

Three traits implicated freezing damage that might be lethal and therefore indicate the survival of the plant after freezing damage: Stem Damage Score, Death Rate and Number of Regrown Leaves. They each show different facets on freezing tolerance and have possible drawbacks. Stem Damage Score was purposefully designed such that a score of 5 or 6 accounted for a stem frozen through the diameter of the epi- or hypocotyl (Table 2.1). The intention here was to indicate severity of the damage as well as probability of survival. In retrospect, it may be questioned whether the combination of those aspects into one trait was an adequate decision with subsequently well-founded results. It was the only trait recorded after Frost not related to the leaves. Death Rate after Regrowth was recorded as a binary trait, 10 days after the frost treatment (Table 2.1). A clear assessment of death or survival of the plant was somewhat difficult at that early time point, but pre-experiments showed that other factors than frost might influence survival of the plantlets, if the regrowth period was dragged out longer than 10 days. The greenhouse used for regrowth was not extensively temperature controlled, so conditions between repetitions varied. The dead plant material facilitated the growth of mold, which might have influenced the plants regrowth. These troubles and the absoluteness of a binary trait might make this trait more prone to experimental errors. In contrast to Stem Damage Score after Frost and Death Rate after Regrowth, which were scores based on more or less subjective observations, the Number of Regrown Leaves was based solely on quantifiable traits (Table 2.1). A plant should not be able to regrow when severely damaged by frost. However, when the shoot apical meristem of the rapeseed plantlet is damaged by frost, the plant has the ability to grow new shoots from the axial meristems. But activating axial meristem might take longer than 10 days and such survival would therefore not be recorded with this trait. The heritabilities showed that Stem Damage Score was the most stable of these three traits with 74%, followed by Death Rate with 62%, while Number of Regrown Leaves had only a heritability of 50% (Table 2.2). Number of Regrown leaves was not significantly different between the parents, Death Rate was only significant with $P \leq 0.10$ and Stem Damage Score with $P \leq 0.05$ (Table 2.3). The QTL analysis of the trait Death Rate had the highest total phenotypic variance explained with a

TR^2 of 42.71%. Stem Damage Score had a TR^2 of 36.39%, and Number of Regrown Leaves had a TR^2 of 32.49% (Table 2.7). The Number of Regrown Leaves was introduced as a good quantitative measure for frost survival. The Number of Regrown Leaves was significantly negatively correlated with the traits Leaf Damage Score, Stem Damage Score and Death Rate ($-0.45 \leq r_S \leq -0.75$ Table 2.4). In comparison to Number of Regrown Leaves, Stem Damage Score and Death Rate were more stable traits with higher heritabilities, showed significant differences between the parents, and resulted in a meaningful QTL analysis. On the other hand, the correlation with Vigor and Number of Leaves after Hardening showed it might have been more influenced by growth factors. The Number of Leaves after Hardening was significantly correlated with the Number of Regrown Leaves, but with a low coefficient of 0.16 (Table 2.4). On chromosomes C02 and C03 QTL for Number of Regrown Leaves had overlapping confidence intervals with QTL for Number of Leaves after Hardening and/or Epicotyl Length (Table 2.7). In conclusion, while Number of Regrown Leaves is quantifiable, it seems to be influenced more by growth factors, which are also responsible for the state of the plant before the frost event. Therefore this trait might be more closely related to winter hardiness and field survival, than the scores of frost damage shortly after the frost treatment. Waalen et al. (2011) measured the number of surviving plants as well as shoot regrowth in percentage of control three weeks after the end of the frost treatment. They concluded that shoot regrowth included the survival rate and the vigor of the plant. In their opinion shoot regrowth is therefore a better trait to estimate survival in the field.

Finding a good system to phenotype freezing damage is very difficult as it is a complex trait which is regulated by a complex gene network (Guo et al. 2018; Rapacz et al. 2015). It is advisable to score many separate aspects of freezing damage in order to increase heritability and effectiveness of QTL analyses and to find traits covering different aspects of frost tolerance.

2.5.2 Are frost damage on the leaves and frost damage on the stem two different traits?

A lot of studies estimate freezing tolerance through electrolyte leakage or chlorophyll fluorescence in the leaves. Also, most transcriptomic studies analyzed only leaf samples (He et al. 2019; Ke et al. 2020; Wei et al. 2021). While the reception of abiotic signals might well take place in the leaves, the protection of the stem is more important for the survival of the plants. In the field, the leaves of winter oilseed rape often freeze off completely and the plant often recovers afterwards by growing new leaves from the shot apical meristem during more favorable conditions. Plants with damaged shoot apex can even grow a new shoot from the axillary meristems. However, most phenotyping does not differentiate between freezing on stem or leaf and often score freezing damage by mixing leaf damage and death (Huang et al. 2018) or only estimate freezing tolerance in the leaves by electrolyte leakage or chlorophyll fluorescence, or simply state plant survival or regrowth.

Therefore the question stands if freezing damage on the leaves and stem is comparable or of different extent. If the latter is true, researching freezing tolerance by only surveying the leaves might not be adequate to conclude on the freezing tolerance of the whole plant. In this

study, damage on the leaves and damage on the stem were scored separately, to test if and how they are connected.

In the ANOVA the heritability of Leaf Damage Score was 68% and the heritability of Stem Damage Score was 74% (Table 2.2). Leaf Damage Score and Stem Damage Score were correlated with a correlation coefficient of 0.69. This correlation does not change much between 'spring' and 'winter' types (Table 2.4 to Table 2.6, Fig. 2.2). The QTL analysis could only explain a total of 34.9% of the observed phenotypic variance (TR^2) for Leaf Damage Score and 36.39% for Stem Damage Score. Their respective main QTL were collocating on C06 and had an explained phenotypic variance of 27.7% for Stem Damage Score (Stem_Dam_F_2) and 11.8% for Leaf Damage Score (Leaf_Dam_F_4). Additive effects of all QTL for both, Leaf Damage Score and Stem Damage Score, were always negative meaning that the winter oilseed rape parent Express617 alleles are causing freezing tolerance in either part of the plant.

Since only one QTL for each, Leaf Damage Score and Stem Damage Score, was collocating, but the correlation between the two traits was so high, the traits were examined for non-significant QTL (Appendix G). The QTL Stem_Dam_F1 on C02 was collocating with a non-significant QTL for Leaf Damage Score. A few more regions could be found where Leaf and Stem Damage Score had collocating, but non-significant, QTL; both traits had non-significant peaks each on C08 between 65 and 72 cM, as well as on C09 between 78 and 82 cM (Appendix G). The LOD Scores ranged between 1.35 and 2.28. The additive effects were positive or negative, while all recorded significant QTL had negative additive effects (Appendix G, Table 2.7).

Overall, both traits can be considered as very stable, since they had a high heritability. They were highly correlated and their main QTL was collocating. Therefore, the same or similar mechanisms may protect all parts of the plant above ground.

However, there were also observed differences. Stem Damage Score had higher values for heritability and total variance explained by the QTL analysis. Even though the QTL analysis explained less phenotypic variance for Leaf Damage Score than for Stem Damage Score, the former had five QTL mapped while the latter had only two (Table 2.7). Both QTL for Stem Damage Score were found to collocate with Leaf Damage Score QTL (see above). The QTL for Leaf Damage Score (Leaf_Dam_F_1, Leaf_Dam_F_2, Leaf_Dam_F_3, Leaf_Dam_F_5) had no collocating significant QTL with Stem Damage Score. Examining for non-significant QTL collocating with these QTL only resulted in a QTL for Stem Damage Score on A02 at 54.7 cM, while Leaf Damage Score QTL Leaf_Dam_F_2 mapped at 36.6 cM, and close by QTL LSurR_F_2 for Leaf Survival Rate mapped in between at 49.0 cM (Appendix G).

Additionally, the Number of Regrown Leaves was negatively correlated with Leaf Damage Score (-0.45) and Stem Damage Score (-0.67, Table 2.4). That the latter was higher supports the hypothesis that damage on stem is more relevant to the survival of the plant and therefore the regrowth process. Also Leaf Damage Score showed lower correlation coefficient with Death Rate and Number of Regrown Leaves in 'winter' (0.58 and -0.36) than 'spring' types (0.66 and -0.51), but Stem Damage Score showed higher correlation coefficients of with Death Rate and Number of Regrown Leaves in 'winter' (0.85 and -0.64, Table 2.6) than 'spring' types (0.78 and -0.68, Table 2.5).

The QTL analysis (Table 2.7) revealed that loci can be general for freezing tolerance or specific to freezing tolerance of leaves. But the striking difference in the correlation of Number of Regrown Leaves and Leaf Damage Score between 'spring' and 'winter' types, might be the biggest indicator that freezing tolerance of the leaves is not a good indicator of chance of survival. Especially the 'winter' types, genotypes with high vernalization requirement, seem more resistant to freezing of the leaves in their ability to survive the frost events. Markowski and Rapacz (1994) compared the vernalization requirement of 14 rapeseed lines with leaf area injury seven days after frost treatment and plant survival rate 14 days after frost treatment. When correlating the presented data, we could find a moderate correlation between vernalization requirement and leaf area injury, but no correlation with plant survival rate (Appendix H). On the other hand, Waalen et al. (2011) found shoot regrowth and visual injury rating highly correlated in winter *Brassica napus* and *B. rapa*. In conclusion, freezing damage on leaves and on stem should be regarded as separate traits as freezing susceptible leaves might not indicate freezing susceptibility of the whole plant and especially plant survival after a frost event.

2.5.3 Transgression

In breeding transgression is a welcome phenomenon as it allows the breeder to find stronger genotypes than before. For example, Teutonico et al. (1995) observed in a DH population from the cross Major × Stellar that F1 and 77% of the DH Lines were more frost tolerant than both parents. For some analyzed traits we could observe transgression.

For Leaf Damage Score no significant differences between the extreme genotypes and the respective parent were found. All additive effects of the QTL for this trait were negative, meaning all alleles for freezing susceptibility were inherited from the spring-type parent, so no transgression was expected. Interestingly, for Leaf Survival Rate the extreme genotype with the maximum value, ergo the freezing tolerant DH line, shows a highly significant difference to Express617 with a value of 0.10 or 10% more viable leaves. Six QTL were found in the QTL analysis, three with positive and negative effects each. As a result of both parents having alleles that increase Leaf Survival Rate, transgression occurs. Stem Damage Score showed a significant difference between the extreme genotype with the maximum value and DH4079, meaning transgression towards freezing susceptibility, although only two QTL with negative effects were found. Unfortunately, freezing susceptibility is not relevant for breeding.

For the traits after Regrowth, transgression can be observed, except for the extreme genotype with lowest Death Rate. The QTL analysis showed minor QTL with both negative and positive effects, ergo alleles from both parents contributed to the traits. The QTL analysis also showed non-significant QTL for traits after Frost and Regrowth (data not shown). This explains the low value for the total variance explained from the QTL analysis in comparison to the heritability. It also adds to the number of possible QTL. As expected, it shows how polygenic the trait of freezing tolerance is.

On the one hand polygenic traits would make breeding easier since transgression occurs frequently in crossings, on the other hand the low phenotypic variance explained makes it hard to breed a very frost hardy genotype, since many loci have to be considered, but

freezing tolerance is not considered a major breeding goal in temperate Europe. Parts of the world with more harsh winters mostly choose to grow spring rapeseed.

2.5.4 How does growth during cold acclimation influence freezing tolerance?

2.5.4.1 Influence of Vigor and Number of Leaves after Hardening

The question, if Vigor has an impact on freezing tolerance, arose after observing winter oilseed rape parent Express617 being significantly more vigorous as well as more freezing tolerant than DH4079. Since growth and vigor were observed in the past to positively influence freezing tolerance, this is a valid hypothesis (Hurry et al. 1995). The means of 'spring' and 'winter' types showed a difference of only 0.1 for Vigor (Table 2.3). Vigor was also not correlated with any freezing tolerance trait when looking at the entire DH population (Table 2.4). There was a weak correlation between Death Rate and Vigor in 'spring' types of -0.19. The QTL analysis only revealed one QTL for Vigor on A05. No traits scored after Frost or Regrowth showed QTL in this region. This indicates no connection between vigor and frost tolerance.

The phenotypic variance of Vigor after Hardening explained by the QTL analysis was only 12.3% (Table 2.7), even though the heritability of Vigor was 74% (Table 2.2). Vigor is a trait recorded by the scientist through scoring, not through a quantitative measurement, and is comprised of a broad spectrum of growth characteristics encompassing leaves as well as stem. Even though the scoring was stable, as indicated by the heritability, it might have been too broad to result in significant QTL and correlations with other traits. Instead of a general trait like Vigor, scientists should concentrate on more specific traits. This might be a reason why this trait was not able to predict freezing tolerance. It should be noted that all plants were well established.

Number of Leaves after Hardening was moderately correlated to Vigor and only showed a correlation with traits after Frost and Regrowth that also used an absolute Number of Leaves (Number of Viable Leaves after Frost, Number of Leaves after Regrowth and Number of Regrown Leaves). They were not correlated with traits that showed the relative number of surviving leaves, like Leaf Survival Rate and Leaf Damage Score, or other traits after Frost or Regrowth. The correlation between Number of Leaves after Hardening and Number of Regrown Leaves might be explained by the hypothesis that the same growth factors enhancing growth before frost treatment are also responsible for higher regrowth ability.

The QTL analysis shows that growth traits are connected: The Number of Regrown Leaves is correlated with Number of Leaves (Table 2.4), and in 'spring' types also with Vigor (Table 2.5). One QTL found on C03 (NewLeaves_R_2) had an overlapping confidence interval with a QTL Number of Leaves after Hardening and Epicotyl Length (Leaves_H_4, EpiL_H_5); and another QTL on C02 (NewLeaves_R_1) had an overlapping confidence interval with a QTL for Epicotyl Length (EpiL_H_4), too (Table 2.7, Appendix B). The QTL Vigor_H on A05 also had an overlapping confidence interval with minor QTL for Epicotyl Length (EpiL_H_1, Table 2.7, Appendix B).

The protection of photosynthesis apparatus, the ability to halt development, and the rate of growth under low temperatures have been argued to have a large influence on freezing

tolerance (Guo et al. 2018; Rapacz and Chilmonik 2000). For *Brassica napus*, Hurry et al. (1995) showed that growth, sugar accumulation and photosynthesis rates were decreased in spring type rape cv. ‘Paroll’ compared to Winter oilseed rape cv. ‘Tor’ under cold hardening conditions. The authors concluded that the plants ability to respond to cold temperature by increasing enzyme and metabolite levels is an important trait to keep growth in cold conditions. The results of Ke et al. (2020) strengthen this hypothesis. They compared the transcriptome of a winter type and semi-winter type after 7 days of cold acclimation and found that genes involved in basic biological processes like DNA replication and translation were more significantly downregulated, inhibiting these processes, in the semi-winter type than in the winter type.

The study of Rapacz et al. (2001), which is similar to Hurry et al. (1995) but with two different cultivars, confirmed that the reduction of freezing tolerance corresponds with the reduction of soluble sugars and higher water content in the roots and the elongated stem, however, they could not reproduce the difference in photosynthesis rate, claiming different methods as a factor. Rapacz et al. (2001) also observed the development of larger leaves in spring type ‘star’ between six and eight weeks, as well as epicotyl elongation, while freezing tolerance went down. Between Number of Leaves after Hardening and Vigor in ‘spring’ types a lower correlation was observed (0.38, Table 2.5), than for ‘winter’ types (0.45, Table 2.6), which could mean larger leaf size. Also there was a weak correlation between Death Rate and Vigor in ‘spring’ types of -0.19. Waalen et al. (2011) could not find significant correlation between leaf number and plant survival or freezing tolerance.

We could not confirm a connection to high vigor or number of leaves and an increased or decreased freezing tolerance of leaves or stem. There is evidence to study leaf size after hardening in ‘spring’ types. This might be connected to the conclusion from 2.5.2, where we established that ‘spring’ type survival is more reliant on freezing damage of the leaves than in ‘winter’ types. If a researcher is more interested in regrowth ability, growth during cold is a good starting point for further research.

2.5.4.2 Influence of stem elongation after Hardening

The three stem length traits, on the other hand, were all significantly correlated with all traits after Frost and Regrowth (Table 2.4). The weakest correlation was -0.16 between Epicotyl Length and Number of Viable Leaves after Frost and the strongest between Stem Damage Score and Stem Length was 0.45. The correlation of Stem Damage Score with Epicotyl Length was 0.36 and with Hypocotyl Length 0.37. In conclusion, a longer stem, irrelevant if caused by elongation in hypo- or epicotyl, made the plant more susceptible to freezing damage. We will therefore focus more on Stem Length after Hardening. Interestingly, in 'winter‘ types Stem Length had no longer significant correlations with Leave Survival Rate and the Number of Viable Leaves after Frost (Table 2.6, Fig. 2.3). The correlation between Stem Damage Score and Stem Length were however always significant.

Waalen et al. (2011) tested seven *Brassica napus* cultivars for freezing tolerance. They measured the crown height over ground level before the frost treatment with 1.3 cm height for the semi-dwarf and 1.5 cm height for the traditional cultivar ‘Californium' up to 2.4 cm for the Hybrid 'Kronos'. But no correlation with freezing tolerance was found. Rapacz and

Chilmonik (2000) observed that spring types became frost susceptible in late winter and early spring, when they also elongated their shoot. However, they also observed higher susceptibility to frost in the two winter types tested, without observing stem elongation. We conclude therefore, that stem elongation seems not to be the only factor. Rapacz et al. (2001), who observed the development of larger leaves in spring type 'star' between six and eight weeks, while freezing tolerance went down as mentioned earlier, also observed that between four and six weeks, spring type started elongating the epicotyl. The reduction of freezing tolerance corresponded with physiological changes like the reduction of soluble sugars and higher water content in the roots and the stem, as well as morphological changes, that is, bigger leaf size and stem elongation. They concluded, that freezing tolerance starts to reduce, when plant enters generative phase.

In the QTL analysis, Epicotyl Length and Stem Length after Hardening showed their major QTL collocating on A07, while all traits after Frost and after Regrowth showed their major QTL on C06. Only Hypocotyl Length showed a QTL HypL_H_5 on C06 with an overlapping confidence interval with traits after Frost (Fig. 2.5). Except Number of Regrown Leaves, traits regarding freezing tolerance and traits regarding stem elongation have no collocating QTL on other chromosomes in the whole genetic map (Appendix B). This is surprising, since it contradicts the correlation seen in our data and the general knowledge of plants with elongated stem being susceptible to freezing damage.
The two regions on A07 and C06 are, however, homologous as discussed in chapter 1 (Chalhoub et al. 2014). It might be the case in other cultivars, that these homologous regions are utilized different, than in this DH population. We could not find any reported QTL in this region.
When examining for non-significant QTL (Appendix G), Stem Damage Score had peaks on A01, A02, A03 and A09 with LOD scores between 1.2 and 1.9, which were located close to significant QTL of either Hypocotyl Length, Epicotyl Length or Stem Length. Additionally, on C08 a non-significant QTL for Stem Damage Score at 71.3 cM with an LOD of 1.9 and a non-significant QTL for Epicotyl Length at 80.5 cM with a LOD of 2.4 were located. Together these non-significant QTL for Stem Damage Score would add 10.7 % to the total of explained variance TR^2 (Appendix G).
All things considered, the non-significant QTL can give more evidence of a genetic connection between stem elongation and Stem Damage Score. Since Stem Damage Score specifically and frost tolerance at large are highly quantitative traits it can be concluded that our QTL analysis did not have the resolution power to gain more significant QTL.

2.5.5 QTL for freezing tolerance: Novel freezing tolerance region on C06

Interestingly, all QTL for Stem Damage Score and all traits after Regrowth were found on the C genome. All traits after Frost had their major QTL on C06. For the QTL Leaf_Dam_F3, DeathRate_R_2 and Stem_Dam_F_2 located between 0 and 9.8 cM (Fig. 2.5) no candidate genes from our list of candidate genes (Appendix F) could be found. Since freezing tolerance is such a complex trait with a complex gene network (Eremina et al. 2016; Guo et al. 2018;

Ke et al. 2020), it would not be surprising if this list was incomplete and potentially candidate genes were overlooked. Many might not have been discovered yet.

The QTL HypL_H_5 and Leaves_R_2 were located between 8.2 and 19.1 cM. The respective traits Hypocotyl Length and Number of Leaves after Regrowth were more connected to growth, yet many freezing tolerance genes were found in this region. BRASSINAZOLE-RESISTANT 1 (BZR1) is part of the brassinosteroid stress response and has a well-known role in freezing tolerance (Lv and Li 2020; Ye et al. 2019). In the stress response it is also able to influence growth (Lv and Li 2020). STEROL METHYLTRANSFERASE 3 (SMT3) acts at the point where sterol biosynthesis branches from brassinosteroid biosynthesis. Sterols are important for plant development, since it influences all cell division and expansion, but also as components of the plasma membrane, where they influence the membranes stability during freeze-induced dehydration (Carland et al. 2010; Webb et al. 1995). Calcium-Dependent Protein Kinases (CDPKs or CPKs) are part of the signaling cascades for abiotic stress response and often influence growth (Atif et al. 2019; Shi et al. 2018). The candidate gene is encoding CDPK1A (also CPK30), which is part of the nutrient-growth network as early part in the nitrate-CPK-NLP signal cascade, however it is more involved in root growth (Liu et al. 2017). *ARABIDOPSIS THALIANA RESPONSE REGULATOR 15* (*ARR15*) is another candidate gene for Hypocotyl Length QTL HypL_H_5 and Number of Regrown Leaves QTL Leaves_R_2. *ARR15* is positively controlled by cytokinin and fulfills diverse role in growth regulation at the meristem, including in early development (Ren et al. 2009; Su et al. 2014). All those Candidate genes for freezing tolerance could therefore very well be responsible for these QTL, however, since genes for growth were not explicitly considered, there might be more.

Another region between 19.9 and 36.7 cM contains the QTL Leaves_R_3 for Number of Leaves after Regrowth, QTL LSur_F_5 for Leave Survival Rate, and QTL Leaves_F_5 for Number of Leaves after Frost (Fig. 2.5). Their candidate gene is another copy of ARR15, located 9843.4 kbps away from the previous discussed copy. Therefore *ARR15* is a candidate gene for QTL related to growth as well as freezing tolerance. *ARR15* expression is increasing freezing tolerance and can be negatively regulated by ethylene (Shi et al. 2012). The candidate gene ARR15 is located at 24,714 kbp. In their transcriptomics analysis Ke et al. (2020) found BnaC06g22430D located on C06 at 24,474 kbp, a gene coding for bZIP transcription factor 44, which is involved in photosynthesis. The two QTL Leaves_F_5 and Leaves_R_3 also have *BASIC TRANSCRIPTION FACTOR 3* (*BTF3*) as candidate gene at the end of their confidence interval. BTF3 is phosphorylated by cold regulated OPEN STOMATA 1 (OST1). After phosphorylation it stabilizes CBF, the central transcription factor responsible for the expression of many *COR* genes (Ding et al. 2018).

On A07 between 58.6 and 67.2 cM the QTL LsurR_F_3 for Leaf Survival Rate is located. This corresponds to 13.2 to 13.9 mil bp in the physical map (Fig. 2.4, Table 2.7). In this region found a significant SNP at 13.5 million bp for freezing tolerance in their rapeseed diversity set. Similarly, a QTL for Death Rate (DeathRate_R_4) on C09 at 98.8 cM in this study (Table 2.7, Appendix B), Wrucke et al. (2019) found a significant SNP at 4.9 million bp. Although they found a large number of significant markers only two of those have positions with the QTL found in this study.

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3 Interrelation of freezing tolerance, growth regulation and flowering time regulation in *Brassica napus* L.

3.1 Abstract

Both flowering time regulation and freezing tolerance rely on the plants ability to sense temperature and day length. Resources have to be allocated efficiently in order to prepare for frost events or to time flowering in a way that insures a successful propagation. Previously, a DH population derived from a cross DH4079 × Express617 of spring and winter oilseed rape was researched in three different experiments for 1) vernalization dependent flowering time, 2) day length and temperature dependent flowering time, and 3) freezing tolerance under climate chamber conditions. Quantitative trait analysis was applied with a SNP-based marker map. Here the results from the freezing tolerance experiment (3) were joined with the results the vernalization experiment (1) and the day length and temperature experiment (2). Vernalization requirement was long discussed to have an influence on freezing tolerance. The results show that the major QTL causing phenotypic differences in the DH population is not responsible for freezing tolerance, but a minor QTL for vernalization response on C02 collocated with QTL for freezing tolerance. On chromosome C06 a QTL for flowering time under short day conditions and QTL for freezing tolerance clustered together. Unexplainably, plants with delay in flowering time under short day conditions were found to be more sensitive to freezing. Traits characterizing growth state and constitution of the plant were found to be correlated with flowering time.

3.2 Introduction

In winter oilseed rape two aspects are said to influence winter hardiness: first, whether the rosette plant starts to elongate its internodia, also known as bolting and a sign for entering the generative phase, and second, the plants vernalization requirement, which is the need of a prolonged cold period to initiate flowering. In the previous chapter the relation between stem elongation and freezing tolerance in a DH population from a cross between German winter oilseed rape Express617 and spring-type rape DH4079 derived from Swedish cultivar Topas was examined, and it was found that the exposure of hypocotyl and epicotyl through elongation was highly correlated with the observed freezing damage, but the QTL analysis lacked evidence of a common genetic cause. This chapter will examine the correlation between flowering time in dependence of vernalization and freezing tolerance in more depth than previously in chapter two.

The literature on this topic is conflicting, but pointing more toward no influence of vernalization requirement on freezing tolerance in *Brassica napus*. While in older varieties, which were released in the 1970, correlation between vernalization requirement and freezing tolerance was found, the correlation was missing in double low cultivars from the 1990 (Rapacz and Markowski 1999). Markowski and Rapacz (1994) showed several winter oilseed rape DH lines with low vernalization requirement and high freezing tolerance and vice versa. Rapacz and Chilmonik (2000) concluded that vernalization requirement is not necessary for a successful cold acclimation, but for maintaining frost resistance through the winter. Waalen et al. (2014) showed that vernalization saturation was reached long before freezing tolerance

decreased and suspected an influence of day length on the ability to maintain freezing tolerance in their discussion. Molecular genetic studies in *Arabidopsis thaliana* could not show a connection between vernalization requirement and freezing tolerance, either (Bond et al. 2011), and point to a connection between flower initiation by circadian rhythm and freezing tolerance (Fornara et al. 2015). Circadian rhythm and photoperiod are known to influence various stress responses, including cold acclimation (Eremina et al. 2016; Roeber et al. 2021). Cold acclimation and freezing tolerance is often regulated by phytohormones (Eremina et al. 2016), which also influence growth and development.

The DH population Express617 x DH4079 showed an important freezing tolerance QTL cluster on C06 (chapter 2.5.5), coincidently in the same region as a QTL cluster regarding traits for flowering time under short days (chapter 1.5.2). To investigate this further, this study does not only examine the connection of freezing tolerance with vernalization requirement, but also the influence of day length on flowering time, freezing tolerance, and growth under cool temperatures and speculates how these regulatory networks might be intertwined.

3.3 Material and Methods

3.3.1 Plant material

The inbred line 617 of the winter oilseed rape cultivar Express (Norddeutsche Pflanzenzucht Hans-Georg Lembke KG) and the doubled haploid line DH4079 (Ferrie 2003) of the Swedish spring-type cultivar Topas were crossed to generate F1 seeds. From clonally propagated F1-plants a DH population consisting of originally 200 lines was developed as described in Valdés et al. (2018).

3.3.2 Previous Phenotyping of the DH Population

The DH population was tested in three separate experimental setups: 1) the vernalization experiment, where the plants were vernalized for 8, 4 and 0 weeks and days to flowering were recorded. The DH population showed a bimodal segregation for days to flowering without vernalization, and therefore for vernalization requirement, the population was divided in half to form two groups referred to as ‘spring’ and ‘winter’ types (see chapter 1, Appendix A). 2) In the day length and temperature experiment the plants were vernalized for nine weeks and grown in four different conditions (long day or short days and 11°C or 22°C) and days to flowering were recorded (LD11, SD11, LD22, SD22). The effect of day length differences was calculated by subtraction DTF under long days from DTF under short days in the same temperature (SD-LD11 and SD-LD22) and effect of temperature differences was calculated by subtracting DTF under 22°C from DTF under 11°C under the same day length (11-22LD and 11-22SD). The results of these two experiments (1 and 2) were presented in chapter one. 3) In the freezing tolerance experiment the plants were hardened for seven weeks and subjected to two frost nights of -14°C. Several traits were recorded after Hardening, after Frost treatment, and after Regrowth. The results were presented and discussed in chapter two.

3.3.3 SNP-Markers used to characterize the population

In the first chapter it was shown, that the DH population showed a bimodal segregation for days to flowering without vernalization, and therefore for vernalization requirement. The

population was divided into two groups referred to as ‘spring’ and ‘winter’ types by the median of the trait days to flowering after 8 weeks of vernalization.
Here the Population was also divided by markers on A07 (Bn-A07-p21478337) and C06 (Bn-A07-p21354084). The haplotypes are denoted with capital letter of the genome (A or C) and in subscript the allele. The spring-type parent allele was denoted as DH, while the winter oilseed parent allele was denoted as Ex. The number of DH lines in each group were $A_{DH}C_{DH}$ =75, $A_{DH}C_{Ex}$ =24, $A_{Ex}C_{DH}$ =25, $A_{Ex}C_{Ex}$ =52. The haplotype of each genotype can be viewed in Appendix D.

3.3.4 Statistical analysis

Statistical analysis was performed in R (R. Core Team 2019). Correlations were calculated with Spearman method (r_S) and a t-test without adjusted p-values was performed to test for the significance of the correlation using package “psych” (Revelle 2019). Figures of the descriptive statistics were done in R with the package ggplot2 (R. Core Team 2019; Wickham 2016). Other statistical analysis as well as SNP marker analysis and linkage map development, QTL analysis, and the search for candidate genes was described in the previous chapters and these previously presented results are here merely combined.

3.4 Results

3.4.1 Correlation of flowering time under different vernalization regimes with plant traits after vernalization or hardening and after frost treatment

When correlating the data from the vernalization experiment and the freezing tolerance experiment (Table 3.1), the Number of Leaves after Hardening was the only trait not showing a significant correlation with days to flowering (DTF) without vernalization (V0), but had significant correlations with DTF after four weeks vernalization (V4) of r_S = -0.25 and DTF after eight weeks vernalization (V8) of r_S = -0.22. The trait Vigor after Hardening was negatively correlated with all three vernalization treatments ($-0.25 \leq r_S \leq -0.34$; Table 3.1).
Of the three traits related to stem length, Hypocotyl Length had the lowest correlation coefficients with r_S = -0.16 (V0) and r_S = -0.14 (V4), and the correlation with V8 was not significant. When only correlating the data of ‘winter’ types (Table 3.2) or ‘spring’ types (Table 3.3), the correlation between Hypocotyl Length after Hardening and DTF in the vernalization experiment was no longer significant (Fig. 3.1). Epicotyl Length after Hardening, on the other hand, showed the strongest of all correlations with DTF after 4 weeks of vernalization (r_S = -0.48). The correlation of Epicotyl Length with V8 (r_S = -0.43) and V0 (r_S = -0.40) were similar (Table 3.1). In ‘winter’ types the correlation was similar with highly significant values ($-0.38 \leq r_S \leq -0.43$; Table 3.2). However, the correlations of Epicotyl Length in ‘spring’ types were weak with r_S = -0.26 (V4), r_S = -0.20 (V8), and not significant for non-vernalized plants (V0). The range of the Epicotyl Length, Hypocotyl Length and Stem Length, was not different between ‘spring’ and ‘winter’ types (Fig. 3.1). The correlation between Stem Length and DTF in the vernalization experiment in the whole population was in between the values of Hypocotyl Length and Epicotyl Length with -0.28 (V8) to -0.39 (V4; Table 3.1). In ‘winter’ types the correlations of Stem Length had a range from highly significant -0.31 with

DTF of non-vernalized plants to not significant with DTF in eight weeks vernalized plants (Table 3.2). In ‘spring’ types the correlations were not significant (Table 3.3).

Table 3.1 Spearman rank correlations between traits of the freezing tolerance experiment from chapter 2 (rows) and vernalization experiment (columns) from chapter 1 with the traits days to flowering (DTF) with 0 (V0), 4 (V4) and 8 (V8) weeks of vernalization treatment in the DH-population DH4079 × Express617.

Trait	DTF V0	DTF V4	DTF V8
After Hardening			
Number of Leaves	-0.11	-0.25 ***	-0.22 ***
Vigor	-0.25 ***	-0.34 ***	-0.31 ***
Hypocotyl Length	-0.16 **	-0.14 *	-0.01
Epicotyl Length	-0.40 ***	-0.48 ***	-0.43 ***
Stem Length	-0.36 ***	-0.39 ***	-0.28 ***
After Frost			
Number of Viable Leaves	0.30 ***	0.12	-0.05
Leaf Survival Rate	0.34 ***	0.20 ***	0.02
Leaf Damage Score	-0.37 ***	-0.20 ***	-0.02
Stem Damage Score	-0.35 ***	-0.22 ***	-0.08
After Regrowth			
Number of Leaves	0.34 ***	0.16 **	-0.01
Death Rate	-0.35 ***	-0.19 **	-0.02
Number of Regrown Leaves	0.26 ***	0.13 *	0.02

* P≤0.10, ** P≤0.05, *** P≤0.01

Table 3.2 Spearman rank correlations between traits of the freezing tolerance experiment from chapter 2 (rows) and vernalization experiment (columns) from chapter 1 with the traits days to flowering (DTF) with 0 (V0), 4 (V4) and 8 (V8) weeks of vernalization treatment in the ‘winter’ type part of DH-population DH4079 × Express617.

Trait (only from ‚winter‘ types)	DTF V0	DTF V4	DTF V8
After Hardening			
Number of Leaves	-0.11	-0.28 ***	-0.26 **
Vigor	-0.24 **	-0.34 ***	-0.25 **
Hypocotyl Length	-0.13	0.00	0.11
Epicotyl Length	-0.38 ***	-0.43 ***	-0.38 ***
Stem Length	-0.31 ***	-0.24 **	-0.16
After Frost			
Number of Viable Leaves	0.14	-0.22 **	-0.34 ***
Leaf Survival Rate	0.18 *	-0.09	-0.22 **
Leaf Damage Score	-0.22 **	0.15	0.25 **
Stem Damage Score	-0.25 **	0.03	0.12
After Regrowth			
Number of Leaves	0.25 **	-0.11	-0.22 **
Death Rate	-0.19 *	0.12	0.19 *
Number of Regrown Leaves	0.24 **	-0.02	-0.08

Table 3.3 Spearman rank correlations between traits of the freezing tolerance experiment from chapter 2 (rows) and vernalization experiment (columns) from chapter 1 with the traits days to flowering (DTF) with 0 (V0), 4 (V4) and 8 (V8) weeks of vernalization treatment in the 'spring' type part of DH-population DH4079 × Express617.

Trait (only from ‚spring' types)	DTF V0	DTF V4	DTF V8
After Hardening			
Number of Leaves	-0.12	-0.31 ***	-0.19 *
Vigor	-0.07	-0.21 **	-0.26 **
Hypocotyl Length	0.16	0.02	0.14
Epicotyl Length	-0.10	-0.26 **	-0.20 *
Stem Length	0.04	-0.15	-0.01
After Frost			
Number of Viable Leaves	0.05	-0.11	-0.17
Leaf Survival Rate	0.10	-0.02	-0.13
Leaf Damage Score	-0.11	0.03	0.15
Stem Damage Score	-0.26 **	-0.15	0.01
After Regrowth			
Number of Leaves	0.21 **	0.01	-0.13
Death Rate	-0.28 ***	-0.13	0.07
Number of Regrown Leaves	0.27 ***	0.1	-0.04

The traits after Frost and after Regrowth from the freezing tolerance experiment showed significant correlations with flowering time without vernalization with correlation coefficients between $\pm 0.26 \leq r_S \leq \pm 0.37$ (Table 3.1). Correlations with V4 were significant, except for Number of Viable Leaves after Frost, and with absolute values up to $r_S = \pm 0.20$, but the correlations of V8 were not significant (Table 3.1). High vernalization requirement, as shown by high number of days to flowering without vernalization, was therefore positively correlated with the survival and regrowth of leaves (Number of Viable Leaves and Leave Survival Rate after Frost, Number of Leaves after Regrowth and Number of Regrown Leaves) and negatively correlated with freezing damage (Leaf Damage Score, Stem Damage Score, and Death Rate (Table 3.1, Fig. 3.2).

When only correlating the data of 'winter' types, the correlations between V0 and traits recorded after Frost and after Regrowth traits got weaker and lost significance (Table 3.2). For example, the correlation of Number of Viable Leaves after Frost with DTF after V4 was significant with a correlation coefficient of $r_S = -0.22$ (Table 3.2), while it was not significant in the whole DH population (Table 3.1). But the correlation between V4 and all other traits after Frost and after Regrowth were no longer significant in 'winter' types, unlike in the whole DH population (Table 3.1, Table 3.2). Additionally, days to flowering after eight weeks of vernalization gained significant correlation with five of the seven traits after Frost and after Regrowth in 'winter' types, none of which were significant in the whole DH population. Interestingly, the direction was opposite of the correlation coefficients with non-vernalized plants. For example, Leaf Damage Score had a Spearman correlation coefficient of $r_S = 0.25$ with days to flowering after eight weeks vernalization versus $r_S = -0.25$ with days to flowering after no vernalization (Table 3.2, Fig. 3.2).

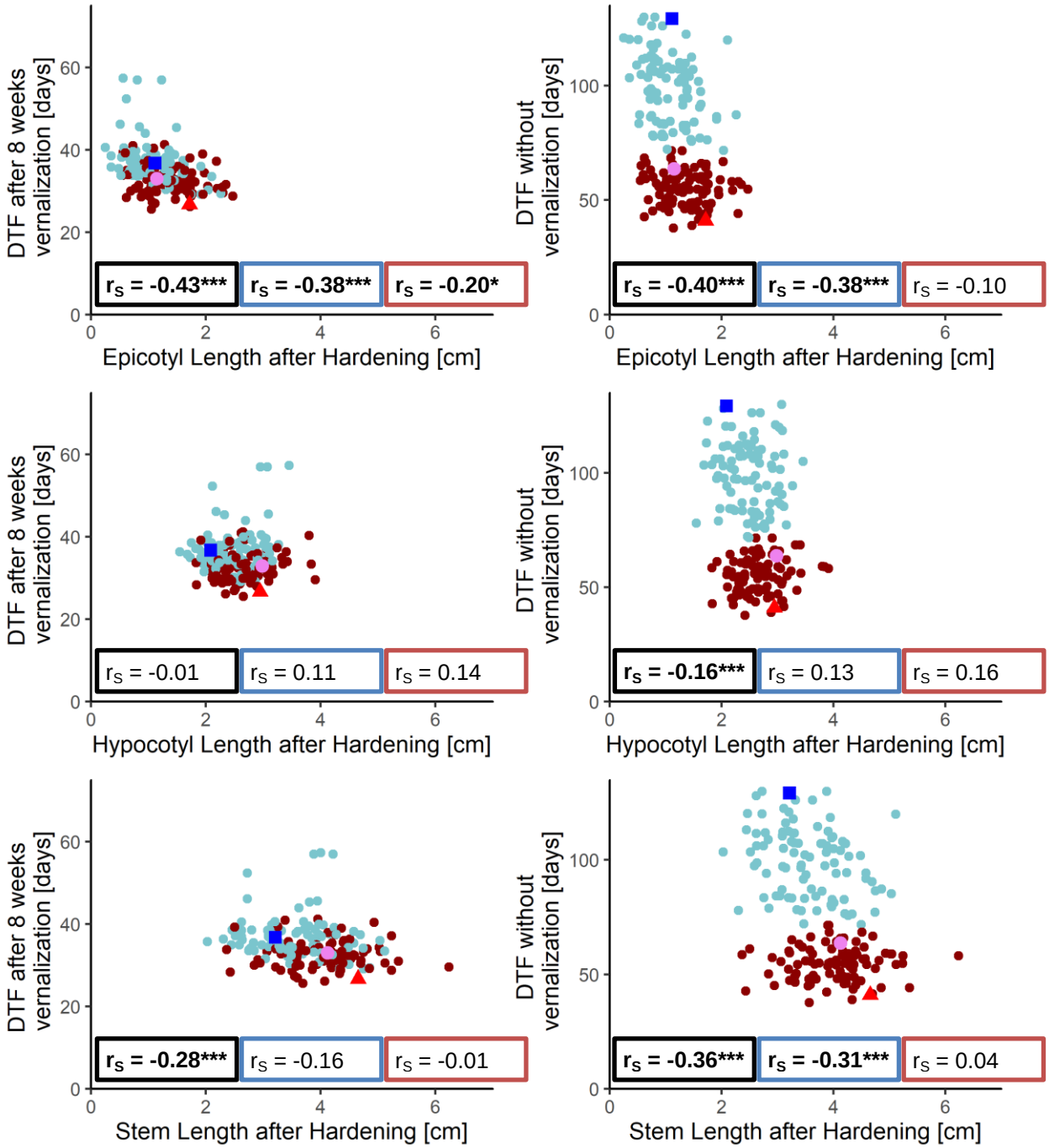


Fig. 3.1 Days to Flowering (DTF) with 8 weeks vernalization (left) and no vernalization (right) from the vernalization experiment from chapter 1 in correlation with Epicotyl Length (upper row), Hypocotyl Length (middle row) and total Stem Length (lower row) after nine weeks of hardening/vernalization conditions from the freezing tolerance experiment from chapter 2. Winter oilseed rape parent Express617 is indicated with blue square, spring-type parent DH4079 indicated with red triangle and F1 with violet circle. The median of the not vernalized population (71.7 days to flowering without vernalization) was used to separate the population into 'spring' types (dark red) and 'winter' types (light blue).

When only correlating the data of 'spring' types (Table 3.3), the correlation coefficients were only significant between DTF without vernalization and Stem Damage Score after Frost (Fig. 3.2), as well as V0 and all traits after Regrowth (Number of Regrown Leaves, Death Rate, and Number of Leaves after Regrowth).

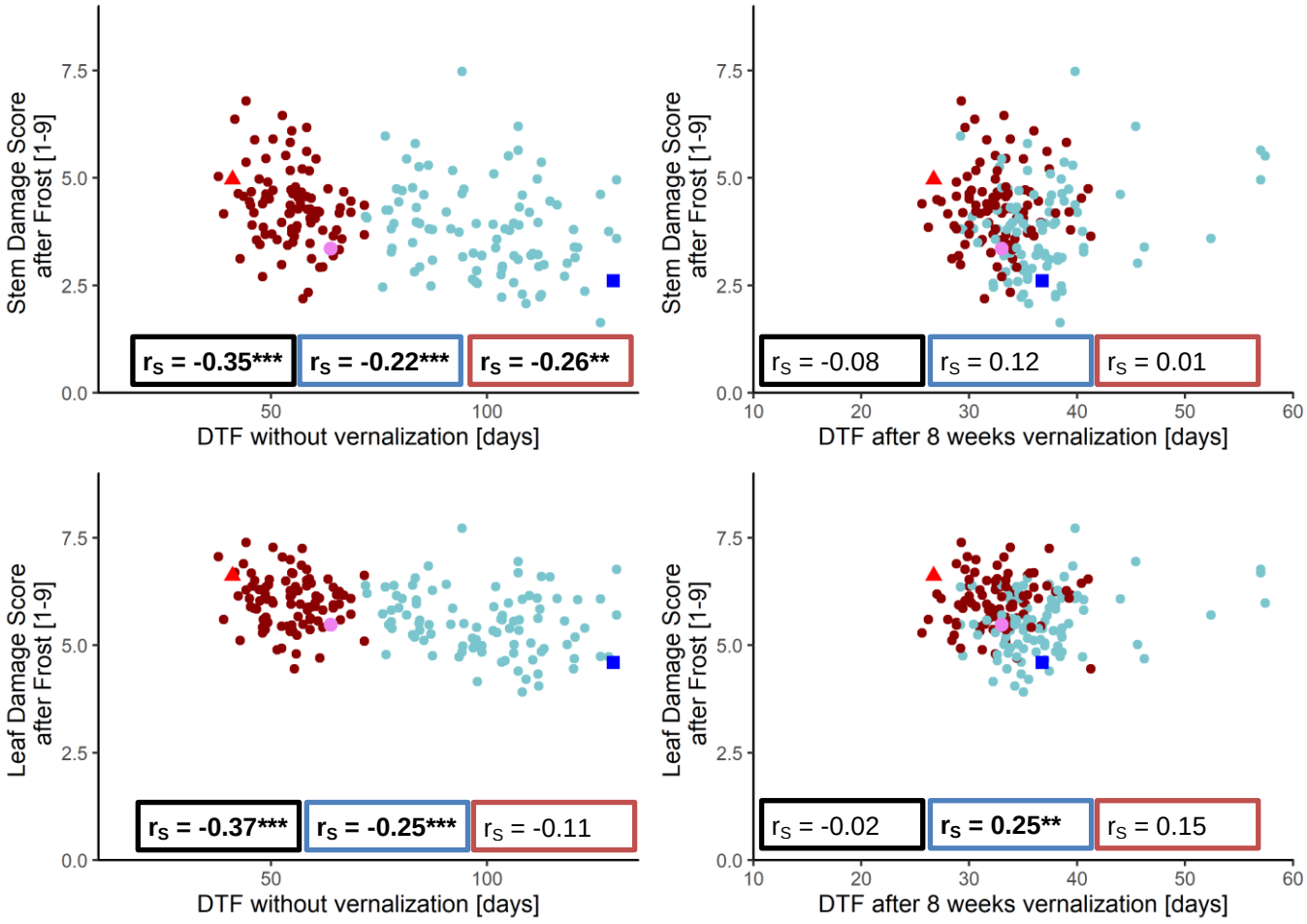
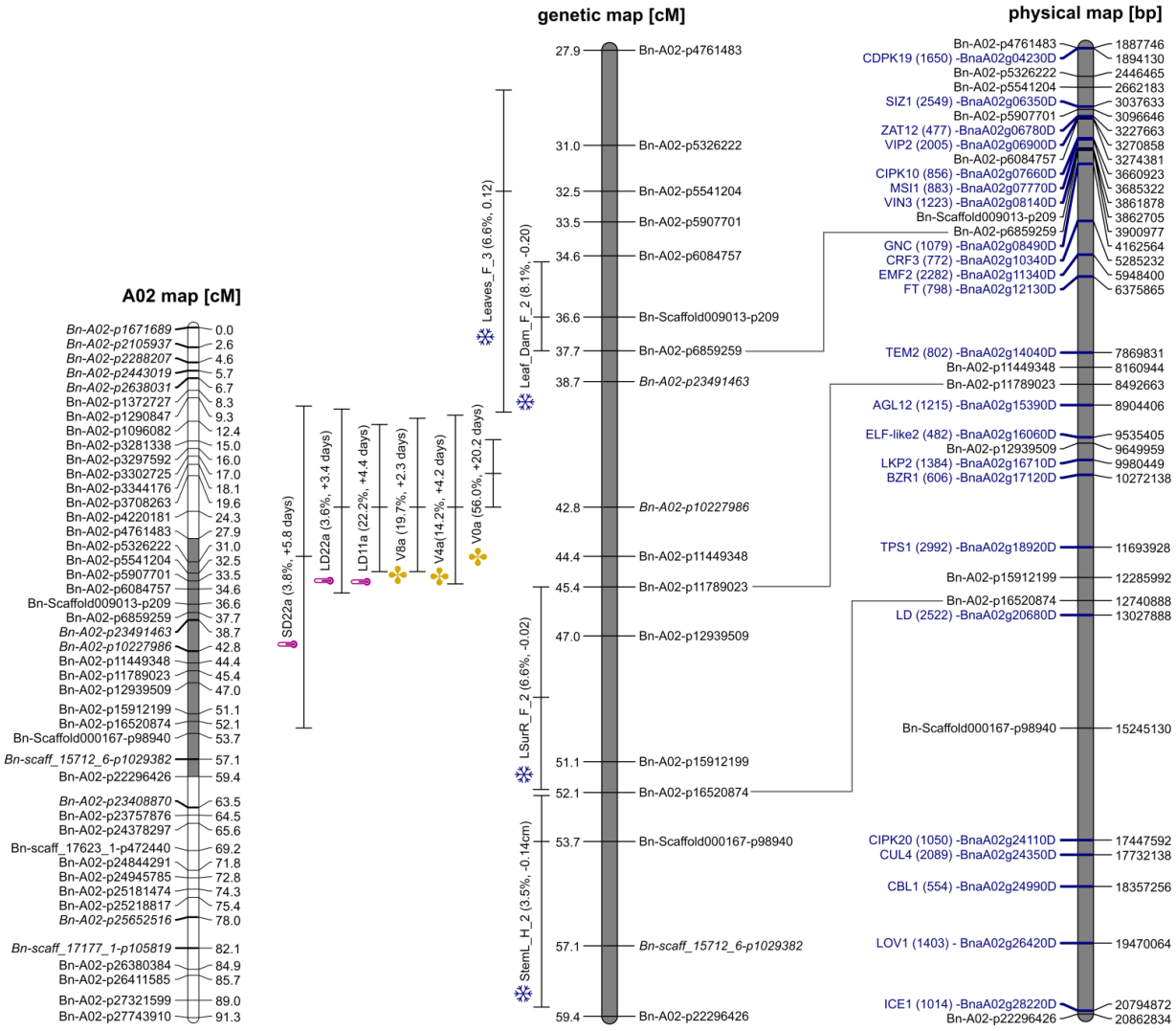


Fig. 3.2 Relation between Stem Damage Score (above) and Leaf Damage Score (below) after Frost from the freezing tolerance experiment from chapter 2 with Days to flowering (DTF) without (left) and with eight weeks vernalization (right) from the vernalization experiment from chapter 1. Spearman rank correlations (rS) are given for the whole population (black frame), only 'winter' types (blue frame) and only 'spring' types (red frame)

3.4.2 Combined QTL Analysis

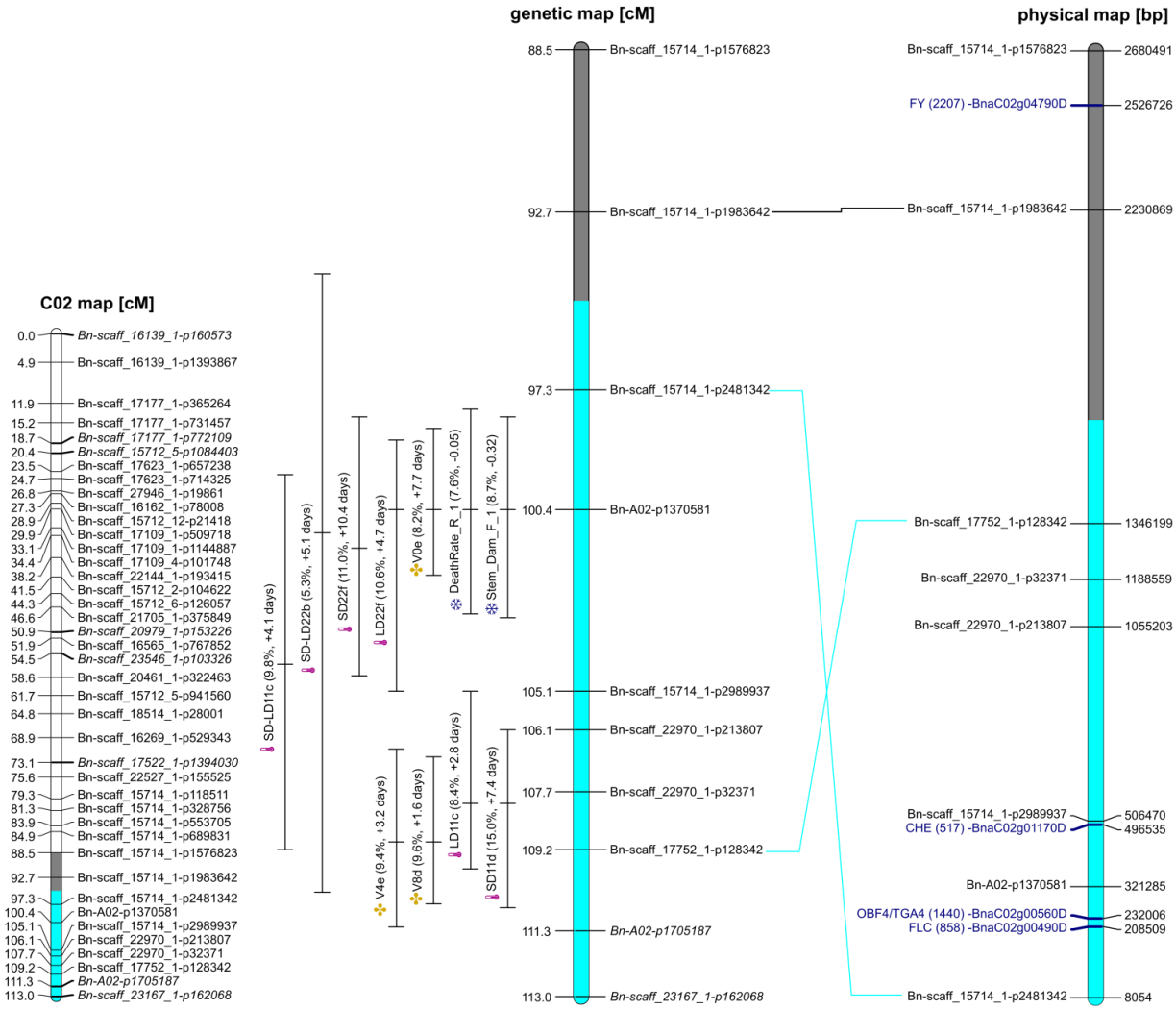
To examine genetic connections between vernalization requirement and freezing tolerance the QTL analyses from chapter 1 and 2 were reexamined in an integrated fashion. In chapter one it was established that the main QTL for vernalization requirement V0a was found on A02 at 42 cM (Table 1.5) and was also characterized as a general flowering time regulator since it was collocating with several other flowering time QTL (Fig. 1.3). *FLOWERING LOCUS T* (*FT*), the gene for a central flowering time regulator was the most likely candidate gene. The QTL from chapter 2 for Number of Leaves after Frost (Leaves_F_3 at 36.6 cM) and Leaf Damage Score (Leaf_dam_F_2 at 32.5cM; Table 2.7) were located on one side of the flowering time QTL; however they had no overlapping confidence intervals (Fig. 3.3). On the other side of the flowering time QTL, a QTL for Leaf Survival Rate (LSurRate_F_2) at 49 cM was found (Table 2.7). This QTL had only an overlapping confidence interval with a QTL for days to flowering under short days (SD22a). Lastly a Stem Length QTL (StemL_H_2) mapped further away at 53.7 cM. All the QTL from the freezing tolerance experiment were



minor QTL with 3.5 to 8.1% explained phenotypic variance. The second largest vernalization

Fig. 3.3 Genetic (middle) and physical (right) map of the QTL clusters region on A02 (left, position of QTL cluster region marked grey). QTL regarding days to flowering from the vernalization experiment (✤) and the day length and temperature experiment (🌡) from chapter 1, and QTL from the freezing tolerance experiment (❄) from chapter 2 are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effects for the respective QTL are given. In the physical map (right), candidate genes (blue) with BLAT scores and the respective gene ID in the reference genome of 'Damor-bzh'.

QTL V0e was located on C02 at 100.4 cM (Table 1.5) and collocated with several flowering time QTL from the day length and temperature experiment like LD22f, SD-LD22b, SD22f and SD-LD11c (Table1.7, Table1.8, Fig. 3.4). On the same position a QTL for Death Rate after Regrowth (DeathRate_R_1) and Stem Damage Score after Frost (Stem_Dam_F_1) mapped (Table 2.7, Fig. 3.4). The additive effects of the flowering time QTL were all positive, while the OTL of the two freezing tolerance traits had negative effects. The explained variance of these QTL ranged between 5.3 and 11.2%, which is quite low, but this was the only instance of significant QTL for vernalization requirement and freezing tolerance of the stem collocating. A search for more non-significant QTL was not successful. On C03 a QTL for days to flowering without vernalization V0f at 4.6cM (Table 1.5) and a QTL for Leaf Survival



Rate (LSurR_F_4) at 7.8cM (Table 2.7) had overlapping confidence intervals, and the additive effects for both were positive.

Fig. 3.4 Genetic (middle) and physical (right) map of the QTL clusters region on C02 (left, position of QTL cluster region marked grey). QTL regarding days to flowering from the vernalization experiment (✤) and the day length and temperature experiment (🌡) from chapter 1, and QTL from the freezing tolerance experiment (❄) from chapter 2 are given with peak and 95% confidence interval. In brackets the variance explained in percent and additive effects for the respective QTL are given. Candidate genes (blue) with BLAT scores and the respective gene ID in the reference genome of 'Damor-bzh'. A chromosome inversion between genetic and physical map is indicated with bright blue.

As described in chapter two, the major QTL of traits for freezing tolerance were clustering on C06 between 0 and 9.6 cM such as for Stem Damage Score (Stem_Dam_F_2) and Leaf Damage Score (Leaf_Dam_F_3) after Frost, and Death Rate (Death_Rate_2) and Number of Regrown Leaves (NewLeaves_R_3) after Regrowth (Fig. 2.5, Appendix B). These were collocating with a cluster with QTL for flowering time regulation under short days, which included QTL for days to flowering under short days (SD11e and SD22g) as well as effect of day length (SD-LD11d, see chapter 1.5.2, Fig.1.5, Appendix B). The additive effects were all negative, except for the effect of temperature differences. The major QTL for Leave Survival Rate after Frost (LSurRate_F_5) at 27.9 cM collocated with a QTL for Number of Viable Leaves after Frost (Leaves_F_5) at 25.8 cM and a QTL for Number of Leaves after Regrowth

(Leaves_R_3) at 26.8 cM (Table 2.7). They were located in the same region as a QTL for days to flowering after 8 weeks vernalization (V8e, Table 1.5), two QTL for the effect of day length (SD-LD22c and SD-LD11e, Table 1.8) and a QTL for the effect of temperature (11-22SDd, Table 1.9, Appendix B). These QTL were identified as part of a temperature × day length cluster (chapter 1.5.3).

The major QTL for Epicotyl Length (EpiL_H_2) and Stem length (StemL_H_3) collocated on A07 at 101 cM (Table 2.7, Fig. 2.4). The region was described as QTL cluster for flowering time, especially regulation of flowering time under short days (see chapter 1.5.2, Fig.1.4). The QTL EpiL_H_2 and StemL_H_3 had overlapping confidence intervals with a major QTL for flowering time under cool short day conditions (SD11b, Table 1.7) and a minor QTL for days to flowering without vernalization (V0d, Table 1.5, Appendix B, Fig. 2.4).

3.4.3 Correlation of the traits from the freezing tolerance experiment with the day length and temperature experiment

3.4.3.1 Traits after Hardening

Because of the collocating QTL on C06 and A07 of traits from the freezing tolerance experiment and of days to flowering (DTF) traits from the day length and temperature experiment, the correlation between the freezing tolerance experiment and the day length and temperature experiment was also examined (Table 3.4). For the correlation between Number of Leaves after Hardening, cool long day conditions (LD11) showed a significant, but poor correlation of r_S = -0.13, and the effect of temperature differences under LD (11-22LD) had a similar significant value with r_S = -0.15. The correlation with Vigor after Hardening was higher under long day (LD) conditions (r_S = -0.21 for LD11 and r_S = -0.26 for LD22) than under short days (-0.16 and -0.17, Table 3.4). Both effects of day length differences (SD-LD11 and SD-LD22) had no significant correlation and both effects of temperature differences (11-22LD and 11-22SD) showed a small positive correlation of 0.13. The correlation with Hypocotyl Length was either non-significant or very small. A strong correlation between early flowering and an increased Epicotyl Length could be observed for all four day length and temperature conditions. The correlation coefficients ranged between $-0.48 \leq r_S \leq -0.55$. The effect of day length differences was correlated with Epicotyl Length (r_S = -0.45 for SD-LD11, r_S = -0.35 for SD-LD22). Both effects for temperature differences showed small positive correlations (r_S = 0.19 for 11-22LD, r_S = 0.24 for 11-22SD). The correlation coefficients with Stem Length were smaller than with Epicotyl Length and lost significance in the effect of temperature differences and the effect of day length difference under warm conditions.

During the analysis of the day length and temperature experiment in chapter 1, epistatic effects between major QTL from two homoeologous regions, which were involved in the regulation of flowering through day length and temperature, on chromosome A07 between 70 and 103 cM and on C06 between 0 and 32 cM were discovered in almost all traits. The DH4079 allele on A07 masked the effect of the C06 locus. Therefore the DH population was separated by the A07 allele to examine the data independent of the epistatic effect.

Table 3.4 Spearman rank correlation between traits of the freezing tolerance experiment (rows) and days to flowering (DTF) from the day length and temperature experiment (columns) under four different temperature and day length conditions with cool long days (LD11), warm long days (LD22), cool short days (SD11) and warm short days (SD22) as well as the effect of temperature differences (11-22LD and 11-22SD) and the effect of day length differences (SD-LD11 and SD-LD22) on DTF, calculated for each genotype in the DH-population DH4079 × Express617.

	Days to flowering under...				The effect of … differences			
	Long days		Short days		day length		temperature	
	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
After Hardening								
Number of Leaves	-0.13 *	-0.02	-0.03	0.02	0.07	0.06	-0.15 **	-0.05
Vigor	-0.21 ***	-0.26 ***	-0.16 **	-0.17 **	-0.05	-0.08	0.13 *	0.13 *
Hypocotyl Length	-0.08	-0.12	-0.00	0.07	0.04	0.14 *	0.09	-0.14 *
Epicotyl Length	-0.50 ***	-0.55 ***	-0.54 ***	-0.48 ***	-0.45 ***	-0.35 ***	0.19 ***	0.24 ***
Stem Length	-0.38 ***	-0.43 ***	-0.34 ***	-0.26 ***	-0.24 ***	-0.14 *	0.17 **	0.07
After Frost								
Number of Viable Leaves	0.08	0.08	-0.05	-0.10	-0.14 *	-0.15 **	0.11	0.13 *
Leaf Survival Rate	0.14 *	0.09	-0.06	-0.14 *	-0.21 ***	-0.21 ***	0.18 **	0.17 **
Leaf Damage Score	-0.16 **	-0.10	0.03	0.12	0.16 **	0.17 **	-0.18 **	-0.17 **
Stem Damage Score	-0.21 ***	-0.17 **	-0.09	-0.01	0.01	0.03	-0.11	-0.08
After Regrowth								
Number of Leaves	0.17 **	0.18 **	0.03	-0.01	-0.07	-0.08	0.06	0.07
Death Rate	-0.19 **	-0.15 **	-0.07	0.01	0.05	0.06	-0.09	-0.09
Number of Regrown Leaves	0.19 **	0.20 ***	0.08	0.05	-0.00	-0.01	0.03	0.02

* P≤0.10, ** P≤0.05, *** P≤0.01

When only regarding the DH lines with the A07 DH4079 allele (Table 3.5), the Number of Leaves after Hardening only had a significant correlation with the effect of temperature differences under long days (11-22LD). Vigor only showed a significant correlation coefficient with DTF under warm long days of r_S = -0.17. When only inspecting the DH lines with the A07 Express617 allele (Table 3.6), the Number of Leaves after Hardening had no significant correlations. Vigor after Hardening had moderately strong correlations between $\pm 0.27 \leq r_S \leq \pm 0.19$ for DTF under all conditions, which was slightly higher than for the whole DH population (Table 3.4). Therefore, the correlation between Vigor and DTF seems to stem from the A07 Express617 allele. The effects of day length and temperature differences were not significantly correlated with Vigor after Hardening.

For the trait Hypocotyl Length after Hardening the correlation coefficients with SD-LD22 and 11-22SD became stronger in both groups (Table 3.5, Table 3.6), and the group with the A07 DH4079 allele gained a significant correlation between Hypocotyl Length and SD22 (Table 3.5) compared to the whole DH population (Table 3.4). For the trait Epicotyl Length the correlation coefficients with all traits from the day length and temperature experiment became weaker in both groups (Table 3.5, Table 3.6) compared to the whole DH population.

Table 3.5 Spearman rank correlation with genotypes which have DH4079 allele at marker Bn-A07-p21478337 on A07, between traits of the freezing tolerance experiment (rows) and days to flowering (DTF) from the day length and temperature experiment (columns) under four different temperature and day length conditions with cool long days (LD11), warm long days (LD22), cool short days (SD11) and warm short days (SD22) as well as the effect of temperature differences (11-22LD and 11-22SD) and the effect of day length differences (SD-LD11 and SD-LD22) on DTF, calculated for each genotype in the DH-population DH4079 × Express617.

	Days to flowering under				The effect of … differences			
	Long days		Short days		day length		temperature	
	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
After Hardening								
Number of Leaves	-0.10	0.02	-0.01	0.08	0.08	0.10	-0.19 *	-0.11
Vigor	-0.08	-0.17 *	-0.03	-0.06	0.07	0.05	0.16	0.09
Hypocotyl Length	0.05	-0.04	0.14	0.18 *	0.15	0.22 **	0.13	-0.17 *
Epicotyl Length	-0.30 ***	-0.37 ***	-0.32 ***	-0.28 ***	-0.22 **	-0.16	0.11	0.13
Stem Length	-0.19 *	-0.28 ***	-0.08	-0.03	0.03	0.09	0.12	-0.05
After Frost								
Number of Viable Leaves	0.18 *	0.19 *	0.08	-0.03	-0.01	-0.11	0.03	0.13
Leaf Survival Rate	0.25 **	0.22 **	0.08	-0.06	-0.08	-0.18 *	0.12	0.18 *
Leaf Damage Score	-0.23 **	-0.17 *	-0.07	0.05	0.06	0.13	-0.12	-0.15
Stem Damage Score	-0.21 **	-0.14	-0.12	-0.01	-0.03	0.03	-0.15	-0.08
After Regrowth								
Number of Leaves	0.26 ***	0.25 **	0.11	0.03	-0.02	-0.06	0.10	0.05
Death Rate	-0.20 **	-0.16	-0.10	-0.01	0.00	0.03	-0.09	-0.06
Number of Regrown Leaves	0.24 **	0.22 **	0.12	0.08	0.00	0.01	0.13	-0.03

* P≤0.10, ** P≤0.05, *** P≤0.01

In the group with the A07 Express617 allele the correlations between Epicotyl Length and DTF under all four conditions were stronger than in the A07 DH4079 allele group, but weaker than in the whole DH population. Interestingly, the correlations with DTF under long day conditions were much higher than under DTF short day conditions. The correlations were no longer significant between Epicotyl Length and the traits effect of day length at 22°C and the effect of temperature under both day length conditions for the DH lines within the A07 DH4079 allele group (Table 3.5). In the group with the A07 Express617 allele only the effect of temperature under long day conditions was significantly correlated with Epicotyl Length (r_S = 0.21; Table 3.6). The Stem Length after Hardening was in both groups only significant for DTF under both long day conditions (LD11, LD22; Table 3.5, Table 3.6). This is a drastic reduction compared to the nearly throughout significant correlations in the whole DH population (Table 3.4).

3.4.3.2 Traits after Frost and after Regrowth

Traits after Frost and after Regrowth had some weak, but significant correlation with DTF in the whole DH population (Table 3.4). Leaf Survival Rate after Frost was negatively correlated

Table 3.6 Spearman rank correlation with genotypes which have Express617 allele at marker Bn-A07-p21478337 on A07, between traits of the freezing tolerance experiment (rows) and days to flowering (DTF) from the day length and temperature experiment (columns) under four different temperature and day length conditions with cool long days (LD11), warm long days (LD22), cool short days (SD11) and warm short days (SD22) as well as the effect of temperature differences (11-22LD and 11-22SD) and the effect of day length differences (SD-LD11 and SD-LD22) on DTF, calculated for each genotype in the DH-population DH4079 × Express617.

	Days to flowering under				The effect of … differences			
	Long days		Short days		day length		temperature	
	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
After Hardening								
Number of Leaves	-0.19	-0.13	-0.08	-0.08	0.06	-0.05	-0.10	0.07
Vigor	-0.26 **	-0.27 **	-0.19 *	-0.23 **	-0.05	-0.16	0.08	0.16
Hypocotyl Length	-0.10	-0.08	0.06	0.17	0.16	0.25 **	0.01	-0.23 **
Epicotyl Length	-0.40 ***	-0.43 ***	-0.33 ***	-0.23 **	-0.19	-0.05	0.21 *	0.04
Stem Length	-0.25 **	-0.22 *	-0.09	0.04	0.04	0.16	0.07	-0.16
After Frost								
Number of Viable Leaves	-0.09	-0.14	-0.32 ***	-0.30 ***	-0.40 ***	-0.29 ***	0.21 *	0.17
Leaf Survival Rate	-0.02	-0.10	-0.32 ***	-0.31 ***	-0.48 ***	-0.33 ***	0.25 **	0.18
Leaf Damage Score	-0.01	0.12	0.32 ***	0.37 ***	0.48 ***	0.37 ***	-0.30 ***	-0.27 **
Stem Damage Score	-0.06	0.05	0.24 **	0.34 ***	0.36 ***	0.38 ***	-0.21 *	-0.29 ***
After Regrowth								
Number of Leaves	0.08	0.04	-0.18	-0.24 **	-0.29 **	-0.29 **	0.12	0.21 *
Death Rate	-0.13	-0.05	0.12	0.23 **	0.27 **	0.30 ***	-0.15	-0.25 **
Number of Regrown Leaves	0.16	0.14	-0.05	-0.14	-0.15	-0.21 *	0.04	0.17

* P≤0.10, ** P≤0.05, *** P≤0.01

with both effects of day length (rS = -0.21 for LD-SD11 and LD-SD22), while it was positive for the effect of temperature (rS = 0.18 for 11-22LD and rS = 0.17 for 11-22SD; Table 3.4). Leaf Damage Score, which was highly negatively correlated with Leaf Survival Rate (Table 2.4), had similar results but in the other direction (Table 3.4). Even though Leaf Damage Score was correlated with Stem Damage Score, Stem Damage Score was only correlated with flowering under long days (rS = -0.21 for LD11 and rS = -0.17 for LD22, Table 3.4). All traits after Regrowth were only correlated with flowering under long days, e.g. Death Rate had correlation of r_S = -0.19 with cool long day and r_S = -0.15 with warm long day conditions.
In the group with the A07 DH4079 allele (Table 3.5) DTF under cool long days was significantly, but moderately correlated with all traits after Frost and after Regrowth. DTF under warm long days had similar or weaker correlations, but Stem Damage Score and Death Rate were no longer significantly correlated. Additionally, Leaf Survival Rate was significantly correlated with the effect of day length differences under 22°C with -0.18 and the effect of temperature differences under short days with 0.18. The group with the A07 Express617 allele, in which the flowering alleles on C06 are not masked, DTF under long

days, both in 11°C and 22°C showed no significant correlations with traits after Frost or after Regrowth (Table 3.6). Instead the DTF under both short day conditions and both effects of day length differences had moderate to strong correlations with all traits after Frost. This is the opposite to the group with the A07 DH4079 and shows how the epistatic effect between A07 and C06 for flowering time heavily influences this result. In contrast to the whole DH population (Table 3.4), the A07 Express617 group showed stronger correlations between the effect of day length under both temperatures and all traits after Frost, even Stem Damage Score (Table 3.6), which was not significant in the whole DH population. The strongest correlation was between Leaf Damage Score and effect of day length under cool temperatures with the highly significant value of 0.48 (Table 3.6).
The correlations between the effects of temperature differences with traits after Frost were stronger in the A07 Express617 group then the whole DH population or the A07 DH4079 group, but the effect of temperature under short days had only significant correlations with Leaf Damage Score and Stem Damage Score with coefficients of r_S = -0.27 and r_S = -0.29, respectively. A correlation with Stem Damage Score was observed, too. The effect of temperature under long days was correlated with r_S = -0.21 (P≤0.10) and the effect of temperature under short days with r_S = -0.29. Death Rate and Number of Leaves after Regrowth had significant correlations with DTF under warm short days, both effects of day length, and the effect of temperature under short days with absolute values between ±0.21 ≤ r_S ≤ ±0.30 (Table 3.6). These correlations were not observed in the A07 DH4079 allele group (Table 3.5) or the whole DH population (Table 3.4).

3.5 Discussion

3.5.1 Is Vernalization requirement connected to freezing tolerance?

Most studies in *Brassica napus* disputed a link between vernalization requirement and freezing tolerance (Hawkins et al. 2002; Markowski and Rapacz 1994; Waalen et al. 2014). This DH population and the different experiments allow for more data to add to this discourse. In chapter 2 the split of the DH population into ‘spring’ and ‘winter’ types, which was based on vernalization requirement, was used to find differences in freezing tolerance between the groups, which were not very big, but statistically significant (Table 2.3). Additionally, Leaf Damage Score and Stem Damage Score were observed to have differences in the correlation with traits scored after Regrowth. In ‘spring’ types Leaf Damage Score had higher correlations with Death Rate and Number of Regrown Leaves after Regrowth, while in ‘winter’ types Stem Damage Score had higher correlations with those two traits after Regrowth (see 2.4.3 and Table 2.5 and Table 2.6).
When correlating the freezing tolerance experiment with flowering time data from the vernalization experiment, a correlation between vernalization requirement and freezing tolerance can be seen (Table 3.1 – Table 3.3). The whole DH population showed significant correlations with the days to flowering (DTF) of non-vernalized plants (V0) with all traits after Frost and after Regrowth (Table 3.1). With application of vernalization these correlations go down and eight weeks vernalized plants (V8) showed no longer a correlation between days to flowering and traits regarding freezing tolerance, which means that this correlation is

dependent on vernalization. The correlations of traits from the freezing tolerance experiment with flowering time data from the vernalization experiment of only ‘spring’ types (Table 3.3) got weaker and had a lower or no significance. Only the traits Stem Damage Score, Number of Leaves after Regrowth, Death Rate and Number of Regrown Leaves were significant with moderate correlations. In the ‘winter’ types (Table 3.2) the correlations got weaker, too, but Leaf Damage Score and Leaf Survival Rate were still significant unlike in ‘spring’ types. When looking at the visualization of the relation between Stem Damage Score as well as Leaf Damage Score and DTF of V0 (Fig. 3.2), the ‘spring‘ and the ‘winter‘ types do not seem to form a continuous linear correlation. Instead they seem to show the same pattern, with a similar range for Stem Damage Score.

The major vernalization QTL V0a on A02 is mainly responsible for the ‘spring’ and ‘winter’ type split (see chapter 1.5). On the same chromosome several minor freezing tolerance QTL were located (Fig. 3.3), but without an overlapping confidence interval with the vernalization QTL. Similarly, Kole et al. (2002) examined a population of a cross between Stellar and Major and next to a strong vernalization QTL on A02 they found several QTL for winter survival, but no QTL for freezing tolerance estimated via electrolyte leakage. Since the confidence intervals of our QTL were not overlapping, a shared genetic cause can be excluded. Therefore, other QTL should be responsible for the correlation between vernalization and freezing tolerance, which would also explain the observed pattern of similar correlation in Fig. 3.2, because the correlation is independent from the ‚spring‘ – ‚winter‘ split on A02. Next to the major QTL for freezing tolerance on C06 no QTL for vernalization were discovered (Appendix B). Hence, this genomic region is also not responsible for the observed correlation between vernalization and freezing tolerance. On C03 a vernalization QTL V0f was found close to a QTL for Leaf Survival Rate (LSurRate_F_4) and the additive effect for both was positive, which is in line with the observed positive correlation observed between DTF without vernalization and Leaf Survival Rate after Frost (Table 3.1). On C02 another vernalization QTL (V0e) and a group of other flowering time QTL collocated with QTL for Death Rate after Regrowth (DeathRate_R_1) and Stem Damage Score after Frost (Stem_Dam_F_1; Fig. 3.4). The additive effects of the flowering time QTL were all positive, while the QTL for the two freezing tolerance traits had negative effects. The opposite additive effects confirmed the negative correlation observed between Stem Damage Score and Death Rate with V0 (Table 3.1). A QTL for DTF under warm long days (LD22f) was collocating with the three QTL. All four had overlapping confidence intervals with three other QTL: DTF under warm short days (SD22f), two QTL for both effects of day length differences (SD-LD22b and SD-LD11c), and, although the peak was further away, a QTL for DTF under cool SD (SD11c, Fig. 3.4). Therefore this region might be involved in reaction to day length and temperature in regards to flowering time regulation and freezing tolerance.

The candidate gene for small vernalization QTL V0e is *FLOWERING LOCUS C* (*FLC*). *FLC* is a known vernalization gene in *Arabidopsis thaliana* and *Brassica napus*, whose protein suppresses flowering by inhibiting *FT* expression (Ietswaart et al. 2012; Schiessl et al. 2014; Tadege et al. 2001; Zou et al. 2012). However, Bond et al. (2011) excluded a regulation of the vernalization pathway via VERNALIZATION INSENSITIVE 3 (VIN3) by known cold acclimation genes. Lee et al. (2015) found evidence of INDUCER OF CBF EXPRESSION 1

(ICE1) upregulating *FLC* and therefore a delay of flowering by a central cold response protein. Two other genes are located in this area. Firstly, *CHE* (*ATTCP21*, *CCA1 HIKING EXPEDITION*, *CHE*, *TCP DOMAIN PROTEIN 21*, *TCP21*) is a repressor of CCA1, a basic circadian rhythm protein (Pruneda-Paz et al. 2009). Secondly, *OBF4* (*OCS ELEMENT BINDING FACTOR 4*, *TGA4*, *TGACG MOTIF-BINDING FACTOR 4*), which was first known to be part of the pathogen response. However, Song et al. (2008) discovered that OBF4 binds on the *FT*-Promotor and can activate flowering. OBF4 can also bind to the CO-protein, the central regulator in the photoperiod and temperature flowering time regulation, and the *OBF4* gene even exhibits a similar circadian expression pattern as *CO* (Song et al. 2008). Since the region discovered in this study was influencing flowering time in response to vernalization as well as day length and high temperature, it is unclear how the effects on freezing tolerance are caused and which of these genes (if any) are also responsible for Stem Damage Score and Death Rate.

While many researchers found that not all *Brassica napus* with high vernalization requirement have high freezing tolerance and vice versa (Hawkins et al. 2002; Markowski and Rapacz 1994; Rapacz and Markowski 1999), this might not mean, that those two are completely independent. The high correlation found in the past (Rapacz and Markowski 1999), which were observed in this study, too, might not be generally true, but with the complexity of the regulation of cold acclimation specifically, a connection should not be excluded yet. For example, Ghanbari and Möllers (2018) found a significant correlation of 0.48 between stem elongation before winter and vernalization requirement, measured by stem elongation three month after being sown in spring. Kole et al. (2002) observed QTL for flowering time without vernalization close to or even overlapping with QTL for winter survival and freezing tolerance in *Brassica napus* and *Brassica rapa*. Rapacz et al. (2001) found, that a spring type rapeseed started to severely loose freezing tolerance earlier than a winter oilseed rape. This corresponded with the spring type starting to elongate the epicotyl and petioles, and the development of larger leaf sizes as well as the reduction of soluble sugars. But also flowering time changed in that time. The spring type rapeseed flowered after 17 days without acclimation and four week cold-acclimated plants flowered 14 days after transfer to warm conditions. But after 6 weeks cold acclimation, when all the morphological and physical changes happened, flowering time was reduced to nine days.

It is clear from this DH population and the literature that low vernalization requirement can be attributed to several loci in the *Brassica napus* genome, and the same is true for freezing tolerance. But only few regulators seem to influence both traits, therefore, while the hypothesis that vernalization requirement and freezing tolerance is generally correlated has to be rejected, common loci are very well possible.

3.5.2 Correlation of freezing tolerance and flowering time regulation after vernalization

3.5.2.1 Freezing tolerance and short day sensitivity

Since the major QTL for traits for freezing tolerance collocated with major QTL for flowering under short days (SD) on chromosome C06, we expected the correlation between freezing tolerance traits and days to flowering (DTF) under SD to be high. However, the values were

only significant between DTF under warm SD and Leaf Survival Rate after Frost (r_S = -0.14, Table 3.4). The effects of temperature differences as well as day length differences had only moderate and significant correlations with leaf traits after Frost.

In chapter one, an epistatic effect between A07 and C06 was discovered, where the DH4079 allele on A07 masked the effect on C06 regarding flowering time under several conditions including SD. Therefore, we divided the DH population by the markers Bn-A07-p21478337 on A07 into haplotypes to study the correlation without the influence of epistasis. This approach was successful since the two groups divided by the A07 allele showed very different correlations between the traits from the freezing tolerance experiment after Frost and after Regrowth and the traits of the day length and temperature experiment (Table 3.5, Table 3.6). The group with the A07 Express617 allele (Table 3.6), in which the flowering alleles on C06 were not masked, the DTF under both SD conditions and both effects of day length differences had moderate to strong correlations with all traits after Frost and partly with traits after Regrowth with correlation coefficients between $\pm 0.24 \leq r_S \leq \pm 0.48$. Both effects of temperature differences had moderate correlations with Leaf Damage Score and Stem Damage Score with values between $\pm 0.21 \leq r_S \leq \pm 0.30$. The correlation between e.g. Stem Damage Score and DTF under SD was positive with r_S = 0.24 for cool SD (SD11) and r_S = 0.34 for warm SD (SD22; Table 3.6), suggesting that DH lines that delay flowering under short days are more prone to freezing damage. In the QTL analysis, the QTL SD11e on chromosome C06 for the trait DTF under warm short days had a negative additive effect of a = -6.9 days and the collocating QTL Stem_Dam_F_2 for the trait Stem Damage Score had a negative additive effect of a = -0.56. The same direction of both additive effects confirms the positive correlation observed. It can be concluded that in the A07 Express617 allele group freezing tolerance is connected to day length sensitivity, short day sensitive plants that delayed flowering under SD through the region on C06 also showed less freezing tolerance in leaves and stem.

This is unexpected, since the abiotic signal of day length is known to both causes the plant to delay flowering (see chapter 1) and to increase freezing tolerance. Roeber et al. (2021) presented in their review the current knowledge about the influence of photoperiod on abiotic stress, and presented the consensus in the literature about short day conditions initiating freezing tolerance, while long day inhibits freezing tolerance. In *Arabidopsis thaliana* SD conditions can increase freezing tolerance by 2 °C (Lee and Thomashow 2012). In their study about the connections of vernalization requirement and freezing tolerance, Waalen et al. (2014) pointed out that the repression of flowering by SD might play an important role in *Brassica napus*.

Since it is unclear, if the traits are caused by the same gene, one can only speculate about the cause of the unusual connection between flowering time under short day conditions and freezing tolerance found in this study. One hypothesis would be linkage drag, meaning two different genes with allelic differences between the parents, which are located in the same region and close to each other. A freezing tolerance gene, where the Express617 allele increases freezing tolerance and a SD influenced flowering gene, where the DH4079 allele delays flowering time. Another hypothesis would be that the cause lies in allelic variation in a gene, as the C06 DH4079 allele can delay flowering more than the C06 Express617 allele,

but C06 DH4079 allele has less contribution for freezing tolerance then the C06 Express617 allele. Basic regulators have been shown to act different on separate traits due to allelic variation (Xie et al. 2015). In chapter 1 the candidate genes *EFS* and *TPS1* were identified (see chapter 1.5.2). Both would be early in the signaling cascade to exhibit such behavior.

3.5.2.2 Flowering under long days and freezing tolerance

As a surprising result, we found significant correlations between tolerance to freezing stress and days to flowering (DTF) of plants after full (8 or 9 weeks) vernalization grown under long day (LD) conditions, first, in 'winter' types (Table 3.2) and second in the A07 DH4079 allele group (Table 3.5).

While in the whole DH population and in the 'spring' types the correlations between DTF after eight weeks vernalization and the traits from the freezing tolerance experiment after Frost and after Regrowth were not significant (Table 3.1, Table 3.3), in the 'winter' types the correlations of DTF after V8 with Number of Viable Leaves, Leaf Survival Rate, and Leaf Damage Score after Frost, as well as Number of Leaves and Death Rate after Regrowth were significant (Table 3.2). The strongest correlation was DTF after V8 with Number of Viable Leaves after Frost (r_S = -0.34) and the weakest with Death Rate after Regrowth (r_S = 0.19). The scatterplot between V8 and Leaf Damage Score shows the positive correlation (Fig. 3.2). Since Spearman correlation was applied, it can be excluded that this correlation was influenced by outliers. The 'spring' – 'winter' split was mainly caused by the vernalization QTL on A02, which was collocating with three QTL for DTF under LD after full vernalization (V8a, LD11a and LD22a; Fig, 1.3). However, since there are two closely located QTL for DTF under V0 and no overlapping QTL for any freezing tolerance trait, this seems not to have a direct cause. An epistatic effect could explain the observed results, but neither LD11a nor V0a showed any epistatic effects, only LD22a had an epistatic effect with LD22d on A07 at 88 cM (Table 1.10).

In the part of the DH population with the A07 DH4079 allele, which would mask the effect of the short day and temperature dependent QTL on C06, the correlation between DTF under SD and traits after Frost and after Regrowth was as expected not significant (Table 3.5), in contrast to the A07 Express allele group, as described in chapter 3.5.2.1. However, DTF under both LD conditions was significantly correlated in the A07 DH4079 allele group with almost all traits after Frost and after Regrowth with the exception of the correlation of DTF under warm LD with Stem Damage Score and Death Rate and absolute values between $\pm 0.17 \leq r_S \leq \pm 0.26$. The correlation between DTF under cool long days and Stem Damage Score, for example, was negative with r_S = -0.21 (Table 3.5), indicating that plants, which were late flowering under LD, had a higher freezing tolerance. Surprisingly, there were no QTL on A07 for either DTF under cool LD conditions or QTL for any freezing tolerance trait found.

A link between flowering under long days and freezing tolerance was found by Cao et al. (2005) with the regulator GIGANTEA (GI). The protein is expressed under LD and accelerates flowering, but is also induced under cold conditions. Cao et al. (2005) showed that *gi* mutants displayed higher sensitivity to freezing than the wild type with as well as without cold acclimation. When *gi* mutant and wild type were grown with 2 – 5h of cold stress

(4°C) per day, flowering was delayed in both, but with a greater effect in *gi* mutants than in the WT. For *Brassica rapa* Xie et al. (2015) proved the function of GI in photoperiod, by using *B. rapa* alleles to rescue a *gi* mutant in *A. thaliana*. However, only one of the two *B. rapa GI* alleles could rescue the freezing tolerance. This shows the genetic variation in *GI* alleles.
LONG VEGETATIVE PHASE 1 (LOV1) is another protein found to delay flowering under LD by inhibiting CO, but positively influencing freezing tolerance (Yoo et al. 2007). In this study, *GI* and *LOV1* were not found to be candidate genes, but the existence of other factors that connect flowering time under LD and freezing tolerance like LOV1 or GI, but are unknown to this date, are very much possible.

3.5.3 How does plant growth affect flowering time?

Hardening and vernalization in both experiments were done under the same conditions, in a temperature of 4 – 6°C and under short day conditions, just for different time periods (7 weeks for hardening in the freezing tolerance experiment, 8 or 4 weeks in the vernalization experiment, and 9 weeks in the day length and temperature experiment). Therefore, the state of the plant after Hardening, recorded during the freezing tolerance experiment from chapter 2, can be assumed to be similar to the state of the plants after vernalization in the vernalization experiment and the day length and temperature experiment from chapter 1, where no growth traits were recorded. The correlation coefficients between all traits after Hardening except Hypocotyl Length and had their highest correlation with days to flowering (DTF) after 4 weeks vernalization (V4, Table 3.1), closely followed by the correlation coefficients of DTF after eight weeks vernalization (V8). The traits regarding DTF of vernalized plants under the four different day length and temperature conditions from the day length and temperature experiment had all significant correlations with Vigor, Epicotyl Length and Stem Length after Hardening. Under long day conditions the correlations were slightly stronger.
In the phenotypic analysis of chapter 2, it was established that elongation of the stem, regardless if elongation of hypocotyl or epicotyl, increased the plants susceptibility to freezing damage. The conclusion was reached since all three traits had similar correlation coefficients, although we could not confirm a strong genetic connection in the QTL analysis. However, the correlation between the three stem length traits and DTF traits showed that the traits Hypocotyl Length and Epicotyl Length are distinctive. Hypocotyl Length after Hardening showed non-significant or weak correlations with flowering traits, while Epicotyl Length after Hardening was highly correlated with DTF, with few exceptions (Table 3.1 – Table 3.6, Fig. 3.1). Stem Length was calculated as the sum of Hypocotyl Length and Epicotyl Length after Hardening (Table 2.1) and since in the present context Hypocotyl Length and Epicotyl Length showed very different results, Stem Length as a sum was not considered a valuable trait and therefore disregarded for this discussion. In the vernalization experiment, DTF in vernalized plants (V4 and V8) was strongly correlated with Epicotyl Length after Hardening from the freezing tolerance experiments in the whole DH population and, with decreasing strength, in ‘winter‘ types and ‘spring’ types (Table 3.1, Table 3.2, Table 3.3). In the day length and temperature experiment, this strong correlation between early flowering and Epicotyl Length, was even more pronounced and correlation coefficients ranged between $-0.48 \leq r_S \leq -0.55$ for

DTF in all four day length and temperature conditions (Table 3.4). Interestingly, even though the four correlations were similar, Epicotyl Length was also significantly correlated with the effects of day length differences (r_S = -0.45 in 11°C and r_S = -0.35 in 22°C) and the effects of temperature differences (r_S = 0.19 under LD and r_S = 0.24 under SD, Table 3.4).
The biggest QTL for Epicotyl Length (EpiL_H_2) was located on chromosome A07 at 101 cM, which was the same position of a QTL cluster regulating flowering under short days (chapter 1.5.2) and had an overlapping confidence interval with a QTL for DTF without vernalization (V0d) and a QTL for DTF under cool short day conditions (SD11b, Appendix B). Other flowering time traits had QTL, which mapped further away, the furthest was a QTL for DTF after 4 weeks vernalization (V4d) at 65 cM. The QTL EpiL_H_2 had an additive effect of a = -0.34, meaning the Express617 allele prevented elongation of the epicotyl, while the QTL for DTF were positive, meaning the Express617 allele delayed flowering. This confirmed the negative correlation observed. Additionally, this region has an epistatic effect with another flowering time QTL cluster on C06, which was not masked with the Express617 allele on A07 (see chapter 1.5.2), which could add to the strength of the correlation, since flowering was delayed under all four conditions with the A07 Express617 allele (Fig.1.6). However, when comparing the correlations of the A07 DH4079 allele group (Table 3.5) with the A07 Express617 allele group (Table 3.6), both had strong and significant correlations between Epicotyl Length after Hardening and DTF under the four day length and temperature conditions. Therefore, this cannot be the only cause of this strong correlation. Epicotyl Length showed a QTL at 74.11 cM on chromosome C02 (EpiL_H_4, Table 2.7), where on both sides of EpiL_H_4 several flowering time QTL were mapped at 35-54 cM and around 100 cM (Appendix B). However, this is quite far away to explain such a strong correlation.
'Spring' types and 'winter' types both showed a negative correlation between Epicotyl Length and flowering time after 4 and 8 weeks of vernalization (Table 3.2, Table 3.3), although the correlation coefficients were lower in 'spring' types. However, while the 'winter' types showed also a significant correlation between Epicotyl Length and DTF without vernalization (r_S = 0.38, Table 3.2), while in 'spring' types the correlation between the two traits was not significant (Table 3.2). The scatterplots in Fig. 3.1 showed that not all early flowering 'spring' types developed a long epicotyl till after Hardening. Since stem elongation before vernalization or hardening treatment was not examined, it can only be speculated if the epicotyl elongated before or during the vernalization treatment. Hence it is unclear if the elongation was also influenced by cold treatment. This is sure an interesting point for further studies.
The Number of Leaves after Hardening and DTF of eight weeks vernalized plants as well as four weeks vernalized plants were significantly correlated with r_S = -0.22 and r_S = -0.24, respectively (Table 3.1). Therefore, DH lines, which managed to grow more leaves till the end of vernalization treatment, tend to flower earlier. This seems to indicate, that early development can have an influence on flowering time. However, when correlating the Number of Leaves after Hardening with the day length and temperature experiment, the correlation coefficients were only significant for DTF under cool long days (LD11, r_S = -0.13) and the effect of temperature differences under long days (11-22LD, r_S = -0.15, Table 3.4).

The QTL analysis revealed no collocating QTL between Number of Leaves after Hardening and any flowering time trait.

Vigor after Hardening was as well significantly correlated with DTF after eight weeks of vernalization (r_S = -0.31) and DTF four weeks after vernalization (r_S = -0.34) in the whole DH population (Table 3.1). With the day length and temperature experiment, the correlations were lower for all four conditions with $-0.16 \leq r_S \leq -0.26$ (Table 3.4). Like with Number of Leaves after Hardening, more developed plants seem to have an advantage to induce flowering time earlier. However, unlike Number of Leaves after Hardening, Vigor also showed a correlation with DTF after V0 with r_S = -0.25 (Table 3.1). This was also observed in 'winter' types (-0.24, Table 3.2), but not in 'spring' types (Table 3.3).

As this study was not focused on exploring factors contributing to growth, the results may be incomplete. Especially in the QTL analysis the search for candidate genes was not focused on investigating genes for growth regulation and is therefore incomplete in regards of this topic. However, many phytohormones that are known to regulate growth are also regulating the plants development. Gibberellin is a well-known growth regulator (Eremina et al. 2016), while also involved in flowering time regulation (Blümel et al. 2015). Circadian clock is an important regulator in flowering time (Blümel et al. 2015) as well as growth (Kinmonth-Schultz et al. 2013) often involving phytohormones like brassinosteroids (Lv and Li 2020). Since flowering requires the plant to invest a lot of resources, and to go through morphological changes, the connection found between growth stage of the plant and flowering time found in this study through correlations is not unexpected. However, the influence of growth and vigor on flowering time is not much researched.

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4 Summary

Two important abiotic factors for plants are temperature and day length. Long day and short day are signals that can induce morphological and developmental changes like flower induction. So-called short day plants need a day length below a critical length, while long day plants need a day length above a critical length to initiate flowering. Day length is also determining the circadian clock, a complex network of genes that change the biochemistry of a plant throughout the day. Such biochemical processes are highly influenced by temperature, too. The temperature optimum and sensitivity of a plant is not only specific, but also dependent on circadian cycle and plant stage.

Brassica napus L. or oilseed rape is the third largest source of vegetable oil in the world and the most important oil crop in the temperate regions of the earth. The European Commission reported a gross production of nearly 17 Mio tonnes of rapeseed in 2021 out of a total oilseeds production of ca. 30 Mio tonnes (including sunflower seed, soybean and linseed). In regions with milder winters like Western Europe, winter oilseed rape is cultivated, while in regions with harsher winters like Canada, Eastern and Northern Europe, spring types are preferred. Winter crops require vernalization, a prolonged period of cold initiating flowering in plants with vernalization requirement. Winter oilseed rape will be autumn sown, while spring oilseed rape lacks vernalization requirement and will be sown in spring. The vernalization requirement in winter types prevents preliminary flowering in autumn. *Brassica napus* is considered a long day plant, meaning that a certain minimum day length is required to initiate flowering. Even after the initiation of flowering a combination of day length and temperature is regulating flowering time by either delaying or accelerating flowering.

Cool temperatures are not only necessary for the fulfillment of vernalization requirement, but also initiate an increase in freezing tolerance to prevent frost damage through a process called hardening. Freezing tolerance is the ability to withstand sub-zero temperatures by preventing lethal damage to the cell membranes by ice crystals. In the winter oilseed rape, an elongated stem before winter is said to indicate lower freezing tolerance. Since hardening and vernalization are happening during the same timeframe in late autumn and winter, a connection between the mechanisms of vernalization and freezing tolerance of *Brassica napus* was generally assumed. However, newer studies question this assumption.

In a nutshell, the abiotic factors temperature and day length influence oilseed rape plants throughout the year and through a plants whole life cycle, specifically on vernalization, flowering time and freezing tolerance.

In this thesis, a doubled haploid (DH) population derived from a cross of a winter and a spring type oilseed rape was examined for the influence of temperature and day length. The following research questions were asked:

a) How does vernalization requirement of DH lines influence days to flowering under greenhouse conditions with and without vernalization treatment?
b) Which effect do day length and temperature have on the flowering time of fully vernalized plants and how do the effects of these two abiotic factors interact?
c) How does freezing tolerance varies in the DH population and can freezing tolerance be predicted by the phenotype before frost treatment?

d) Is there a connection between the gene networks of freezing tolerance and vernalization requirement?

The DH population consisted of 194 lines derived from a cross between the inbred line 617 of the German winter oilseed rape cultivar ‘Express’ and spring-type doubled haploid line DH4079 derived from the Swedish cultivar ‘Topas’. A published linkage marker map consisting of 21,583 SNP markers distributed over 19 linkage groups was used to develop a framework map consisting of 767 markers. QTL mapping was performed with WinQTL Cartographer software version 2.5 for all experiments. Candidate genes were searched in the reference genome of rapeseed line ‘Damor-*bzh*’. The following three sets of replicated experiments were performed:

1. In the vernalization experiment, the plants were vernalized for 0, 4, and 8 weeks and grown in the greenhouse in five replications. Days to flowering (DTF) were recorded starting from the end of vernalization when plants were transferred to the greenhouse until the opening of the first flower. Plants that did not flower after 100 days but showed flower buds were recorded with a value of 115 days and those that did not show flower buds with 130 days.
2. The effect of day length and temperature on flowering time of nine weeks vernalized plants was determined in the day length and temperature experiment. The experiment was a split-split plot design with two factor levels in the main factor temperature (11 and 22°C) and two factor levels in the split factor day length (8 and 16 h) with 5 replications. A reduced set of 188 DH lines, the parental genotypes, and the F1 were used. The experiment was terminated at day 135. Genotypes that did not flower at day 135 but showed buds were recorded with a value of 150 days and if they did not show buds were recorded with a value of 165 days.
3. In the freezing tolerance experiment a reduced set of 184 DH lines was used. The DH lines, the parents and the F1 (200 plants in total) were sown in Styrofoam boxes and hardened for seven weeks at 4 °C and 8 hours artificial light. The experimental design was a simple rectangular lattice design with two sets. This experiment was repeated nine times. The plants were scored for several traits after hardening (e.g. Epicotyl Length and total Stem Length in cm), four days after the frost treatment (e.g. Stem Damage and Leaf Damage sored 1-9), and after a regrowth period (11 days after the end of the frost treatment, e.g. Death as binary).

Correlation coefficients of all the traits recorded from all three experiments were calculated and studied.

The vernalization experiment revealed a bimodal distribution of the DH Population regarding days to flowering without vernalization. This allowed for a separation of the DH population into ‘spring’ and ‘winter’ types. A major QTL for DTF without vernalization (V0a), located on A02 at 42 cM, explained 56% of the phenotypic variance and had an additive effect of 20.2 days. QTL V0a was discovered to have an overlapping confidence interval with QTL for several other flowering time traits: A QTL for DTF after 4 weeks vernalization (V4a) and a QTL for DTF after eight weeks of vernalization (V8a) mapped at 43 cM. In the temperature

and day length experiment the QTL analysis revealed a QTL for DTF under warm long day conditions (LD22a) and one QTL for flowering under cool long day conditions (LD11a) collocating with the QTL V8a and V4a. Furthermore, a QTL for DTF under warm short days (SD22a) mapped at 44 cM on the same chromosome. In all these treatments, vernalization was applied, and the additive effects of the QTL were ranging from 2.3 (V8a) to 5.8 days (SD22a). This led to the conclusion, that this locus was also a general flowering time loci. The most likely candidate gene was the well-known flowering time gene *FLOWERING LOCUS T*.

The day length and temperature experiment showed the great influence of day length. The ANOVA showed a component of variance for day length of 656.9 days², while for temperature it was only 34.9 days². Flowering tended to be delayed under short days. The delay depended on the genotype and ranged from 7 to 100 days under 22°C. Interestingly, the interaction between day length and temperature had a bigger effect than temperature alone (variance components of 53.4 days² vs 34.9 days²). Under short days, high temperature led more to a delay of flowering in some DH lines, but acceleration in others (with a range of -44 to 40 days), compared to flowering time under cool short day conditions (-20 to 44 days). The QTL analysis revealed effects on two homologous regions on chromosome C06 and A07. On C06, spring-type alleles delayed flowering under short days and warmer temperature, while on A07, winter-type alleles showed the same effect. On A07 there was also a minor vernalization QTL V0d located. For both regions the candidate gene *EARLY FLOWERING IN SHORT DAYS* was found. The QTL on these homologous regions had epistatic effects where the DH4079 alleles on A07 masked the allelic effect on C06.

In the freezing tolerance experiment, a strong correlation between stem elongation and freezing tolerance was found. The highest correlation coefficient was r_S= 0.45 between the Stem Damage and Stem Length. However, the QTL analysis found only weak evidence connecting the two traits genetically. The correlation coefficients of DTF without vernalization with Stem Damage after frost treatment r_S= -0.25, and with Leaf Damage after frost treatment r_S= -0.22. No QTL for traits after frost treatment was collocating with the major QTL for vernalization requirement V0a on A02. However, vernalization QTL V0e as well as a QTL for Stem Damage (Stem_ Dam_F_1) and a QTL for Death Rate (DeathRate_R_1) mapped in the same position on C02 at 100.4 cM. As a surprising result, the major QTL for traits after frost treatment were located on C06, in the same region that was a hot spot for flowering time under short days and warm temperatures, but DH lines which did delay flowering under short days were observed to be more sensitive to freezing damage. This is contradictory to the current literature.

The research questions can be answered as following:

(a) In this DH rape seed population, vernalization requirement is mainly determined by one locus. This locus showed also an effect on flowering time after vernalization treatment. The major flowering time QTL V0a is therefore a part of a general flowering time locus.

(b) The difference in day length between 8h and 16 h had a large effect on flowering time in this DH population. Short days delay the flowering time. Temperature (11°C and 22°C) alone had a smaller impact than the interaction of temperature and day length. These two abiotic factors should therefore be studied in dependence of each other.

Two homologous regions on A07 and C06 were hot spots for temperature and day length dependent flowering time in this DH population.

(c) The connection between stem elongation and low freezing tolerance could clearly be confirmed with a high correlation, but less convincingly with the QTL analysis. This might be due to the highly quantitative and complex nature of the trait freezing tolerance.

(d) The hypothesis that high vernalization requirement is correlated with high freezing tolerance could be confirmed. The traits were significantly correlated, and a minor QTL for vernalization collocated with QTL for two traits regarding freezing tolerance, Stem Damage and Death Rate. The major QTL for freezing tolerance mapped in the same region as major QTL for flowering time under short days and warm temperatures. In conclusion, the gene network of sensing day length and temperature to regulate flowering are connected to the gene network for freezing tolerance.

In the future unpredictable winters, warmer spring temperatures, late frost and other unusual and extreme climate conditions will happen more often due to climate change, and pose increased challenges for agriculture, specifically a secure crop production. Here it is shown, how the genetic networks of temperature and day length response as well as vernalization, flowering time regulation, and freezing tolerance are interconnected. Such a genetic diversity and complexity in crops like oilseed rape are posing a huge challenge for breeders. But the utilization of different genes as well as gene homologs will also be a chance for plant breeders to combat the emerging challenges by climate change.

5 Zusammenfassung

Zwei wichtige abiotische Faktoren für Pflanzen sind Temperatur und Tageslänge. Langtag und Kurztag sind Signale, die morphologische und entwicklungsbedingte Veränderungen wie die Blüteninduktion auslösen können. Sogenannte Kurztagspflanzen benötigen eine Tageslänge unterhalb einer kritischen Länge, während Langtagspflanzen eine Tageslänge oberhalb einer kritischen Länge für die Blühinduktion benötigen. Die Tageslänge bestimmt auch die zirkadiane („innere“) Uhr, ein komplexes Netzwerk von Genen, die die Biochemie einer Pflanze im Laufe des Tages verändern. Solche biochemischen Prozesse werden auch stark von der Temperatur beeinflusst. Das Temperaturoptimum und die Temperaturempfindlichkeit einer Pflanze sind nicht nur artspezifisch, sondern hängen auch vom zirkadianen Zyklus und dem Pflanzenstadium ab.

Brassica napus L. (Raps) ist die drittgrößte Quelle für Pflanzenöl in der Welt und die wichtigste Ölpflanze in den gemäßigten Regionen der Erde. Die Europäische Kommission meldete für 2021 eine Bruttoproduktion von fast 17 Mio. Tonnen Raps bei einer Gesamtproduktion von ca. 30 Mio. Tonnen Ölsaaten (einschließlich Sonnenblume, Sojabohne und Lein). In Regionen mit milderen Wintern wie Westeuropa wird Winterraps angebaut, während in Regionen mit strengeren Wintern wie Kanada, Ost- und Nordeuropa Sommerraps bevorzugt werden. Winterkulturen erfordern eine Vernalisation, eine längere Kälteperiode, die bei Pflanzen, die eine Vernalisation benötigen, die Blüte ermöglicht. Winterraps wird im Herbst gesät, während Sommerraps keine Vernalisation benötigt und im Frühjahr gesät wird. Die Vernalisationsanforderung bei den Wintersorten verhindert eine

verfrühte Blüte im Herbst. *Brassica napus* gilt als Langtagspflanze, was bedeutet, dass eine bestimmte Mindesttageslänge für die Blühinduktion erforderlich ist. Auch nach der Blühinduktion reguliert eine Kombination aus Tageslänge und Temperatur den Blühzeitpunkt, indem sie die Blüte entweder verzögert oder beschleunigt.
Kühle Temperaturen sind nicht nur für die Erfüllung der Vernalisationsanforderung notwendig, sondern bewirken auch eine Erhöhung der Frosttoleranz durch einen als Abhärtung bezeichneten Prozess. Frosttoleranz ist die Fähigkeit, Minusgrade zu überstehen, indem letale Schäden an den Zellmembranen durch Eiskristalle verhindert werden. Bei Winterraps gilt ein elongierter Stängel vor dem Winter als Hinweis auf eine geringere Frosttoleranz. Da Abhärtung und Vernalisation zum gleichen Zeitraum im Spätherbst und Winter stattfinden, wurde ein Zusammenhang zwischen den Mechanismen der Vernalisation und der Frosttoleranz von *Brassica napus* allgemein angenommen. Neuere Studien stellen diese Vermutung jedoch in Frage.
Zusammenfassend lässt sich sagen, dass Raps während des ganzen Jahres und über den gesamten Lebenszyklus hinweg von den abiotischen Faktoren Temperatur und Tageslänge beeinflusst wird, insbesondere durch Vernalisation, in der Blütezeit und für die Frosthärtung.
In dieser Arbeit wurde eine doppelt haploide (DH) Population, die aus einer Kreuzung eines Winter- und eines Sommerrapses stammt, auf den Einfluss von Temperatur und Tageslänge untersucht. Die folgenden Forschungsfragen wurden gestellt:

a) Wie beeinflusst der Vernalisationsbedarf der DH-Linien die Tage bis zur Blüte unter Gewächshausbedingungen mit und ohne Vernalisationsbehandlung?
b) Welchen Einfluss haben Tageslänge und Temperatur auf die Blütezeit von voll vernalisierten Pflanzen und wie interagieren die Effekte dieser beiden abiotischen Faktoren?
c) Wie variiert die Frosttoleranz in der DH-Population und kann die Frosttoleranz durch den Phänotyp vor der Frostbehandlung vorhergesagt werden?
d) Gibt es einen Zusammenhang zwischen den Gennetzwerken der Frosttoleranz und dem Vernalisationsbedürfnis?

Die DH-Population bestand aus 194 Linien, die aus einer Kreuzung zwischen der Inzuchtlinie 617 der deutschen Winterrapssorte 'Express' und der doppelhaploiden Linie DH4079 aus der schwedischen Sommersorte 'Topas' stammten. Eine veröffentlichte Kopplungsmarkerkarte, die aus 21.583 SNP-Markern besteht, die auf 19 Kopplungsgruppen verteilt sind, wurde verwendet, um eine aus 767 Markern bestehende „Framework“-Karte zu entwickeln. Die QTL-Kartierung wurde für alle Experimente mit der Software WinQTL Cartographer Version 2.5 durchgeführt. Die Kandidatengene wurden im Referenzgenom der Rapslinie 'Damor-bzh' gesucht. Es wurden die folgenden drei Gruppen von wiederholten Versuchen durchgeführt:
1. Bei den Vernalisationsversuchen wurden die Pflanzen 0, 4 und 8 Wochen vernalisiert und in fünf Wiederholungen im Gewächshaus angebaut. Die Tage bis zur Blüte („days to flowering“ - DTF) wurden ab dem Ende der Vernalisation, als die Pflanzen ins Gewächshaus gestellt wurden, bis zum Öffnen der ersten Blüte gemessen. Pflanzen, die nach 100 Tagen nicht blühten, aber Blütenknospen aufwiesen, wurden mit einem Wert von 115 Tagen erfasst, Pflanzen, die keine Blütenknospen aufwiesen, mit 130 Tagen.

2. Die Wirkung von Tageslänge und Temperatur auf die Blütezeit von neun Wochen vernalisierten Pflanzen wurde in den Versuchen zu Tageslänge und Temperatur ermittelt. Der Versuch war ein Split-Split-Plot-Design mit zwei Faktorebenen im Hauptfaktor Temperatur (11 und 22 °C) und zwei Faktorebenen im Split-Faktor Tageslänge (8 und 16 h) mit 5 Wiederholungen. Es wurde ein reduzierter Satz von 188 DH-Linien, die elterlichen Genotypen und die F1 verwendet. Der Versuch wurde am Tag 135 beendet. Genotypen, die am Tag 135 nicht blühten, aber Knospen aufwiesen, wurden mit einem Wert von 150 Tagen erfasst, und wenn sie keine Knospen aufwiesen, wurden sie mit einem Wert von 165 Tagen erfasst.
3. Bei den Versuchen zur Frosttoleranz wurde ein reduzierter Satz von 184 DH-Linien verwendet. Die DH-Linien, die Eltern und die F1 (insgesamt 200 Pflanzen) wurden in Styroporkisten ausgesät und sieben Wochen lang bei 4 °C und 8 Stunden Kunstlicht abgehärtet. Der Versuchsplan war ein einfacher rechteckiger Gitterversuch mit zwei Gruppen. Dieser Versuch wurde neunmal wiederholt. Die Pflanzen wurden zu drei Zeitpunkten auf verschiedene Merkmale hin untersucht: nach der Abhärtung (z. B. Epikotyllänge und Gesamtstängellänge in cm), vier Tage nach der Frostbehandlung (z. B. Stängelschäden und Blattschäden, bonitiert mit 1-9) und nach einer Erholungsphase (11 Tage nach Ende der Frostbehandlung, z. B. Absterben als binäres Merkmal).
Die Korrelationskoeffizienten aller Merkmale, die in allen drei Versuchen erfasst wurden, wurden berechnet und untersucht.

Die Vernalisationsversuche zeigten eine bimodale Verteilung der DH-Population hinsichtlich der Tage bis zur Blüte ohne Vernalisation. Dies ermöglichte eine Unterteilung der DH-Population in "Sommer" und "Winter"-Typen. Ein wichtiger QTL für DTF ohne Vernalisation (V0a), der auf A02 bei 42 cM lag, erklärte 56 % der phänotypischen Varianz und hatte einen additiven Effekt von 20,2 Tagen. Der QTL V0a wies ein überlappendes Konfidenzintervall mit QTL für mehrere andere Blütezeitmerkmale auf: Ein QTL für DTF nach 4 Wochen Vernalisation (V4a) und ein QTL für DTF nach acht Wochen Vernalisation (V8a) wurden auf 43 cM kartiert. In den Temperatur- und Tageslängenexperimenten ergab die QTL-Analyse einen QTL für DTF unter warmen Langtagsbedingungen (LD22a) und einen QTL für Blüte unter kühlen Langtagsbedingungen (LD11a), die mit den QTL V8a und V4a kollokieren. Darüber hinaus wurde ein QTL für DTF unter warmen, kurzen Tagen (SD22a) bei 44 cM auf demselben Chromosom kartiert. Bei all diesen Behandlungen wurde eine Vernalisation durchgeführt, und die additiven Effekte des QTL lagen zwischen 2,3 (V8a) und 5,8 Tagen (SD22a). Dies führte zu der Schlussfolgerung, dass es sich bei diesem Locus auch um einen allgemeinen Blütezeitlocus handelt. Das wahrscheinlichste Kandidatengen war das bekannte Blühgen FLOWERING LOCUS T.
Die Versuche zur Tageslänge und Temperatur zeigten den großen Einfluss der Tageslänge. Die ANOVA ergab eine Varianzkomponente für die Tageslänge von 656,9 Tagen², während sie für die Temperatur nur 34,9 Tage² betrug. Die Blüte verzögerte sich tendenziell bei kurzen Tagen. Die Verzögerung hing vom Genotyp ab und reichte von 7 bis 100 Tagen bei 22 °C. Interessanterweise hatte die Wechselwirkung zwischen Tageslänge und Temperatur einen größeren Effekt als die Temperatur allein (Varianzkomponente von 53,4 Tagen²

gegenüber 34,9 Tagen[2]). Bei kurzen Tagen führte eine hohe Temperatur bei einigen DH-Linien eher zu einer Verzögerung der Blüte, bei anderen jedoch zu einer Beschleunigung (mit einer Spanne von -44 bis 40 Tagen), verglichen mit der Blütezeit unter kühlen Kurztagsbedingungen (-20 bis 44 Tage). Die QTL-Analyse ergab Auswirkungen auf zwei homologe Regionen auf den Chromosomen C06 und A07. Auf C06 waren es Sommerrapsallele, die die Blüte bei kurzen Tagen und wärmeren Temperaturen verzögerten, aber auf A07 waren es Winterrapsallele, die die Blüte unter gleichen Bedingungen verzögerten. Auf A07 befand sich auch ein kleiner Vernalisations-QTL V0d. Für beide Regionen wurde das Kandidatengen EARLY FLOWERING IN SHORT DAYS gefunden. Die QTL auf diesen homologen Regionen hatten epistatische Effekte, wobei das DH4079-Allel auf A07 den allelischen Effekt auf C06 maskierte.

Bei den Versuchen zur Frosttoleranz wurde eine starke Korrelation zwischen Stängelelongation und Frosttoleranz festgestellt. Der höchste Korrelationskoeffizient war r_S= 0,45 zwischen der Stängelschädigung nach der Frostbehandlung und der Stängellänge davor. Die QTL-Analyse ergab jedoch nur schwache Hinweise auf einen genetischen Zusammenhang zwischen den beiden Merkmalen. Die Korrelationskoeffizienten von DTF ohne Vernalisation mit Stängelschäden nach der Frostbehandlung r_S= -0,25 und mit Blattschäden nach der Frostbehandlung r_S= -0,22. Kein QTL für Merkmale nach Frostbehandlung war mit dem Haupt-QTL für die Vernalisationsanforderung V0a auf A02 kollokiert. Der Vernalisations-QTL V0e sowie ein QTL für Stängelschäden (Stem_ Dam_F_1) und ein QTL für die Absterberate (DeathRate_R_1) wurden jedoch an der gleichen Stelle auf C02 bei 100,4 cM kartiert. Überraschenderweise befanden sich die wichtigsten QTL für Merkmale nach Frostbehandlung auf C06, in derselben Region, die ein Hotspot für die Blütezeit bei kurzen Tagen und warmen Temperaturen war, allerdings wurde beobachtet wie die DH Linien, die unter Kurztag ihren Blühzeitpunkt verzögerten, eine höhere Empfindlichkeit gegenüber Frost aufwiesen. Dies ist gegensätzlich zur derzeitigen Literatur.

Die Forschungsfragen können wie folgt beantwortet werden:

(a) In dieser DH-Rapspopulation wird der Vernalisationsbedarf hauptsächlich durch einen Locus bestimmt. Dieser Locus zeigte auch eine Wirkung auf die Blütezeit nach einer Vernalisationsbehandlung. Der Haupt-QTL für die Blütezeit V0a ist daher Teil eines allgemeinen Locus für die Blütezeit.

(b) Der Unterschied in der Tageslänge zwischen 8 h und 16 h hatte in dieser DH-Population einen großen Einfluss auf die Blütezeit. Kurze Tage verzögern die Blütezeit. Die Temperatur (11°C und 22°C) allein hatte einen geringeren Einfluss als die Interaktion von Temperatur und Tageslänge. Diese beiden abiotischen Faktoren sollten daher in Abhängigkeit voneinander untersucht werden. Zwei homologe Regionen auf A07 und C06 waren Hotspots für die temperatur- und tageslängenabhängige Blütezeit in dieser DH Population.

(c) Der Zusammenhang zwischen Stängelelongation und geringer Frosttoleranz konnte mit einer hohen Korrelation eindeutig bestätigt werden, jedoch weniger überzeugend mit der QTL-Analyse. Dies könnte auf die hoch quantitative und komplexe Natur des Merkmals Frosttoleranz zurückzuführen sein.

(d) Die Hypothese, dass ein hoher Vernalisationsbedarf mit hoher Frosttoleranz korreliert ist, konnte bestätigt werden. Die Merkmale waren signifikant miteinander korreliert, und ein QTL für die Vernalisation kollokierte mit QTL für zwei Merkmale der Frosttoleranz: Stängelschäden und Absterberate. Die Haupt-QTL für Frosttoleranz wurde in derselben Region wie die Haupt-QTL für die Blütezeit bei kurzen Tagen und warmen Temperaturen kartiert. Zusammenfassend lässt sich sagen, dass das Gennetzwerk für die Antwort auf Tageslänge und die Temperatur in Bezug auf die Regulation des Blühzeitpunktes verbunden ist mit dem Gennetzwerk für Frosttoleranz.

In Zukunft werden unvorhersehbare Winter, wärmere Frühlingstemperaturen, Spätfrost und andere ungewöhnliche und extreme Klimabedingungen aufgrund des Klimawandels häufiger auftreten und die Landwirtschaft vor große Herausforderungen, wie die Sicherung der Nahrungsproduktion, stellen. Hier wird gezeigt, wie die genetischen Netzwerke der Reaktion auf Temperatur- und Tageslängen sowie der Vernalisation, der Blühzeitregulation und der Frosttoleranz miteinander verbunden sind. Eine solche genetische Vielfalt und Komplexität in Kulturpflanzen wie dem Raps stellt eine große Herausforderung für die Züchter dar. Die Nutzung verschiedener Gene und Gen-Homologe ist aber auch eine Chance für die Pflanzenzüchtung, die neuen Herausforderungen des Klimawandels zu bewältigen.

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7 Appendix

Appendix A: Phenotypic flowering time data from the vernalization experiment and the day length and temperature experiment for each DH line as well as parental genotypes and F1 as means over replications in days.

DH Line		Vernalization experiment			Temperature and day length experiment							
No.	type	V0	V4	V8	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
1	'winter'	75.8	47.5	32.3	54.2	37.4	80.0	77.8	25.8	40.4	16.8	2.2
2	'winter'	79.0	47.5	33.6	58.0	43.3	116.0	112.0	58.0	68.8	14.8	4.0
4	'winter'	76.4	37.8	29.2	41.8	24.0	63.0	49.0	21.2	25.0	17.8	14.0
5	'winter'	112.6	55.0	38.8	58.4	69.0	109.0	125.0	50.6	56.0	-10.6	-16.0
6	'winter'	87.0	47.3	38.5	62.6	42.4	97.8	77.5	35.2	35.1	20.2	20.3
7	'winter'	83.6	42.8	33.8	53.8	44.8	109.0	129.7	55.2	84.9	9.0	-20.7
8	'winter'	102.0	45.8	34.4	57.4	43.3	90.3	94.8	32.9	51.5	14.2	-4.4
9	'spring'	64.4	38.8	32.0	46.0	28.0	81.8	57.6	35.8	29.6	18.0	24.2
12	'spring'	64.4	38.5	29.0	45.3	27.0	63.4	43.5	18.2	16.5	18.3	19.9
16	'spring'	48.0	35.3	25.6	41.0	26.2	56.6	33.3	15.6	7.1	14.8	23.3
19	'spring'	48.6	34.8	27.0	39.4	25.8	64.0	68.2	24.6	42.5	13.7	-4.2
20	'winter'	108.2	58.5	37.6	58.8	39.6	85.6	92.3	26.8	52.7	19.2	-6.7
21	'winter'	104.0	53.8	39.2	NA	NA	NA	NA	NA	NA	NA	NA
22	'spring'	60.8	38.0	31.6	46.4	26.2	69.8	50.3	23.4	24.1	20.2	19.6
23	'spring'	42.8	36.8	28.4	43.6	30.8	74.8	59.7	31.2	28.9	12.8	15.1
24	'spring'	55.6	42.5	33.4	48.8	35.8	97.8	113.3	49.0	77.5	13.0	-15.6
25	'spring'	68.5	40.5	35.0	55.2	33.0	115.2	121.2	60.0	88.2	22.2	-6.0
26	'spring'	45.4	36.8	35.6	40.2	25.3	73.0	83.2	32.8	58.0	15.0	-10.2
27	'spring'	66.0	45.5	33.4	69.6	25.8	92.0	66.0	22.4	40.3	43.9	26.0
28	'winter'	94.4	46.3	38.2	51.8	45.0	97.0	115.8	45.2	70.8	6.8	-18.8
32	'winter'	118.0	44.3	35.4	60.2	40.5	82.2	112.3	22.0	71.8	19.7	-30.1
36	'spring'	41.6	30.5	30.5	33.8	17.8	42.3	28.0	8.5	10.2	16.0	14.3
39	'winter'	86.4	52.5	39.6	75.0	81.0	139.0	150.3	64.0	69.3	-6.0	-11.3
40	'winter'	106.3	41.5	33.2	51.2	30.2	71.8	56.0	20.6	25.8	21.0	15.8
41	'winter'	76.6	41.5	32.6	57.0	38.2	75.4	81.5	18.4	43.3	18.8	-6.1
43	'spring'	48.2	34.8	26.2	38.0	17.2	49.8	29.2	11.8	12.0	20.8	20.6
45	'winter'	96.8	40.3	33.8	50.6	38.8	100.8	89.0	50.2	50.2	11.8	11.8
46	'winter'	125.2	48.8	42.8	NA	NA	NA	NA	NA	NA	NA	NA
49	'winter'	78.4	36.8	35.0	54.6	48.0	88.6	118.4	34.0	70.4	6.6	-29.8
50	'spring'	39.0	33.3	28.0	45.2	26.2	66.5	48.8	21.3	22.6	19.0	17.7
52	'winter'	111.8	48.3	34.0	63.2	37.8	91.3	62.2	28.1	24.4	25.4	29.1
54	'spring'	54.8	34.5	28.8	40.8	18.8	56.3	33.5	15.5	14.7	22.0	22.8
55	'spring'	50.4	35.8	30.2	61.0	27.0	71.8	58.8	10.8	31.8	34.0	13.0
56	'spring'	61.2	50.3	39.3	59.4	51.7	105.3	86.3	45.9	34.7	7.7	19.0
57	'spring'	49.0	35.5	30.0	44.2	27.8	60.2	56.6	16.0	28.8	16.4	3.6
59	'spring'	59.0	38.0	33.4	52.2	36.6	70.6	78.3	18.4	41.7	15.6	-7.7
62	'winter'	107.5	46.3	34.4	56.8	43.8	84.5	76.0	27.7	32.2	13.0	8.5
63	'winter'	77.8	41.3	35.4	54.8	35.8	78.4	74.3	23.7	38.5	19.0	4.2
64	'winter'	82.8	42.3	30.8	44.6	23.2	64.6	45.0	20.0	21.8	21.4	19.6
65	'winter'	111.8	45.3	34.8	48.8	26.6	72.6	97.2	23.8	70.6	22.2	-24.6
66	'winter'	93.5	45.0	34.4	60.4	33.2	84.2	89.8	23.8	56.6	27.2	-5.6

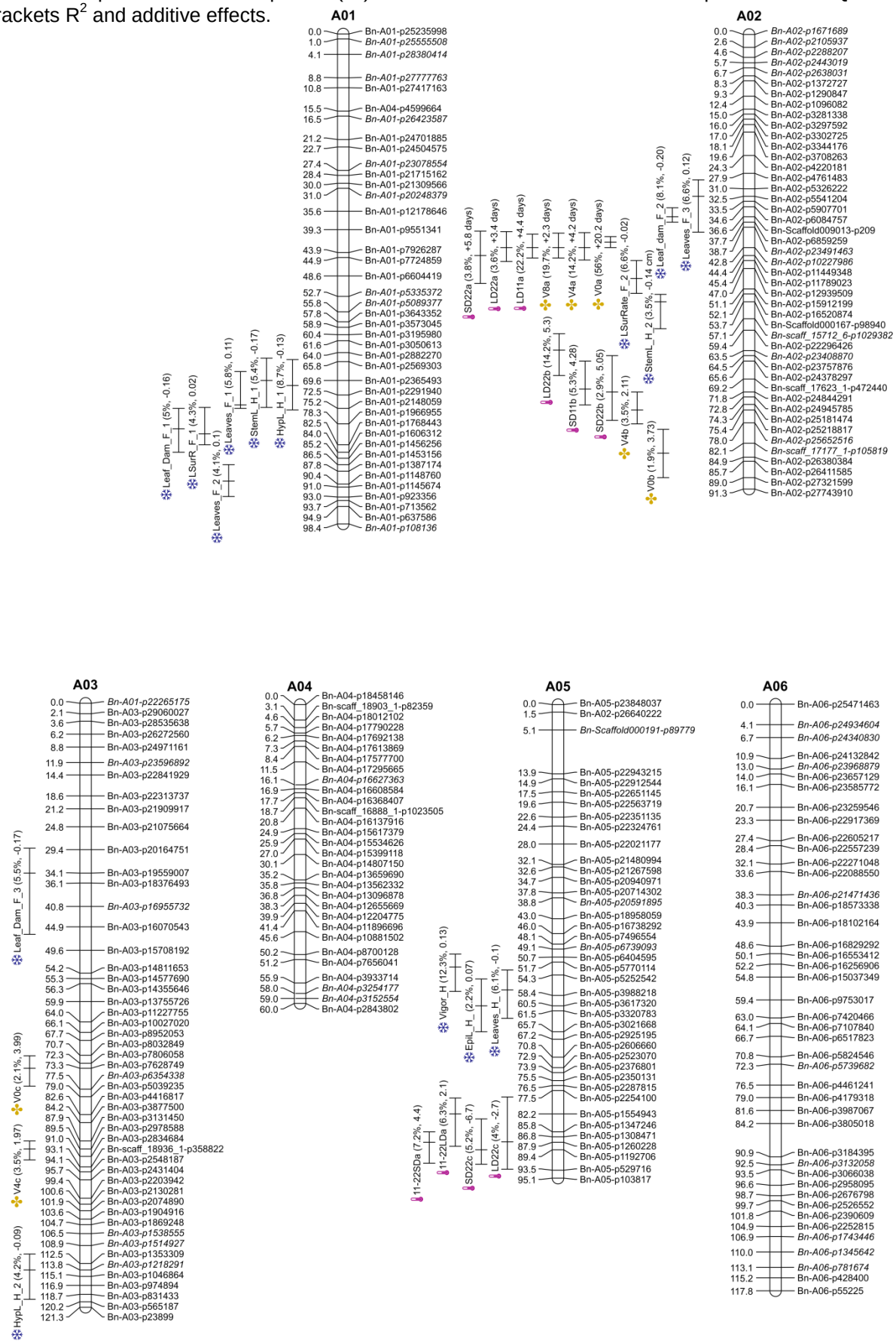
DH Line		Vernalization experiment			Temperature and day length experiment							
No.	type	V0	V4	V8	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
67	'spring'	42.4	36.0	30.0	43.2	28.6	69.0	62.6	25.8	34.0	14.6	6.4
68	'winter'	103.2	43.0	35.4	52.2	30.4	82.4	61.0	30.2	30.6	21.8	21.4
69	'spring'	62.0	38.0	32.6	50.8	26.0	80.5	74.4	29.7	48.4	24.8	6.1
70	'spring'	44.0	33.3	27.6	NA	NA	NA	NA	NA	NA	NA	NA
71	'winter'	81.4	40.8	33.0	53.2	49.2	75.8	66.4	22.6	17.2	4.0	9.4
72	'spring'	49.6	34.8	30.0	44.2	25.7	74.2	67.3	30.0	41.6	18.5	7.0
73	'winter'	122.6	64.5	38.6	55.8	51.8	77.6	59.5	21.8	7.7	4.0	18.1
74	'spring'	65.8	39.0	34.0	49.0	31.4	81.0	60.0	32.0	28.6	17.6	21.0
75	'spring'	54.4	36.5	32.4	46.2	27.8	84.5	82.0	38.3	54.2	18.4	2.5
76	'spring'	52.4	35.5	29.2	41.2	22.0	59.6	42.8	18.4	20.8	19.2	16.8
80	'spring'	62.0	45.0	35.8	49.4	28.6	84.2	90.5	34.8	61.9	20.8	-6.3
81	'winter'	84.6	41.3	35.2	NA	NA	NA	NA	NA	NA	NA	NA
82	'winter'	72.2	39.5	34.6	56.0	33.0	93.6	115.0	37.6	82.0	23.0	-21.4
84	'spring'	58.2	42.5	33.4	48.2	25.5	74.2	69.3	26.0	43.8	22.7	5.0
85	'winter'	77.3	44.3	34.2	49.6	31.3	65.0	56.0	15.4	24.8	18.4	9.0
88	'winter'	94.6	46.0	39.2	56.2	34.5	84.8	65.8	28.6	31.3	21.7	19.0
89	'spring'	54.4	41.0	39.0	50.4	26.2	86.6	87.4	36.2	61.2	24.2	-0.8
90	'spring'	44.2	35.8	31.0	37.4	19.0	58.8	35.4	21.4	16.4	18.4	23.4
91	'spring'	60.4	36.3	35.0	40.6	23.0	60.6	42.6	20.0	19.6	17.6	18.0
92	'spring'	57.2	46.3	37.4	57.6	30.5	117.5	117.3	59.9	86.8	27.1	0.2
93	'winter'	130.0	95.5	57.0	89.4	105.0	152.8	165.0	63.4	60.0	-15.6	-12.2
94	'spring'	55.0	38.5	33.6	44.5	22.5	71.4	45.0	26.9	22.5	22.0	26.4
95	'winter'	102.3	42.5	32.4	47.6	27.2	68.0	52.2	20.4	25.0	20.4	15.8
96	'winter'	98.8	43.8	37.0	59.0	48.6	83.6	96.6	24.6	48.0	10.4	-13.0
97	'spring'	44.2	36.8	29.3	38.3	17.8	53.4	39.0	15.2	21.2	20.5	14.4
98	'spring'	45.3	33.0	30.6	40.0	17.3	63.8	50.3	23.8	33.0	22.8	13.5
99	'winter'	101.6	53.8	37.5	60.0	45.2	97.8	99.6	37.8	54.4	14.8	-1.8
100	'spring'	46.6	37.3	32.8	49.6	35.0	78.3	91.0	28.7	56.0	14.6	-12.8
101	'spring'	56.8	35.0	31.6	42.6	24.0	66.6	54.0	24.0	30.0	18.6	12.6
103	'spring'	56.2	38.5	34.0	48.0	29.0	79.2	76.0	31.2	47.0	19.0	3.2
104	'spring'	54.8	37.5	36.0	44.2	27.6	63.6	60.3	19.4	32.7	16.6	3.4
105	'winter'	106.2	41.3	33.6	49.2	32.8	76.4	63.2	27.2	30.4	16.4	13.2
106	'winter'	107.2	47.3	45.4	46.8	33.0	63.2	43.0	16.4	10.0	13.8	20.2
107	'spring'	71.6	38.0	33.4	46.2	26.4	58.7	49.4	12.5	23.0	19.8	9.3
109	'spring'	66.8	37.0	31.2	44.8	30.8	58.6	57.6	13.8	26.8	14.0	1.0
110	'winter'	126.3	67.3	38.4	64.6	45.4	96.8	86.8	32.2	41.4	19.2	10.0
111	'spring'	48.6	35.8	32.2	47.2	24.2	71.2	62.6	24.0	38.4	23.0	8.6
112	'winter'	103.6	45.8	37.2	57.6	40.4	83.8	82.6	26.2	42.2	17.2	1.2
113	'spring'	43.6	35.0	28.8	40.2	22.6	60.5	41.6	20.3	19.0	17.6	18.9
114	'spring'	59.0	36.8	34.4	48.2	32.2	82.8	85.2	34.6	53.0	16.0	-2.5
115	'spring'	54.6	38.3	35.2	46.4	33.6	78.4	79.2	32.0	45.6	12.8	-0.8
116	'spring'	71.6	38.8	35.4	55.6	31.8	94.5	103.2	38.9	71.4	23.8	-8.7
117	'winter'	90.8	47.7	40.8	NA	NA	NA	NA	NA	NA	NA	NA
118	'winter'	106.2	44.3	37.0	62.4	45.5	92.8	120.6	30.4	75.1	16.9	-27.9
119	'spring'	54.2	37.3	31.0	48.2	25.8	65.8	46.2	17.6	20.5	22.5	19.6
120	'winter'	94.3	48.7	39.8	58.3	54.3	111.8	125.0	53.4	70.7	4.0	-13.3
121	'spring'	54.4	36.5	30.6	42.4	23.8	57.2	72.4	14.8	48.6	18.6	-15.2

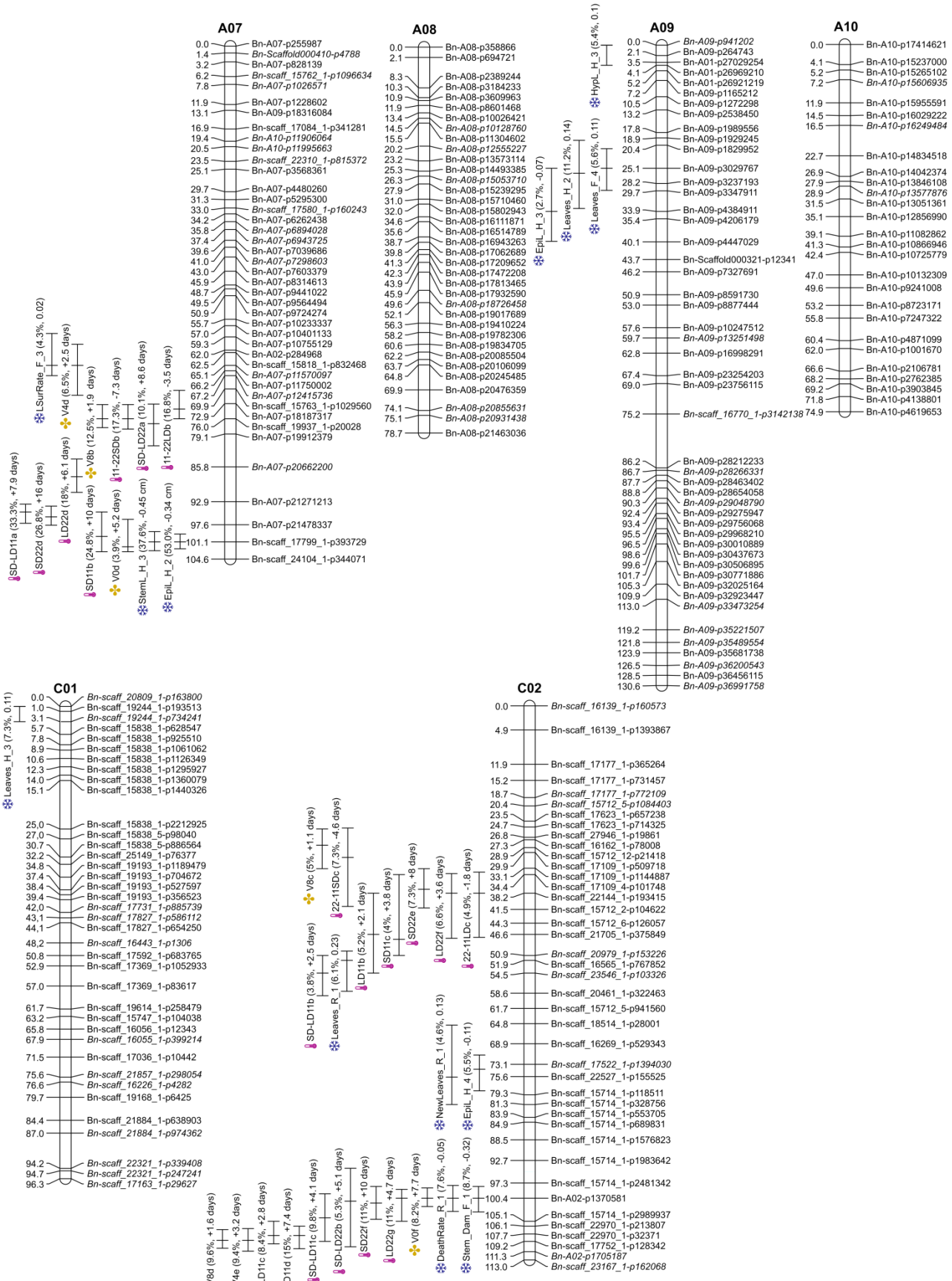
DH Line		Vernalization experiment			Temperature and day length experiment							
No.	type	V0	V4	V8	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
123	'winter'	107.3	50.8	37.4	52.0	30.8	81.4	81.5	29.4	50.8	21.3	-0.1
124	'winter'	90.6	40.3	37.4	66.6	41.8	94.0	107.4	27.4	65.6	24.8	-13.4
125	'spring'	57.0	41.0	32.6	39.8	23.8	61.8	36.0	22.0	12.2	16.0	25.8
127	'spring'	47.4	36.5	29.6	41.0	21.0	69.8	89.3	28.8	68.3	20.0	-19.5
128	'winter'	110.6	41.0	37.0	67.0	48.8	103.5	97.0	36.5	48.3	18.3	6.5
129	'winter'	105.2	47.5	36.8	65.4	40.6	88.0	94.8	22.6	54.2	24.8	-6.8
130	'winter'	110.2	46.7	37.0	52.4	37.0	75.0	105.3	22.6	68.3	15.4	-30.3
131	'spring'	58.2	34.5	29.6	47.4	24.3	70.0	87.7	22.6	63.4	23.2	-17.7
132	'winter'	84.2	40.0	32.8	51.6	38.4	75.5	85.7	23.9	47.3	13.2	-10.2
133	'winter'	114.6	73.8	38.8	63.3	54.2	73.8	102.0	10.4	47.8	9.1	-28.3
136	'spring'	59.2	34.5	31.8	50.2	24.4	62.8	65.0	12.6	40.6	25.8	-2.2
137	'spring'	64.0	58.7	39.6	NA	NA	NA	NA	NA	NA	NA	NA
138	'winter'	101.4	49.8	37.8	51.8	32.0	77.5	68.4	25.8	36.4	19.8	9.1
139	'spring'	56.0	37.8	28.6	44.4	26.4	70.6	49.8	26.2	23.4	18.0	20.8
140	'spring'	48.4	32.5	27.4	NA	NA	NA	NA	NA	NA	NA	NA
141	'winter'	83.2	41.3	33.4	51.8	33.0	81.8	57.3	30.0	24.3	18.8	24.5
144	'winter'	113.2	54.5	35.0	49.0	34.8	78.0	69.5	29.0	34.7	14.2	8.5
145	'spring'	59.3	39.0	40.4	44.2	25.4	82.8	72.2	38.6	46.8	18.8	10.6
146	'spring'	55.0	33.5	31.0	39.6	21.6	56.6	51.0	17.0	29.4	18.0	5.6
147	'spring'	58.8	36.8	32.6	44.0	26.0	70.2	66.3	26.2	40.3	18.0	4.0
148	'winter'	92.0	50.5	35.4	49.8	29.0	77.0	68.0	27.2	39.0	20.8	9.0
149	'winter'	79.6	42.5	37.4	57.8	40.6	109.3	97.8	51.5	57.2	17.2	11.5
150	'winter'	91.6	49.3	30.4	48.2	29.6	73.6	54.4	25.4	24.8	18.6	19.2
151	'winter'	116.2	79.5	39.8	73.8	76.0	123.0	143.7	49.2	67.7	-2.2	-20.7
152	'spring'	45.6	34.3	30.0	42.4	25.6	63.5	53.8	21.1	28.2	16.8	9.7
153	'winter'	71.8	36.3	30.3	42.8	29.8	56.0	56.0	13.3	26.2	13.0	0.0
155	'spring'	48.8	35.0	32.8	44.8	29.5	76.6	71.5	31.8	42.0	15.3	5.1
156	'spring'	52.6	37.3	33.2	40.8	20.4	53.0	43.4	12.2	23.0	20.4	9.6
157	'winter'	87.4	38.0	29.4	42.8	27.0	61.8	39.4	19.0	12.4	15.8	22.4
158	'spring'	56.3	38.0	32.2	46.8	27.4	71.4	81.0	24.6	53.6	19.4	-9.6
161	'spring'	46.2	36.8	31.6	46.6	26.0	100.2	95.4	53.6	69.4	20.6	4.8
162	'spring'	58.4	37.5	31.8	47.6	24.4	64.0	50.4	16.4	26.0	23.2	13.6
163	'winter'	83.6	49.0	38.0	63.0	35.0	107.5	130.0	44.5	95.0	28.0	-22.5
164	'winter'	98.8	45.0	36.2	53.2	32.0	80.8	63.0	27.6	31.0	21.2	17.8
165	'spring'	58.2	43.8	37.2	55.0	34.8	91.0	134.5	36.0	99.7	20.2	-43.5
169	'spring'	52.4	43.5	36.6	65.8	40.4	102.2	89.8	36.4	49.4	25.4	12.4
176	'winter'	104.2	39.5	32.6	47.6	30.0	70.2	77.0	22.6	47.0	17.6	-6.8
177	'spring'	63.2	46.3	41.0	53.4	60.0	96.6	118.5	43.2	58.5	-6.6	-21.9
178	'winter'	96.6	48.5	35.4	51.4	31.2	82.6	80.2	31.2	49.0	20.2	2.4
179	'winter'	112.6	44.8	38.0	67.2	47.2	97.0	119.0	29.8	71.8	20.0	-22.0
181	'winter'	107.4	41.8	33.8	51.2	45.0	72.0	95.8	20.8	50.8	6.2	-23.8
183	'winter'	120.4	48.8	38.6	60.6	60.8	98.4	98.4	37.8	37.6	-0.2	0.0
184	'spring'	49.4	37.3	32.5	40.3	28.6	61.4	41.4	21.2	12.8	11.7	20.0
187	'spring'	66.4	44.3	34.2	54.4	41.4	86.4	87.8	32.0	46.4	13.0	-1.4
188	'spring'	59.0	36.3	33.4	45.2	32.2	77.8	108.8	32.6	76.6	13.0	-31.1
193	'spring'	46.0	34.5	29.4	37.2	17.8	57.0	42.2	19.8	24.4	19.4	14.8
195	'spring'	55.4	43.0	41.3	47.8	27.0	73.5	78.8	25.8	51.8	20.8	-5.3

DH Line		Vernalization experiment			Temperature and day length experiment							
No.	type	V0	V4	V8	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
196	'winter'	97.8	40.0	32.2	47.6	29.8	61.8	44.2	14.2	14.5	17.9	17.6
197	'spring'	48.8	36.8	33.4	45.0	22.8	80.6	106.8	35.6	84.0	22.2	-26.2
199	'spring'	47.2	36.3	32.4	46.8	43.4	81.4	75.5	34.6	32.1	3.4	5.9
200	'winter'	82.8	38.3	33.0	46.8	30.2	80.0	53.3	33.2	23.1	16.6	26.8
204	'winter'	97.5	41.3	36.6	59.0	41.0	79.0	81.3	20.0	40.3	18.0	-2.3
205	'winter'	83.4	40.8	35.4	54.2	42.2	82.0	101.6	27.8	59.4	12.0	-19.6
206	'winter'	118.6	55.5	45.6	64.5	43.6	92.3	88.3	27.8	44.7	20.9	4.0
207	'winter'	105.0	78.0	57.4	77.0	54.2	73.5	65.5	-3.5	11.3	22.8	8.0
208	'winter'	120.2	65.0	46.2	60.2	45.4	90.0	88.5	29.8	43.1	14.8	1.5
209	'spring'	57.4	36.0	31.4	47.0	28.2	71.0	62.5	24.0	34.3	18.8	8.5
210	'winter'	77.8	44.0	40.6	54.6	44.0	93.6	101.3	39.0	57.3	10.6	-7.7
218	'spring'	65.8	39.8	38.0	45.8	23.0	51.8	56.5	6.1	33.5	22.8	-4.7
230	'spring'	48.0	37.3	33.0	50.8	27.0	74.2	84.2	23.4	57.2	23.8	-10.0
234	'winter'	94.2	65.8	38.6	61.8	41.4	90.7	53.0	28.9	11.6	20.4	37.7
237	'spring'	51.4	37.0	31.2	40.4	23.8	64.0	53.8	23.6	30.1	16.7	10.2
238	'spring'	68.5	44.5	36.4	52.4	34.8	100.2	119.2	47.8	84.5	17.7	-19.0
239	'winter'	96.5	73.5	47.4	NA	NA	NA	NA	NA	NA	NA	NA
240	'spring'	54.4	40.0	33.0	42.4	24.8	79.5	69.5	37.1	44.7	17.6	10.0
243	'spring'	60.2	36.8	30.6	54.3	26.8	73.6	61.8	19.3	35.0	27.5	11.9
244	'spring'	50.4	36.8	33.8	47.0	32.2	97.8	82.2	50.8	50.0	14.8	15.6
246	'spring'	53.4	36.3	32.4	40.8	23.0	61.4	45.8	20.6	22.8	17.8	15.7
249	'spring'	65.2	39.0	39.4	57.2	43.2	110.3	138.2	53.1	95.0	14.0	-28.0
250	'spring'	58.6	41.5	33.8	46.0	29.8	77.0	64.6	31.0	34.8	16.2	12.4
252	'winter'	126.3	60.3	44.0	69.4	73.8	128.0	148.7	58.6	74.9	-4.4	-20.7
253	'winter'	87.4	51.0	38.2	53.2	72.8	113.0	144.8	59.8	72.0	-19.6	-31.8
256	'spring'	49.2	34.3	28.8	39.6	20.4	61.2	54.5	21.6	34.1	19.2	6.7
257	'winter'	120.0	42.0	33.5	53.2	30.4	83.0	48.8	29.8	18.4	22.8	34.2
258	'winter'	107.3	58.3	57.0	63.2	62.8	109.8	137.6	46.6	74.9	0.5	-27.9
262	'spring'	60.2	43.5	35.0	55.8	34.5	81.0	114.0	25.2	79.5	21.3	-33.0
263	'winter'	103.5	45.5	35.8	60.0	44.0	88.6	84.6	28.6	40.6	16.0	4.0
264	'winter'	86.6	37.0	29.2	41.0	21.6	54.5	45.2	13.5	23.6	19.4	9.3
266	'spring'	54.8	39.0	35.4	58.2	32.5	74.8	63.7	16.6	31.2	25.7	11.1
267	'winter'	80.3	39.8	34.6	52.6	34.8	80.5	72.8	27.9	38.0	17.8	7.8
269	'winter'	97.6	46.3	35.0	57.0	34.6	80.0	57.8	23.0	23.2	22.4	22.3
270	'winter'	109.0	45.3	35.5	50.2	30.6	72.3	69.4	22.1	38.8	19.6	2.9
271	'spring'	55.8	38.0	32.4	45.0	48.2	79.5	60.6	34.5	12.4	-3.2	18.9
273	'spring'	45.0	34.8	27.4	38.2	19.4	59.4	42.0	21.2	22.6	18.8	17.4
276	'spring'	38.5	36.0	28.8	NA	NA	NA	NA	NA	NA	NA	NA
279	'winter'	84.4	42.0	35.0	46.0	28.8	62.8	52.3	16.8	23.5	17.3	10.6
280	'winter'	112.0	54.0	34.2	54.8	38.2	78.2	82.3	23.4	44.1	16.6	-4.1
281	'winter'	97.3	41.0	34.5	58.0	44.8	79.4	85.2	21.4	40.4	13.2	-5.8
282	'winter'	108.2	44.0	35.0	59.4	41.4	93.8	80.0	34.4	38.6	18.0	13.8
283	'winter'	121.0	65.8	40.6	70.3	67.0	136.0	139.3	65.7	72.3	3.3	-3.3
285	'winter'	112.3	56.8	38.0	62.5	44.8	93.2	125.3	30.7	80.5	17.7	-32.1
286	'winter'	103.4	41.3	34.8	56.0	36.6	82.0	66.4	26.0	29.8	19.4	15.6
287	'winter'	85.4	41.3	36.0	43.0	24.2	57.8	43.3	14.8	19.1	18.8	14.6
289	'spring'	37.8	34.0	29.8	40.2	24.8	67.2	76.5	27.0	51.7	15.4	-9.3

DH Line		Vernalization experiment			Temperature and day length experiment							
No.	type	V0	V4	V8	LD11	LD22	SD11	SD22	SD-LD11	SD-LD22	11-22LD	11-22SD
290	'winter'	130.0	59.0	52.4	60.5	60.6	109.6	126.0	49.1	65.4	-0.1	-16.4
291	'spring'	53.8	37.8	33.8	45.4	25.8	63.4	78.6	18.0	52.9	19.7	-15.2
292	'spring'	64.4	39.5	36.0	52.2	30.6	94.0	99.6	41.8	69.0	21.6	-5.6
293	'spring'	59.4	38.5	34.0	51.0	29.2	81.2	57.0	30.2	27.8	21.8	24.2
295	'spring'	61.3	39.3	34.4	50.6	25.0	77.0	37.0	26.4	12.0	25.6	40.0
296	'winter'	111.6	75.0	38.5	70.3	72.0	106.8	118.5	36.4	46.5	-1.7	-11.8
299	'winter'	84.4	38.3	31.6	40.4	25.6	58.0	59.6	17.6	34.0	14.8	-1.6
300	'winter'	109.8	52.0	40.0	70.0	45.8	96.0	109.7	26.0	63.9	24.3	-13.7
301	'winter'	128.2	75.0	40.5	70.0	49.8	93.4	101.8	23.4	52.1	20.3	-8.4
302	'spring'	46.3	36.8	35.0	NA	NA	NA	NA	NA	NA	NA	NA
303	'spring'	50.2	34.5	30.0	45.4	26.0	72.0	50.0	26.6	24.0	19.4	22.0
304	'winter'	78.0	42.3	36.4	53.6	31.8	84.0	68.4	30.4	36.7	21.9	15.6
Express617		129.3	65.5	36.8	71.7	57.7	103.3	117.8	31.6	60.1	14.0	-14.5
F1		63.8	39.0	33.0	48.7	29.5	75.0	63.0	26.3	33.5	19.2	12.0
DH4079		41.0	32.1	26.7	37.8	17.0	52.5	33.1	14.7	16.1	20.8	19.4

Appendix B: Overview of the genetic framework map with units in cM. Markers with no physical position in the reference genome are written in italics. Results of the QTL analysis of the vernalization experiment (✤) and the temperature and day length experiment (🌡) from chapter 1, and the freezing tolerance experiment from chapter 2 (❄) with 95% confidence interval and peaks of the QTL. In brackets R^2 and additive effects.

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SD22f (11%, +10 days)
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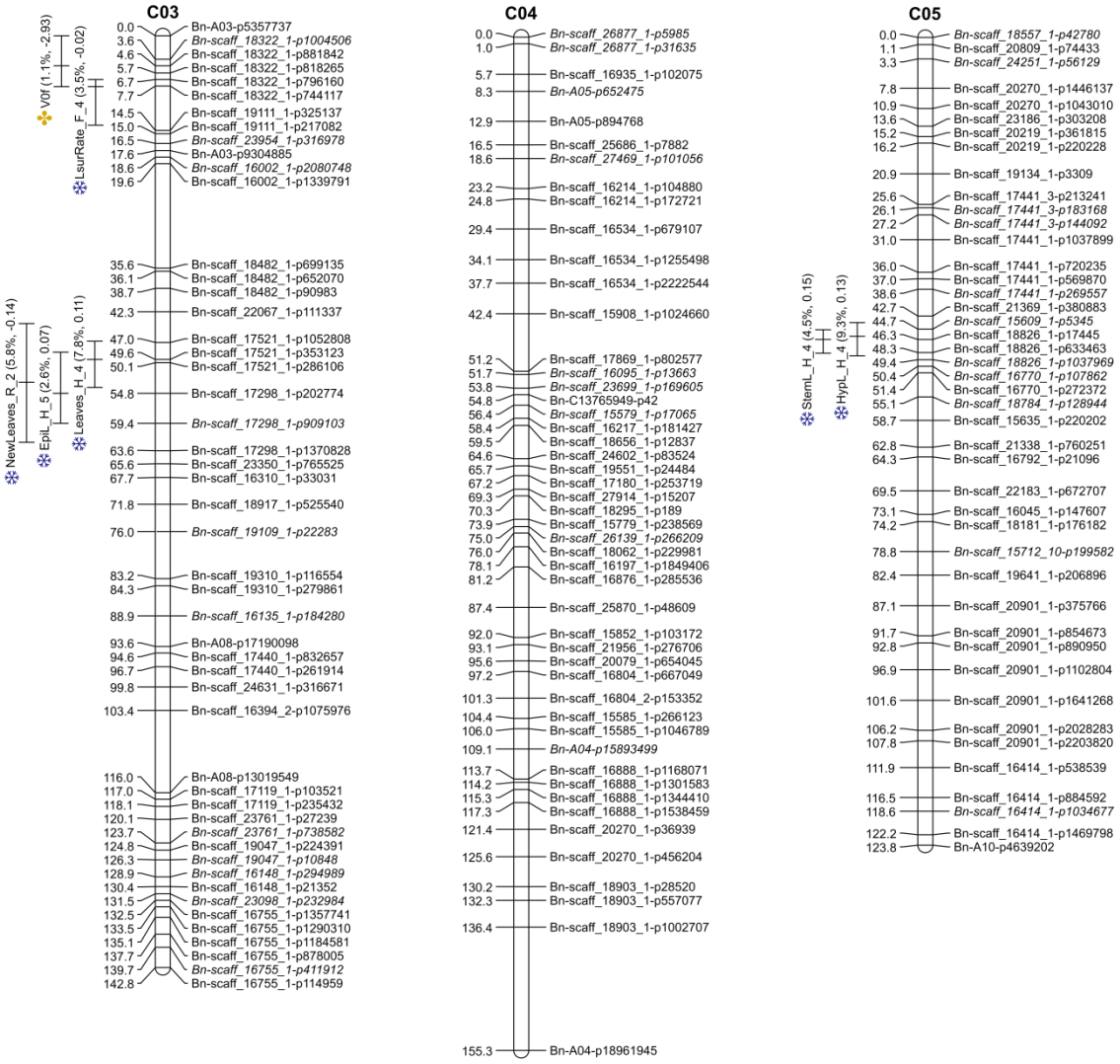
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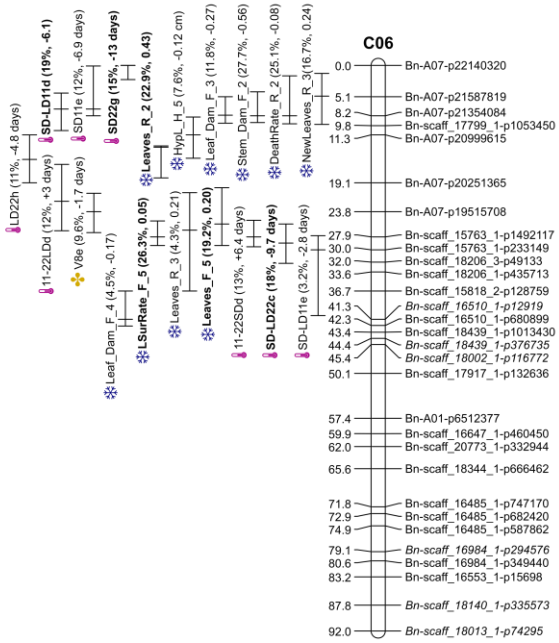
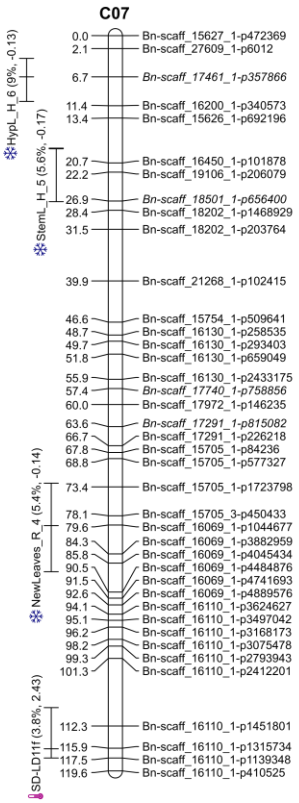
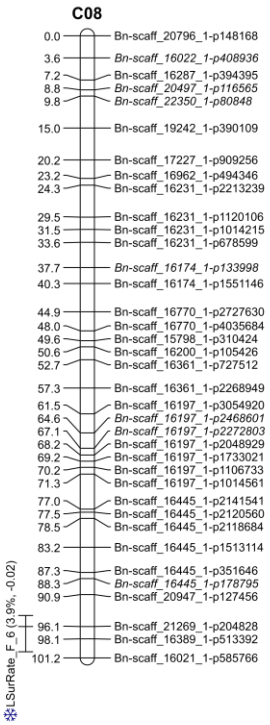
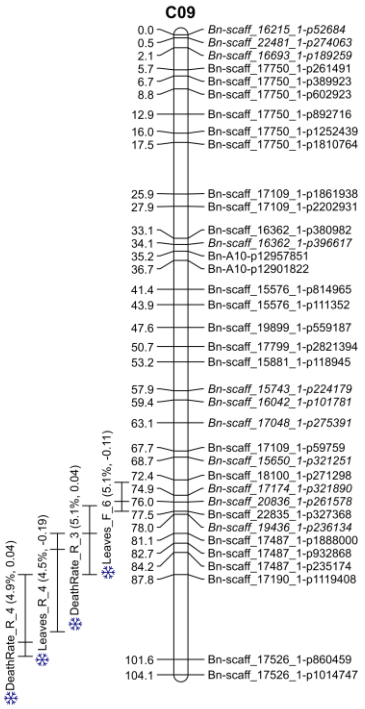
67.7 Bn-scaff_16310_1-p33031
71.8 Bn-scaff_18917_1-p525540
76.0 Bn-scaff_19109_1-p22283
83.2 Bn-scaff_19310_1-p116554
84.3 Bn-scaff_19310_1-p279861
88.9 Bn-scaff_16135_1-p184280
93.6 Bn-A08-p17190098
94.6 Bn-scaff_17440_1-p832657
96.7 Bn-scaff_17440_1-p261914
99.8 Bn-scaff_24631_1-p316671
103.4 Bn-scaff_16394_2-p1075976
116.0 Bn-A08-p13019549
117.0 Bn-scaff_17119_1-p103521
118.1 Bn-scaff_17119_1-p235432
120.1 Bn-scaff_23761_1-p27239
123.7 Bn-scaff_23761_1-p738582
124.8 Bn-scaff_19047_1-p224391
126.3 Bn-scaff_19047_1-p10848
128.9 Bn-scaff_16148_1-p294989
130.4 Bn-scaff_16148_1-p21352
131.5 Bn-scaff_23098_1-p232984
132.5 Bn-scaff_16755_1-p1357741
133.5 Bn-scaff_16755_1-p1290310
135.1 Bn-scaff_16755_1-p1184581
137.7 Bn-scaff_16755_1-p878005
139.7 Bn-scaff_16755_1-p411912
142.8 Bn-scaff_16755_1-p114959
V0f (1.1%, -2.93)
LsurRate_F_4 (3.5%, -0.02)
NewLeaves_R_2 (5.8%, -0.14)
EpiL_H_5 (2.6%, 0.07)
Leaves_H_4 (7.8%, 0.11)
C04
0.0 Bn-scaff_26877_1-p5985
1.0 Bn-scaff_26877_1-p31635
5.7 Bn-scaff_16935_1-p102075
8.3 Bn-A05-p652475
12.9 Bn-A05-p894768
16.5 Bn-scaff_25686_1-p7882
18.6 Bn-scaff_27469_1-p101056
23.2 Bn-scaff_16214_1-p104880
24.8 Bn-scaff_16214_1-p172721
29.4 Bn-scaff_16534_1-p679107
34.1 Bn-scaff_16534_1-p1255498
37.7 Bn-scaff_16534_1-p2222544
42.4 Bn-scaff_15908_1-p1024660
51.2 Bn-scaff_17869_1-p802577
51.7 Bn-scaff_16095_1-p13663
53.8 Bn-scaff_23699_1-p169605
54.8 Bn-C13765949-p42
56.4 Bn-scaff_15579_1-p17065
58.4 Bn-scaff_16217_1-p181427
59.5 Bn-scaff_18656_1-p12837
64.6 Bn-scaff_24602_1-p83524
65.7 Bn-scaff_19551_1-p24484
67.2 Bn-scaff_17180_1-p253719
69.3 Bn-scaff_27914_1-p15207
70.3 Bn-scaff_18295_1-p189
73.9 Bn-scaff_15779_1-p238569
75.0 Bn-scaff_26139_1-p266209
76.0 Bn-scaff_18062_1-p229981
78.1 Bn-scaff_16197_1-p1849406
81.2 Bn-scaff_16876_1-p285536
87.4 Bn-scaff_25870_1-p48609
92.0 Bn-scaff_15852_1-p103172
93.1 Bn-scaff_21956_1-p276706
95.6 Bn-scaff_20079_1-p654045
97.2 Bn-scaff_16804_1-p667049
101.3 Bn-scaff_16804_2-p153352
104.4 Bn-scaff_15585_1-p266123
106.0 Bn-scaff_15585_1-p1046789
109.1 Bn-A04-p15893499
113.7 Bn-scaff_16888_1-p1168071
114.2 Bn-scaff_16888_1-p1301583
115.3 Bn-scaff_16888_1-p1344410
117.3 Bn-scaff_16888_1-p1538459
121.4 Bn-scaff_20270_1-p36939
125.6 Bn-scaff_20270_1-p456204
130.2 Bn-scaff_18903_1-p28520
132.3 Bn-scaff_18903_1-p557077
136.4 Bn-scaff_18903_1-p1002707
155.3 Bn-A04-p18961945
C05
0.0 Bn-scaff_18557_1-p42780
1.1 Bn-scaff_20809_1-p74433
3.3 Bn-scaff_24251_1-p56129
7.8 Bn-scaff_20270_1-p1446137
10.9 Bn-scaff_20270_1-p1043010
13.6 Bn-scaff_23186_1-p303208
15.2 Bn-scaff_20219_1-p361815
16.2 Bn-scaff_20219_1-p220228
20.9 Bn-scaff_19134_1-p3309
25.6 Bn-scaff_17441_3-p213241
26.1 Bn-scaff_17441_3-p183168
27.2 Bn-scaff_17441_3-p144092
31.0 Bn-scaff_17441_1-p1037899
36.0 Bn-scaff_17441_1-p720235
37.0 Bn-scaff_17441_1-p569870
38.6 Bn-scaff_17441_1-p269557
42.7 Bn-scaff_21369_1-p380883
44.7 Bn-scaff_15609_1-p5345
46.3 Bn-scaff_18826_1-p17445
48.3 Bn-scaff_18826_1-p633463
49.4 Bn-scaff_18826_1-p1037969
50.4 Bn-scaff_16770_1-p107862
51.4 Bn-scaff_16770_1-p272372
55.1 Bn-scaff_18784_1-p128944
58.7 Bn-scaff_15635_1-p220202
62.8 Bn-scaff_21338_1-p760251
64.3 Bn-scaff_16792_1-p21096
69.5 Bn-scaff_22183_1-p672707
73.1 Bn-scaff_16045_1-p147607
74.2 Bn-scaff_18181_1-p176182
78.8 Bn-scaff_15712_10-p199582
82.4 Bn-scaff_19641_1-p206896
87.1 Bn-scaff_20901_1-p375766
91.7 Bn-scaff_20901_1-p854673
92.8 Bn-scaff_20901_1-p890950
96.9 Bn-scaff_20901_1-p1102804
101.6 Bn-scaff_20901_1-p1641268
106.2 Bn-scaff_20901_1-p2028283
107.8 Bn-scaff_20901_1-p2203820
111.9 Bn-scaff_16414_1-p538539
116.5 Bn-scaff_16414_1-p884592
118.6 Bn-scaff_16414_1-p1034677
122.2 Bn-scaff_16414_1-p1469798
123.8 Bn-A10-p4639202
StemL_H_4 (4.5%, 0.15)
HypL_H_4 (9.3%, 0.13)


C06
LD22h (11%, -4.8 days)
11-22LDd (12%, +3 days)
V8e (9.6%, -1.7 days)
Leaf_Dam_F_4 (4.5%, -0.17)
SD-LD11d (19%, -6.1)
SD11e (12%, -6.9 days)
SD22g (15%, -13 days)
LSurRate_F_5 (26.3%, 0.05)
Leaves_R_2 (22.9%, 0.43)
Leaves_R_3 (4.3%, 0.21)
HypL_H_5 (7.6%, -0.12 cm)
Leaves_F_5 (19.2%, 0.20)
Leaf_Dam_F_3 (11.8%, -0.27)
11-22SDd (13%, +6.4 days)
Stem_Dam_F_2 (27.7%, -0.56)
SD-LD22c (18%, -9.7 days)
DeathRate_R_2 (25.1%, -0.08)
SD-LD11e (3.2%, -2.8 days)
NewLeaves_R_3 (16.7%, 0.24)
0.0 Bn-A07-p22140320
5.1 Bn-A07-p21587819
8.2 Bn-A07-p21354084
9.8 Bn-scaff_17799_1-p1053450
11.3 Bn-A07-p20999615
19.1 Bn-A07-p20251365
23.8 Bn-A07-p19515708
27.9 Bn-scaff_15763_1-p1492117
30.0 Bn-scaff_15763_1-p233149
32.0 Bn-scaff_18206_3-p49133
33.6 Bn-scaff_18206_1-p435713
36.7 Bn-scaff_15818_2-p128759
41.3 Bn-scaff_16510_1-p12919
42.3 Bn-scaff_16510_1-p680899
43.4 Bn-scaff_18439_1-p1013430
44.4 Bn-scaff_18439_1-p376735
45.4 Bn-scaff_18002_1-p116772
50.1 Bn-scaff_17917_1-p132636
57.4 Bn-A01-p6512377
59.9 Bn-scaff_16647_1-p460450
62.0 Bn-scaff_20773_1-p332944
65.6 Bn-scaff_18344_1-p666462
71.8 Bn-scaff_16485_1-p747170
72.9 Bn-scaff_16485_1-p682420
74.9 Bn-scaff_16485_1-p587862
79.1 Bn-scaff_16984_1-p294576
80.6 Bn-scaff_16984_1-p349440
83.2 Bn-scaff_16553_1-p15698
87.8 Bn-scaff_18140_1-p335573
92.0 Bn-scaff_18013_1-p74295


C07
HypL_H_6 (9%, -0.13)
StemL_H_5 (5.6%, -0.17)
NewLeaves_R_4 (5.4%, -0.14)
SD-LD11f (3.8%, 2.43)
0.0 Bn-scaff_15627_1-p472369
2.1 Bn-scaff_27609_1-p6012
6.7 Bn-scaff_17461_1-p357866
11.4 Bn-scaff_16200_1-p340573
13.4 Bn-scaff_15626_1-p692196
20.7 Bn-scaff_16450_1-p101878
22.2 Bn-scaff_19106_1-p206079
26.9 Bn-scaff_18501_1-p656400
28.4 Bn-scaff_18202_1-p1468929
31.5 Bn-scaff_18202_1-p203764
39.9 Bn-scaff_21268_1-p102415
46.6 Bn-scaff_15754_1-p509641
48.7 Bn-scaff_16130_1-p258535
49.7 Bn-scaff_16130_1-p293403
51.8 Bn-scaff_16130_1-p659049
55.9 Bn-scaff_16130_1-p2433175
57.4 Bn-scaff_17740_1-p758856
60.0 Bn-scaff_17972_1-p146235
63.6 Bn-scaff_17291_1-p815082
66.7 Bn-scaff_17291_1-p226218
67.8 Bn-scaff_15705_1-p84236
68.8 Bn-scaff_15705_1-p577327
73.4 Bn-scaff_15705_1-p1723798
78.1 Bn-scaff_15705_3-p450433
79.6 Bn-scaff_16069_1-p1044677
84.3 Bn-scaff_16069_1-p3882959
85.8 Bn-scaff_16069_1-p4045434
90.5 Bn-scaff_16069_1-p4484876
91.5 Bn-scaff_16069_1-p4741693
92.6 Bn-scaff_16069_1-p4889576
94.1 Bn-scaff_16110_1-p3624627
95.1 Bn-scaff_16110_1-p3497042
96.2 Bn-scaff_16110_1-p3168173
98.2 Bn-scaff_16110_1-p3075478
99.3 Bn-scaff_16110_1-p2793943
101.3 Bn-scaff_16110_1-p2412201
112.3 Bn-scaff_16110_1-p1451801
115.9 Bn-scaff_16110_1-p1315734
117.5 Bn-scaff_16110_1-p1139348
119.6 Bn-scaff_16110_1-p410525


C08
LSurRate_F_6 (3.9%, -0.02)
0.0 Bn-scaff_20796_1-p148168
3.6 Bn-scaff_16022_1-p408936
7.2 Bn-scaff_16287_1-p394395
8.8 Bn-scaff_20497_1-p116565
9.8 Bn-scaff_22350_1-p80848
15.0 Bn-scaff_19242_1-p390109
20.2 Bn-scaff_17227_1-p909256
23.2 Bn-scaff_16962_1-p494346
24.3 Bn-scaff_16231_1-p2213239
29.5 Bn-scaff_16231_1-p1120106
31.5 Bn-scaff_16231_1-p1014215
33.6 Bn-scaff_16231_1-p678599
37.7 Bn-scaff_16174_1-p133998
40.3 Bn-scaff_16174_1-p1551146
44.9 Bn-scaff_16770_1-p2727630
48.0 Bn-scaff_16770_1-p4035684
49.6 Bn-scaff_15798_1-p310424
50.6 Bn-scaff_16200_1-p105426
52.7 Bn-scaff_16361_1-p727512
57.3 Bn-scaff_16361_1-p2268949
61.5 Bn-scaff_16197_1-p3054920
64.6 Bn-scaff_16197_1-p2468601
67.1 Bn-scaff_16197_1-p2272803
68.2 Bn-scaff_16197_1-p2048929
69.2 Bn-scaff_16197_1-p1733021
70.2 Bn-scaff_16197_1-p1106733
71.3 Bn-scaff_16197_1-p1014561
77.0 Bn-scaff_16445_1-p2141541
77.5 Bn-scaff_16445_1-p2120560
78.5 Bn-scaff_16445_1-p2118684
83.2 Bn-scaff_16445_1-p1513114
87.3 Bn-scaff_16445_1-p351646
88.3 Bn-scaff_16445_1-p178795
90.9 Bn-scaff_20947_1-p127456
96.1 Bn-scaff_21269_1-p204828
98.1 Bn-scaff_16389_1-p513392
101.2 Bn-scaff_16021_1-p585766


C09
DeathRate_R_4 (4.9%, 0.04)
Leaves_R_4 (4.5%, -0.19)
DeathRate_R_3 (5.1%, 0.04)
Leaves_F_6 (5.1%, -0.11)
0.0 Bn-scaff_16215_1-p52684
0.5 Bn-scaff_22481_1-p274063
2.1 Bn-scaff_16693_1-p189259
5.7 Bn-scaff_17750_1-p261491
6.7 Bn-scaff_17750_1-p389923
8.8 Bn-scaff_17750_1-p602923
12.9 Bn-scaff_17750_1-p892716
16.0 Bn-scaff_17750_1-p1252439
17.5 Bn-scaff_17750_1-p1810764
25.9 Bn-scaff_17109_1-p1861938
27.9 Bn-scaff_17109_1-p2202931
33.1 Bn-scaff_16362_1-p380982
34.1 Bn-scaff_16362_1-p396617
35.2 Bn-A10-p12957851
36.7 Bn-A10-p12901822
41.4 Bn-scaff_15576_1-p814965
43.9 Bn-scaff_15576_1-p111352
47.6 Bn-scaff_19899_1-p559187
50.7 Bn-scaff_17799_1-p2821394
53.2 Bn-scaff_15881_1-p118945
57.9 Bn-scaff_15743_1-p224179
59.4 Bn-scaff_16042_1-p101781
63.1 Bn-scaff_17048_1-p275391
67.7 Bn-scaff_17109_1-p59759
68.7 Bn-scaff_15650_1-p321251
72.4 Bn-scaff_18100_1-p271298
74.9 Bn-scaff_17174_1-p321890
76.0 Bn-scaff_20836_1-p261578
77.5 Bn-scaff_22835_1-p327368
78.0 Bn-scaff_19436_1-p236134
81.1 Bn-scaff_17487_1-p1888000
82.7 Bn-scaff_17487_1-p932868
84.2 Bn-scaff_17487_1-p235174
87.8 Bn-scaff_17190_1-p1119408
101.6 Bn-scaff_17526_1-p860459
104.1 Bn-scaff_17526_1-p1014747

Appendix C: Flowering time candidate genes from *Arabidopsis thaliana* and homologous positions in reference genome of 'Damor-bzh'.

Arabidopsis thaliana (TAIR)				Reference genome (genoscope)		
Gene name	Locus name	Synonyms	gene size [bp]	BLAT score	Chromosome	Postion [bp]
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	1215	chrA02	8'904'406
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	576	chrA07	17'668'217
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	1044	chrA07	21'069'351
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	1107	chrC02	17'190'504
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	1044	chrC06	32'747'244
AGL12	AT1G71692	AGAMOUS-LIKE 12, AGL12, XAANTAL1, XAL1	2583	850	chrUn_random	12'296'521
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	685	chrA04	1'587'657
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	818	chrA07	14'469'176
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	849	chrA09	26'494'571
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	482	chrC04	25'270'502
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	824	chrC08	28'999'758
AGL18	AT3G57390	AGAMOUS-LIKE 18, AGL18	2507	842	chrUn_random	11'432'677
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	966	chrA01	6'344'696
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	1046	chrA03	23'232'703
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	1146	chrA08	9'745'671
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	950	chrC01	9'679'266
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	621	chrC07	39'349'719
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	650	chrUn_random	90'153'299
AGL19	AT4G22950	AGAMOUS-LIKE 19, AGL19, GL19	4181	999	chrUn_random	42'764'710
AGL24	AT4G24540	AGAMOUS-LIKE 24, AGL24	3210	1134	chrA01	7'068'783
AGL24	AT4G24540	AGAMOUS-LIKE 24, AGL24	3210	1076	chrA03	23'990'499
AGL24	AT4G24540	AGAMOUS-LIKE 24, AGL24	3210	1131	chrC01	11'242'903
AGL24	AT4G24540	AGAMOUS-LIKE 24, AGL24	3210	1031	chrC07	40'103'285
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	1305	chrA02_random	545'583
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	1417	chrA07	20'115'728
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	1469	chrA07	18'230'152
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	542	chrA08	15'077'963
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	807	chrC02_random	302'667
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	415	chrC03	45'929'960
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	1465	chrC06	30'791'744
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	1510	chrC06	27'150'089
AP1	AT1G69120	AGAMOUS-LIKE 7, AGL7, AP1, APETALA1, ATAP1	4056	526	chrUn_random	134'299'011
ARP6	AT3G33520	ACTIN-RELATED PROTEIN 6, ARP6, ATARP6, EARLY IN SHORT DAYS 1, ESD1, SUF3, SUPPRESSOR OF FRI 3	2751	856	chrA08	75'633
ARP6	AT3G33520	ACTIN-RELATED PROTEIN 6, ARP6, ATARP6, EARLY IN SHORT DAYS 1, ESD1, SUF3, SUPPRESSOR OF FRI 3	2751	881	chrC03	60'500'721

AS1	AT2G37630	ARABIDOPSIS PHANTASTICA-LIKE 1, AS1, ASYMMETRIC LEAVES 1, ATMYB91, ATPHAN, MYB DOMAIN PROTEIN 91, MYB91	2249	1001	chrA03	8'127'096
AS1	AT2G37630	ARABIDOPSIS PHANTASTICA-LIKE 1, AS1, ASYMMETRIC LEAVES 1, ATMYB91, ATPHAN, MYB DOMAIN PROTEIN 91, MYB91	2249	994	chrA05	3'742'951
AS1	AT2G37630	ARABIDOPSIS PHANTASTICA-LIKE 1, AS1, ASYMMETRIC LEAVES 1, ATMYB91, ATPHAN, MYB DOMAIN PROTEIN 91, MYB91	2249	872	chrC03	11'081'260
AS1	AT2G37630	ARABIDOPSIS PHANTASTICA-LIKE 1, AS1, ASYMMETRIC LEAVES 1, ATMYB91, ATPHAN, MYB DOMAIN PROTEIN 91, MYB91	2249	929	chrC04	5'769'379
ATX	AT1G50320	ATHX, ATX, THIOREDOXIN X, THX	1153	357	chrC06	4'139'470
BBX19	AT4G38960	B-BOX DOMAIN PROTEIN 19, BBX19	2234	468	chrA06	24'316'523
BBX19	AT4G38960	B-BOX DOMAIN PROTEIN 19, BBX19	2234	794	chrA08	13'565'045
BBX19	AT4G38960	B-BOX DOMAIN PROTEIN 19, BBX19	2234	762	chrC03	49'433'343
BBX19	AT4G38960	B-BOX DOMAIN PROTEIN 19, BBX19	2234	580	chrC07	44'674'076
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	755	chrA08	18'701'231
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	560	chrA09	33'212'698
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	720	chrA10	2'114'556
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	745	chrC05	1'999'798
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	581	chrC08	37'729'006
BBX24	AT1G06040	B-BOX DOMAIN PROTEIN 24, BBX24, SALT TOLERANCE, STO	1644	757	chrC08	1'249'232
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	355	chrA07	18'230'284
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	369	chrA07	20'117'472
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	1160	chrA08	15'077'963
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	861	chrC03	45'928'650
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	1139	chrC03	45'928'650
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	357	chrC06	30'793'267
CAL	AT1G26310	AGAMOUS-LIKE 10, AGL10, CAL, CAL1, CAULIFLOWER	3651	403	chrC06	27'150'221
CDC73	AT3G22590	CDC73, PHP, PLANT HOMOLOGOUS TO PARAFIBROMIN	2005	927	chrA05	11'763'448
CDC73	AT3G22590	CDC73, PHP, PLANT HOMOLOGOUS TO PARAFIBROMIN	2005	1013	chrC05	28'702'066
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	595	chrA03	1'123'051
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	395	chrA09	2'635'731
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	414	chrC02	44'909'678
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	517	chrC02	496'535
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	606	chrC03	1'706'298
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	369	chrC09	2'855'677
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	687	chrC09	46'834'787
CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	511	chrUn_random	14'870'954

CHE	AT5G08330	ATTCP21, CCA1 HIKING EXPEDITION, CHE, TCP DOMAIN PROTEIN 21, TCP21	1593	645	chrUn_random	86'353'809
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	1979	chrA04	10'180'891
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	2509	chrA04	9'911'833
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	3511	chrA04	9'911'833
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	639	chrA07	13'399'090
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	724	chrA07	13'399'693
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	994	chrA07	5'686'040
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	1217	chrA07	5'686'040
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	3453	chrA07	13'398'076
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	1594	chrC06_random	1'967'829
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	968	chrC07	1'941'908
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	467	chrUn_random	94'711'574
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	496	chrUn_random	94'712'359
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	1000	chrUn_random	19'076'100
CIP1	AT5G41790	CIP1, COP1-INTERACTIVE PROTEIN 1	5318	1567	chrUn_random	94'710'652
CLF	AT2G23380	CLF, CURLY LEAF, ICU1, INCURVATA 1, SDG1, SET1, SETDOMAIN 1, SETDOMAIN GROUP 1	5295	2615	chrA04	12'079'072
CLF	AT2G23380	CLF, CURLY LEAF, ICU1, INCURVATA 1, SDG1, SET1, SETDOMAIN 1, SETDOMAIN GROUP 1	5295	2509	chrC04	37'428'665
CO	AT5G15840	B-BOX DOMAIN PROTEIN 1, BBX1, CO, CONSTANS, FG	2924	906	chrA10	13'358'445
CO	AT5G15840	B-BOX DOMAIN PROTEIN 1, BBX1, CO, CONSTANS, FG	2924	978	chrC09	43'745'461
CRY1	AT4G08920	ATCRY1, BLU1, BLUE LIGHT UNINHIBITED 1, CRY1, CRYPTOCHROME 1, ELONGATED HYPOCOTYL 4, HY4, OOP2, OUT OF PHASE 2	3618	1895	chrC09	25'053'226
CRY1	AT4G08920	ATCRY1, BLU1, BLUE LIGHT UNINHIBITED 1, CRY1, CRYPTOCHROME 1, ELONGATED HYPOCOTYL 4, HY4, OOP2, OUT OF PHASE 2	3618	1802	chrUn_random	40'540'392
CRY2	AT1G04400	AT-PHH1, ATCRY2, CRY2, CRYPTOCHROME 2, FHA, PHH1	2879	1573	chrA08	18'439'413
CRY2	AT1G04400	AT-PHH1, ATCRY2, CRY2, CRYPTOCHROME 2, FHA, PHH1	2879	955	chrA10	1'356'852
CRY2	AT1G04400	AT-PHH1, ATCRY2, CRY2, CRYPTOCHROME 2, FHA, PHH1	2879	374	chrA10_random	3'886
CRY2	AT1G04400	AT-PHH1, ATCRY2, CRY2, CRYPTOCHROME 2, FHA, PHH1	2879	1371	chrC05	1'230'897
CRY2	AT1G04400	AT-PHH1, ATCRY2, CRY2, CRYPTOCHROME 2, FHA, PHH1	2879	1587	chrC08	474'429
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2089	chrA02	17'732'138
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2274	chrA06	23'710'912
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2105	chrA09	11'006'126
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2131	chrC02	34'638'699
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2300	chrC07	25'628'561
CUL4	AT5G46210	ATCUL4, CUL4, CULLIN4	5445	2284	chrC09	16'065'389
EBI	AT5G05660	ARABIDOPSIS NF-X LIKE 2, ATNFXL2, EARLY BIRD, EBI, NFX1-LIKE 2, NFXL2	4987	2207	chrA10	16'164'315
EBI	AT5G05660	ARABIDOPSIS NF-X LIKE 2, ATNFXL2, EARLY BIRD, EBI, NFX1-LIKE 2, NFXL2	4987	2429	chrC09	48'000'026
EDL3	AT3G63060	EDL3, EID1-LIKE 3	1576	439	chrA05	4'808'950
EDL3	AT3G63060	EDL3, EID1-LIKE 3	1576	539	chrC04	7'421'399
EFS	AT1G77300	ASH1 HOMOLOG 2, ASHH2, CAROTENOID CHLOROPLAST REGULATORY1, CCR1, EARLY FLOWERING IN SHORT DAYS, EFS, LAZ2, LAZARUS 2, SDG8, SET DOMAIN GROUP 8	9533	3440	chrA07	22'947'417

EFS	AT1G77300	ASH1 HOMOLOG 2, ASHH2, CAROTENOID CHLOROPLAST REGULATORY1, CCR1, EARLY FLOWERING IN SHORT DAYS, EFS, LAZ2, LAZARUS 2, SDG8, SET DOMAIN GROUP 8	9533	1849	chrC06	35'772'647
EFS	AT1G77300	ASH1 HOMOLOG 2, ASHH2, CAROTENOID CHLOROPLAST REGULATORY1, CCR1, EARLY FLOWERING IN SHORT DAYS, EFS, LAZ2, LAZARUS 2, SDG8, SET DOMAIN GROUP 8	9533	3378	chrC06	35'772'221
EFS	AT1G77300	ASH1 HOMOLOG 2, ASHH2, CAROTENOID CHLOROPLAST REGULATORY1, CCR1, EARLY FLOWERING IN SHORT DAYS, EFS, LAZ2, LAZARUS 2, SDG8, SET DOMAIN GROUP 8	9533	1052	chrUn_random	15'153'706
ELF3	AT2G25930	EARLY FLOWERING 3, ELF3, PYK20	4381	1099	chrA04	13'248'508
ELF3	AT2G25930	EARLY FLOWERING 3, ELF3, PYK20	4381	974	chrA09	28'573'334
ELF3	AT2G25930	EARLY FLOWERING 3, ELF3, PYK20	4381	1112	chrC08	31'767'434
ELF3	AT2G25930	EARLY FLOWERING 3, ELF3, PYK20	4381	998	chrUn_random	77'090'565
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	389	chrA03	8'892'086
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	401	chrA04	17'558'796
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	390	chrA05	2'910'114
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	362	chrC03_random	650'565
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	411	chrC04	3'764'060
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	393	chrC04_random	4'305'411
ELF4	AT2G40080	EARLY FLOWERING 4, ELF4	660	366	chrUn_random	76'255'843
ELF5	AT5G62640	ATELF5, EARLY FLOWERING 5, ELF5	3109	1403	chrA06	15'466'805
ELF5	AT5G62640	ATELF5, EARLY FLOWERING 5, ELF5	3109	365	chrC02_random	5'007'262
ELF5	AT5G62640	ATELF5, EARLY FLOWERING 5, ELF5	3109	1318	chrC03	36'207'078
ELF-like2	AT1G72630	ELF4-L2, ELF4-LIKE 2	1405	482	chrA02	9'535'405
ELF-like2	AT1G72630	ELF4-L2, ELF4-LIKE 2	1405	524	chrA07	21'508'148
ELF-like2	AT1G72630	ELF4-L2, ELF4-LIKE 2	1405	363	chrC02	18'453'485
ELF-like2	AT1G72630	ELF4-L2, ELF4-LIKE 2	1405	396	chrC06	25'941'038
ELF-like2	AT1G72630	ELF4-L2, ELF4-LIKE 2	1405	524	chrC06	33'547'359
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	2282	chrA02	5'948'400
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	497	chrA03	5'998'369
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	1098	chrA03	6'001'849
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	472	chrA10	6'783'715
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	2331	chrA10	6'780'087
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	2186	chrC02	11'515'669
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	973	chrC03	8'094'295
EMF2	AT5G51230	ATEMF2, CYR1, CYTOKININ RESISTANT 1, EMBRYONIC FLOWER 2, EMF2, VEF2	6001	2323	chrC09	29'249'147
FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	607	chrA05	13'500'268
FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	873	chrA08	6'279'162

FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	769	chrC06	9'707'491
FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	858	chrC08	9'369'552
FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	708	chrUn_random	100'589'161
FBH1	AT1G35460	ATCFL1 ASSOCIATED PROTEIN 2, CFLAP2, FBH1, FLOWERING BHLH 1	2500	741	chrUn_random	54'873'586
FBH3	AT1G51140	ABA-RESPONSIVE KINASE SUBSTRATE 1, AKS1, ATCFL1 ASSOCIATED PROTEIN 1, CFLAP1, FBH3, FLOWERING BHLH 3	2366	877	chrA06	1'429'755
FBH3	AT1G51140	ABA-RESPONSIVE KINASE SUBSTRATE 1, AKS1, ATCFL1 ASSOCIATED PROTEIN 1, CFLAP1, FBH3, FLOWERING BHLH 3	2366	1071	chrC06	5'007'350
FBH4	AT2G42280	ABA-RESPONSIVE KINASE SUBSTRATE 3, AKS3, FBH4, FLOWERING BHLH 4	2476	993	chrA04	18'411'326
FBH4	AT2G42280	ABA-RESPONSIVE KINASE SUBSTRATE 3, AKS3, FBH4, FLOWERING BHLH 4	2476	919	chrA05	1'458'057
FBH4	AT2G42280	ABA-RESPONSIVE KINASE SUBSTRATE 3, AKS3, FBH4, FLOWERING BHLH 4	2476	913	chrC04	1'916'736
FBH4	AT2G42280	ABA-RESPONSIVE KINASE SUBSTRATE 3, AKS3, FBH4, FLOWERING BHLH 4	2476	965	chrC04	46'926'513
FCA	AT4G16280	FCA, FLOWERING CONTROL LOCUS A	8229	3222	chrA01	9'237'224
FCA	AT4G16280	FCA, FLOWERING CONTROL LOCUS A	8229	673	chrA01_random	568'207
FCA	AT4G16280	FCA, FLOWERING CONTROL LOCUS A	8229	3196	chrC01	15'311'460
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	531	chrA01	868'402
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	846	chrA01	868'193
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	929	chrA01	868'193
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	942	chrA08	12'446'567
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	976	chrC01	1'446'631
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	955	chrC03_random	5'398'859
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	819	chrC07	43'707'282
FD	AT4G35900	ATBZIP14, FD, FD-1	1787	808	chrUn_random	22'433'596
FES1	AT2G33835	FES1, FRIGIDA-ESSENTIAL 1	3003	651	chrA03	7'224'608
FES1	AT2G33835	FES1, FRIGIDA-ESSENTIAL 1	3003	1084	chrA05	5'417'915
FES1	AT2G33835	FES1, FRIGIDA-ESSENTIAL 1	3003	735	chrC03	9'642'676
FES1	AT2G33835	FES1, FRIGIDA-ESSENTIAL 1	3003	976	chrUn_random	7'514'302
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	1320	chrA01	17'831'729
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	482	chrA05	15'618'391
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	830	chrA05	15'590'755
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	1002	chrA05	15'624'909
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	1349	chrC01	31'800'540
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	845	chrC05	30'905'512

FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	640	chrUn_random	92'039'395
FIE	AT3G20740	FERTILIZATION-INDEPENDENT ENDOSPERM, FERTILIZATION-INDEPENDENT ENDOSPERM 1, FIE, FIE1, FIS3	3644	1125	chrUn_random	43'890'860
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	939	chrA02	135'303
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	727	chrA03	1'361'796
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	956	chrA03	6'239'950
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	713	chrA10	14'998'498
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	858	chrC02	208'509
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	594	chrC03	8'403'102
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	1043	chrC03	2'000'958
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	683	chrC09	46'366'545
FLC	AT5G10140	AGAMOUS-LIKE 25, AGL25, FLC, FLF, FLOWERING LOCUS C, FLOWERING LOCUS F, REDUCED STEM BRANCHING 6, RSB6	6067	1095	chrC09	46'345'275
FLD	AT3G10390	FLD, FLOWERING LOCUS D, REDUCED SYSTEMIC IMMUNITY 1, RSI1	3053	1482	chrA03	15'078'446
FLD	AT3G10390	FLD, FLOWERING LOCUS D, REDUCED SYSTEMIC IMMUNITY 1, RSI1	3053	1513	chrC03	22'063'771
FLK	AT3G04610	FLK, FLOWERING LOCUS KH DOMAIN	4432	1981	chrA03	13'978'151
FLK	AT3G04610	FLK, FLOWERING LOCUS KH DOMAIN	4432	2108	chrC03	20'562'865
FLK	AT3G04610	FLK, FLOWERING LOCUS KH DOMAIN	4432	1973	chrUn_random	65'472'236
FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	874	chrA02	24'581'991
FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	606	chrA06	16'592'636
FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	369	chrC02	45'610'182
FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	396	chrC02	45'641'051
FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	946	chrC02	45'609'768

FLM	AT1G77080	AGAMOUS-LIKE 27, AGL27, FLM, FLOWERING LOCUS M, MADS AFFECTING FLOWERING 1, MAF1	4590	725	chrC03	34'168'505
FPA	AT2G43410	FPA	6009	1776	chrA05	1'848'841
FPA	AT2G43410	FPA	6009	552	chrA09	27'193'961
FPA	AT2G43410	FPA	6009	1767	chrC04	2'067'366
FPF1	AT5G24860	ARABIDOPSIS FLOWERING PROMOTING FACTOR 1, ATFPF1, FLOWERING PROMOTING FACTOR 1, FPF1	723	392	chrA09	2'344'574
FPF1	AT5G24860	ARABIDOPSIS FLOWERING PROMOTING FACTOR 1, ATFPF1, FLOWERING PROMOTING FACTOR 1, FPF1	723	384	chrC07	34'411'709
FPF1	AT5G24860	ARABIDOPSIS FLOWERING PROMOTING FACTOR 1, ATFPF1, FLOWERING PROMOTING FACTOR 1, FPF1	723	420	chrC09	2'398'323
FRI	AT4G00650	FLA, FLOWERING LOCUS A, FRI, FRIGIDA, REDUCED STEM BRANCHING 7, RSB7	2603	473	chrA03	6'053'059
FRI	AT4G00650	FLA, FLOWERING LOCUS A, FRI, FRIGIDA, REDUCED STEM BRANCHING 7, RSB7	2603	828	chrA10	4'019'409
FRI	AT4G00650	FLA, FLOWERING LOCUS A, FRI, FRIGIDA, REDUCED STEM BRANCHING 7, RSB7	2603	749	chrC03	8'149'554
FRI	AT4G00650	FLA, FLOWERING LOCUS A, FRI, FRIGIDA, REDUCED STEM BRANCHING 7, RSB7	2603	830	chrC09	29'041'837
FRL1	AT1G20330	COTYLEDON VASCULAR PATTERN 1, CVP1, FRILL1, FRL1, SMT2, STEROL METHYLTRANSFERASE 2	1705	522	chrA07	22'437'077
FRL1	AT1G20330	COTYLEDON VASCULAR PATTERN 1, CVP1, FRILL1, FRL1, SMT2, STEROL METHYLTRANSFERASE 2	1705	615	chrC06	35'129'057
FRL1	AT1G20330	COTYLEDON VASCULAR PATTERN 1, CVP1, FRILL1, FRL1, SMT2, STEROL METHYLTRANSFERASE 2	1705	770	chrUn_random	31'218'136
FRL1	AT1G20330	COTYLEDON VASCULAR PATTERN 1, CVP1, FRILL1, FRL1, SMT2, STEROL METHYLTRANSFERASE 2	1705	788	chrUn_random	126'855'445
FRL2	AT1G31814	FRIGIDA LIKE 2, FRL2	2111	351	chrA09	17'659'583
FRL2	AT1G31814	FRIGIDA LIKE 2, FRL2	2111	432	chrUn_random	89'780'322
FT	AT1G65480	FLOWERING LOCUS T, FT, REDUCED STEM BRANCHING 8, RSB8	2508	798	chrA02	6'375'865
FT	AT1G65480	FLOWERING LOCUS T, FT, REDUCED STEM BRANCHING 8, RSB8	2508	498	chrA07	18'855'249
FT	AT1G65480	FLOWERING LOCUS T, FT, REDUCED STEM BRANCHING 8, RSB8	2508	727	chrC02_random	996'723
FT	AT1G65480	FLOWERING LOCUS T, FT, REDUCED STEM BRANCHING 8, RSB8	2508	397	chrC06	28'554'321
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1577	chrA03	19'890'980
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1539	chrA09	2'718'607
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1432	chrC02	44'718'031
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1529	chrC07_random	2'192'013
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1149	chrUn_random	80'359'808
FUL	AT5G60910	AGAMOUS-LIKE 8, AGL8, FRUITFULL, FUL	3836	1360	chrUn_random	16'313'807
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	849	chrA01	3'397'289
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1290	chrA01	10'508'843
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	943	chrA07	848'062

FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1712	chrA09	30'348'839
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1720	chrA09	5'017'240
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	794	chrC01	4'956'907
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	448	chrC07	2'338'266
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1470	chrC07	2'410'139
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1684	chrC08	33'815'740
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	1735	chrC09	6'545'557
FVE	AT2G19520	ACG1, ATMSI4, FVE, MSI4, MULTICOPY SUPPRESSOR OF IRA1 4, NFC04, NFC4	3887	735	chrUn_random	109'895'210
FY	AT5G13480	FY	5499	2232	chrA02	773'810
FY	AT5G13480	FY	5499	2326	chrA03	2'037'083
FY	AT5G13480	FY	5499	2207	chrC02	2'526'726
FY	AT5G13480	FY	5499	2287	chrC03	2'863'424
GI	AT1G22770	FB, GI, GIGANTEA	6040	377	chrA08	15'529'390
GI	AT1G22770	FB, GI, GIGANTEA	6040	2975	chrA09	22'588'063
GI	AT1G22770	FB, GI, GIGANTEA	6040	2972	chrC05	11'779'335
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	366	chrA01	2'522'303
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	548	chrA04	11'047'343
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	370	chrC01	79'820
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	582	chrC08_random	4'165'961
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	514	chrUn_random	116'187'206
GRP7	AT2G21660	"COLD, CIRCADIAN RHYTHM, AND RNA BINDING 2", ATGRP7, CCR2, GLYCINE RICH PROTEIN 7, GLYCINE-RICH RNA-BINDING PROTEIN 7, GR-RBP7, GRP7, RBGA3, RNA-BINDING GLYCINE-RICH PROTEIN A3	1474	640	chrUn_random	132'674'347
HAP2	AT4G11720	GCS1, GENERATIVE CELL-SPECIFIC 1, HAP2, HAPLESS 2	3624	1562	chrA09	14'153'605
HAP2	AT4G11720	GCS1, GENERATIVE CELL-SPECIFIC 1, HAP2, HAPLESS 2	3624	1652	chrUn_random	46'814'400

HAP3	AT2G38880	"NUCLEAR FACTOR Y, SUBUNIT B1", ATHAP3, ATNF-YB1, HAP3, HAP3A, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3A, NF-YB1, NUCLEAR FACTOR Y SUBUNIT B1	2290	393	chrA03	8'535'129
HAP3	AT2G38880	"NUCLEAR FACTOR Y, SUBUNIT B1", ATHAP3, ATNF-YB1, HAP3, HAP3A, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3A, NF-YB1, NUCLEAR FACTOR Y SUBUNIT B1	2290	542	chrA05	3'333'223
HAP3	AT2G38880	"NUCLEAR FACTOR Y, SUBUNIT B1", ATHAP3, ATNF-YB1, HAP3, HAP3A, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3, HEME ACTIVATOR PROTEIN (YEAST) HOMOLOG 3A, NF-YB1, NUCLEAR FACTOR Y SUBUNIT B1	2290	577	chrC04	4'729'142
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	3555	chrA07	7'598'431
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	1107	chrA08	13'779'762
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	2914	chrA08	13'788'867
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	1108	chrA09	32'684'663
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	363	chrC03	49'016'017
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	3241	chrC03	49'000'848
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	3625	chrC07	14'108'631
HAP5	AT1G30450	ATCCC1, CATION-CHLORIDE CO-TRANSPORTER 1, CCC1, HAP5, HAPLESS 5	6909	1490	chrUn_random	32'907'546
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	3388	chrA02	23'647'916
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	3343	chrA03	19'727'243
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	894	chrA10	15'366'011
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	3430	chrC02	44'519'198
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	3532	chrC07_random	2'164'806
HUA2	AT5G23150	ENHANCER OF AG-4 2, HUA2	6860	638	chrC09	46'904'370
LD	AT4G02560	LD, LUMINIDEPENDENS	5016	1602	chrA02	13'028'651
LD	AT4G02560	LD, LUMINIDEPENDENS	5016	2522	chrA02	13'027'888
LD	AT4G02560	LD, LUMINIDEPENDENS	5016	2537	chrC02	24'961'665
LDL1	AT1G62830	ARABIDOPSIS LYSINE-SPECIFIC HISTONE DEMETHYLASE, ATLSD1, ATSWP1, LDL1, LSD1, LSD1-LIKE 1, LYSINE-SPECIFIC HISTONE DEMETHYLASE, SWP1	2736	1330	chrA09	6'743'820
LDL1	AT1G62830	ARABIDOPSIS LYSINE-SPECIFIC HISTONE DEMETHYLASE, ATLSD1, ATSWP1, LDL1, LSD1, LSD1-LIKE 1, LYSINE-SPECIFIC HISTONE DEMETHYLASE, SWP1	2736	1311	chrC09	9'570'405
LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	626	chrA06_random	1'264'186
LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	1217	chrA06_random	1'264'186
LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	541	chrUn_random	75'773'821

LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	889	chrUn_random	136'063'353
LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	993	chrUn_random	135'705'425
LFY	AT5G61850	LEAFY, LEAFY 3, LFY, LFY3	2639	1212	chrUn_random	36'144'394
LHP1	AT5G17690	ATLHP1, LHP1, LIKE HETEROCHROMATIN PROTEIN 1, TERMINAL FLOWER 2, TFL2	5669	1533	chrA10	12'768'026
LHP1	AT5G17690	ATLHP1, LHP1, LIKE HETEROCHROMATIN PROTEIN 1, TERMINAL FLOWER 2, TFL2	5669	966	chrC02	3'989'842
LHP1	AT5G17690	ATLHP1, LHP1, LIKE HETEROCHROMATIN PROTEIN 1, TERMINAL FLOWER 2, TFL2	5669	1850	chrC09	42'746'336
LHP1	AT5G17690	ATLHP1, LHP1, LIKE HETEROCHROMATIN PROTEIN 1, TERMINAL FLOWER 2, TFL2	5669	740	chrUn_random	50'029'482
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	401	chrA09	33'804'381
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	1800	chrA10	376'918
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	1493	chrC03	11'396
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	1706	chrC05	428'561
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	987	chrC07	3'550'670
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	465	chrC08_random	4'342'522
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	359	chrC09	3'128'340
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	356	chrUn_random	66'186'753
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	1049	chrUn_random	66'180'825
LHY	AT1G01060	LATE ELONGATED HYPOCOTYL, LATE ELONGATED HYPOCOTYL 1, LHY, LHY1	4179	1383	chrUn_random	56'311'226
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	1384	chrA02	9'980'449
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	1019	chrA07	880'130
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	1084	chrA07	875'091
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	1153	chrA07	869'402
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	992	chrC07	3'533'821
LKP2	AT2G18915	ADAGIO 2, ADO2, LKP2, LOV KELCH PROTEIN 2	2972	1277	chrC07	3'537'257
LUX	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	483	chrA01	11'570'506
LUX	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	754	chrA06	10'231'884
LUX	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	582	chrC01	19'833'161
LUX	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	784	chrUn_random	54'856'156
MAF2	AT5G65050	AGAMOUS-LIKE 31, AGL31, MADS AFFECTING FLOWERING 2, MAF2	4182	801	chrA02	24'582'091
MAF2	AT5G65050	AGAMOUS-LIKE 31, AGL31, MADS AFFECTING FLOWERING 2, MAF2	4182	502	chrA06	16'592'743
MAF2	AT5G65050	AGAMOUS-LIKE 31, AGL31, MADS AFFECTING FLOWERING 2, MAF2	4182	553	chrC02	45'609'914
MAF2	AT5G65050	AGAMOUS-LIKE 31, AGL31, MADS AFFECTING FLOWERING 2, MAF2	4182	630	chrC02	45'640'963
MAF3	AT5G65060	AGAMOUS-LIKE 70, AGL70, FCL3, MADS AFFECTING FLOWERING 3, MAF3	4104	850	chrA02	24'582'175

MAF3	AT5G65060	AGAMOUS-LIKE 70, AGL70, FCL3, MADS AFFECTING FLOWERING 3, MAF3	4104	569	chrA06	16'592'664
MAF3	AT5G65060	AGAMOUS-LIKE 70, AGL70, FCL3, MADS AFFECTING FLOWERING 3, MAF3	4104	693	chrC02	45'609'914
MAF4	AT5G65070	AGAMOUS-LIKE 69, AGL69, FCL4, MADS AFFECTING FLOWERING 4, MAF4	3932	685	chrA02	24'582'131
MAF4	AT5G65070	AGAMOUS-LIKE 69, AGL69, FCL4, MADS AFFECTING FLOWERING 4, MAF4	3932	674	chrA06	16'600'642
MAF4	AT5G65070	AGAMOUS-LIKE 69, AGL69, FCL4, MADS AFFECTING FLOWERING 4, MAF4	3932	381	chrC02	45'609'904
MAF4	AT5G65070	AGAMOUS-LIKE 69, AGL69, FCL4, MADS AFFECTING FLOWERING 4, MAF4	3932	686	chrC03	34'155'431
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	883	chrA02	3'685'322
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	1062	chrA03	4'451'137
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	395	chrA03_random	1'792'092
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	409	chrA05	16'899'737
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	946	chrA10_random	1'614'423
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	982	chrC02	6'275'166
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	1062	chrC03	6'033'502
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	432	chrC05_random	324'322
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	434	chrC07	43'435'535
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	990	chrC09	36'922'324
MSI1	AT5G58230	ARABIDOPSIS MULTICOPY SUPRESSOR OF IRA1, ATMSI1, MATERNAL EFFECT EMBRYO ARREST 70, MEE70, MSI1, MULTICOPY SUPRESSOR OF IRA1	2234	428	chrUn_random	32'195'100
OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1457	chrA02	111'472
OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1424	chrA10	15'036'480
OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	382	chrC02	45'804'623
OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1440	chrC02	232'006

OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1427	chrC09	46'435'924
OBF4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	564	chrUn_random	13'452'360
PCL1	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	483	chrA01	11'570'506
PCL1	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	754	chrA06	10'231'884
PCL1	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	582	chrC01	19'833'161
PCL1	AT3G46640	LUX, LUX ARRHYTHMO, PCL1, PHYTOCLOCK 1	2285	784	chrUn_random	54'856'156
PEP	AT4G26000	PEP, PEPPER	2773	531	chrA01	7'732'450
PEP	AT4G26000	PEP, PEPPER	2773	1168	chrA03	24'506'469
PEP	AT4G26000	PEP, PEPPER	2773	641	chrC01_random	750'987
PEP	AT4G26000	PEP, PEPPER	2773	1211	chrC07	40'590'833
PEP	AT4G26000	PEP, PEPPER	2773	1066	chrC08	17'306'667
PFT1	AT1G25540	GLH1, MED25, MEDIATOR 25, PFT1, PHYTOCHROME AND FLOWERING TIME 1	5751	2510	chrA08	14'975'483
PFT1	AT1G25540	GLH1, MED25, MEDIATOR 25, PFT1, PHYTOCHROME AND FLOWERING TIME 1	5751	2549	chrA09	21'525'125
PFT1	AT1G25540	GLH1, MED25, MEDIATOR 25, PFT1, PHYTOCHROME AND FLOWERING TIME 1	5751	2609	chrC05	14'003'876
PFT1	AT1G25540	GLH1, MED25, MEDIATOR 25, PFT1, PHYTOCHROME AND FLOWERING TIME 1	5751	2509	chrUn_random	6'744'503
PHP	AT3G22590	CDC73, PHP, PLANT HOMOLOGOUS TO PARAFIBROMIN	2005	927	chrA05	11'763'448
PHP	AT3G22590	CDC73, PHP, PLANT HOMOLOGOUS TO PARAFIBROMIN	2005	1013	chrC05	28'702'066
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	3246	chrA06	3'098'539
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	2990	chrA09	32'433'592
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	353	chrC03	8'991'863
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	1481	chrC08	36'747'084
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	2846	chrC08	36'745'983
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	399	chrUn_random	13'282'016
PHY A	AT1G09570	ELONGATED HYPOCOTYL 8, FAR RED ELONGATED 1, FAR RED ELONGATED HYPOCOTYL 2, FHY2, FRE1, HY8, PHYA, PHYTOCHROME A	5660	3144	chrUn_random	30'130'929
PHY B	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	649	chrA03	16'746'223
PHY B	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2627	chrA05	17'432'648

PHY B	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2125	chrC03	24'846'334
PHY B	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2686	chrC05	35'604'638
PHY C	AT5G35840	PHYC, PHYTOCHROME C	4037	2510	chrA05	7'402'904
PHY C	AT5G35840	PHYC, PHYTOCHROME C	4037	2521	chrC06	14'042'549
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1356	chrA03	9'501'931
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1300	chrA04	18'575'801
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	842	chrC01	38'735'396
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	972	chrC03	2'586'906
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1330	chrC03	13'424'755
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1260	chrC04	47'145'131
REF6	AT3G48430	JMJ12, JUMONJI DOMAIN-CONTAINING PROTEIN 12, REF6, RELATIVE OF EARLY FLOWERING 6	5537	2937	chrA06	9'325'931
REF6	AT3G48430	JMJ12, JUMONJI DOMAIN-CONTAINING PROTEIN 12, REF6, RELATIVE OF EARLY FLOWERING 6	5537	2847	chrUn_random	14'697'023
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	715	chrA01	21'707'960
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	433	chrA03	280'499
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	956	chrA05	20'369'865
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	389	chrA10	17'053'572
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	400	chrC03	440'722
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	931	chrC05	40'263'051
RVE8	AT3G09600	LCL5, LHY-CCA1-LIKE5, REVEILLE 8, RVE8	2779	477	chrUn_random	3'663'518
SEF	AT5G37055	ATSWC6, SEF, SERRATED LEAVES AND EARLY FLOWERING	1072	475	chrA10	9'913'064
SEF	AT5G37055	ATSWC6, SEF, SERRATED LEAVES AND EARLY FLOWERING	1072	425	chrUn_random	46'149'824
SEF	AT5G37055	ATSWC6, SEF, SERRATED LEAVES AND EARLY FLOWERING	1072	426	chrUn_random	116'292'971
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	415	chrA07	8'941'824
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	843	chrA07	8'933'968
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	962	chrA09	20'975'906
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	803	chrC03	46'857'933
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	981	chrC05	14'941'104
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	372	chrC07	16'965'437
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	942	chrC07	16'990'322
SEP3	AT1G24260	AGAMOUS-LIKE 9, AGL9, SEP3, SEPALLATA3	2523	680	chrUn_random	74'513'834
SLY1	AT4G24210	SLEEPY1, SLY1	1204	360	chrA01	6'972'840
SLY1	AT4G24210	SLEEPY1, SLY1	1204	437	chrC01	11'104'839
SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	535	chrA02	21'775'120
SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	474	chrA06	20'542'099
SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	498	chrA09	1'451'972
SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	538	chrC02	41'362'009
SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	483	chrC07_random	1'782'677

SLY2	AT5G48170	SLEEPY2, SLY2, SNE, SNEEZY	1121	491	chrC09	1'307'827
SMZ	AT3G54990	SCHLAFMUTZE, SMZ	2805	1049	chrA09_random	2'781'251
SMZ	AT3G54990	SCHLAFMUTZE, SMZ	2805	891	chrC06	18'280'762
SMZ	AT3G54990	SCHLAFMUTZE, SMZ	2805	993	chrC08	27'410'410
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1540	chrA03_random	901'871
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1168	chrA04	19'286'989
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1589	chrA05	2'626'930
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1337	chrC04	48'074'797
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1553	chrC04_random	867'094
SOC1	AT2G45660	AGAMOUS-LIKE 20, AGL20, ATSOC1, SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1	3621	1469	chrUn_random	53'591'089
SPA1	AT2G46340	SPA1, SUPPRESSOR OF PHYA-105 1	5375	2265	chrA03	10'135'719
SPA1	AT2G46340	SPA1, SUPPRESSOR OF PHYA-105 1	5375	2578	chrA05	854'366
SPA1	AT2G46340	SPA1, SUPPRESSOR OF PHYA-105 1	5375	2243	chrC03	14'429'813
SPA1	AT2G46340	SPA1, SUPPRESSOR OF PHYA-105 1	5375	2450	chrC04	916'366
SPA2	AT4G11110	SPA1-RELATED 2, SPA2	5621	2389	chrA09	14'674'318
SPA2	AT4G11110	SPA1-RELATED 2, SPA2	5621	2384	chrC09	25'996'733
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	2244	chrA01	20'005'402
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	959	chrA05	9'158'671
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	2316	chrA05	18'186'014
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	2332	chrC01	35'494'941
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	2344	chrC05	37'058'462
SPA3	AT3G15354	SPA1-RELATED 3, SPA3	3943	1017	chrC06	12'097'948
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	1078	chrA01	20'005'659
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	1134	chrA05	18'186'839
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	1879	chrA05	9'158'333
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	1118	chrC01	35'495'614
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	1085	chrC05	37'059'072
SPA4	AT1G53090	SPA1-RELATED 4, SPA4	3718	2112	chrC06	12'097'707
SRCAP	AT3G12810	CHR13, PHOTOPERIOD-INDEPENDENT EARLY FLOWERING 1, PIE1, SRCAP	9153	5402	chrA05	19'333'825
SRCAP	AT3G12810	CHR13, PHOTOPERIOD-INDEPENDENT EARLY FLOWERING 1, PIE1, SRCAP	9153	404	chrC01	37'413'256
SRCAP	AT3G12810	CHR13, PHOTOPERIOD-INDEPENDENT EARLY FLOWERING 1, PIE1, SRCAP	9153	5309	chrUn_random	34'808'873
SUF4	AT1G30970	SUF4, SUPPRESSOR OF FRIGIDA4	3502	1122	chrA09	18'549'785
SUF4	AT1G30970	SUF4, SUPPRESSOR OF FRIGIDA4	3502	1122	chrC08	14'152'599
SUF4	AT1G30970	SUF4, SUPPRESSOR OF FRIGIDA4	3502	983	chrUn_random	32'851'076
SUF4	AT1G30970	SUF4, SUPPRESSOR OF FRIGIDA4	3502	1114	chrUn_random	17'263'413
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	691	chrA04	11'515'101
SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	691	chrA04	11'515'101
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1458	chrA09	29'590'841
SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1458	chrA09	29'590'841
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	479	chrC04	36'478'381

SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	479	chrC04	36'478'381
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1172	chrC04	36'477'980
SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1172	chrC04	36'477'980
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1251	chrC08	32'995'413
SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	1251	chrC08	32'995'413
SVP	AT2G22540	GAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	435	chrUn_random	111'630'073
SVP	AT2G22540	AGAMOUS-LIKE 22, AGL22, FAQ1, FLOWERING ARABIDOPSIS QTL1, SHORT VEGETATIVE PHASE, SVP	4255	435	chrUn_random	111'630'073
SWN	AT4G02020	EZA1, SDG10, SET DOMAIN-CONTAINING PROTEIN 10, SWINGER, SWN	5408	2480	chrA09	243'575
SWN	AT4G02020	EZA1, SDG10, SET DOMAIN-CONTAINING PROTEIN 10, SWINGER, SWN	5408	2273	chrA10	8'730'890
SWN	AT4G02020	EZA1, SDG10, SET DOMAIN-CONTAINING PROTEIN 10, SWINGER, SWN	5408	2387	chrUn_random	2'413'184
TEM1	AT1G25560	ATTEM1, EDF1, ETHYLENE RESPONSE DNA BINDING FACTOR 1, TEM1, TEMPRANILLO 1	1759	878	chrA08	14'982'788
TEM1	AT1G25560	ATTEM1, EDF1, ETHYLENE RESPONSE DNA BINDING FACTOR 1, TEM1, TEMPRANILLO 1	1759	1026	chrA09	21'598'264
TEM1	AT1G25560	ATTEM1, EDF1, ETHYLENE RESPONSE DNA BINDING FACTOR 1, TEM1, TEMPRANILLO 1	1759	989	chrC05	13'975'008
TEM1	AT1G25560	ATTEM1, EDF1, ETHYLENE RESPONSE DNA BINDING FACTOR 1, TEM1, TEMPRANILLO 1	1759	848	chrUn_random	6'727'572
TEM2	AT1G68840	ATRAV2, EDF2, ETHYLENE RESPONSE DNA BINDING FACTOR 2, RAP2.8, RAV2, RELATED TO ABI3/VP1 2, RELATED TO AP2 8, TEM2, TEMPRANILLO 2	1801	802	chrA02	7'869'831
TEM2	AT1G68840	ATRAV2, EDF2, ETHYLENE RESPONSE DNA BINDING FACTOR 2, RAP2.8, RAV2, RELATED TO ABI3/VP1 2, RELATED TO AP2 8, TEM2, TEMPRANILLO 2	1801	578	chrA09	21'598'407
TEM2	AT1G68840	ATRAV2, EDF2, ETHYLENE RESPONSE DNA BINDING FACTOR 2, RAP2.8, RAV2, RELATED TO ABI3/VP1 2, RELATED TO AP2 8, TEM2, TEMPRANILLO 2	1801	817	chrC02	14'843'532
TEM2	AT1G68840	ATRAV2, EDF2, ETHYLENE RESPONSE DNA BINDING FACTOR 2, RAP2.8, RAV2, RELATED TO ABI3/VP1 2, RELATED TO AP2 8, TEM2, TEMPRANILLO 2	1801	526	chrC05	13'975'474
TEM2	AT1G68840	ATRAV2, EDF2, ETHYLENE RESPONSE DNA BINDING FACTOR 2, RAP2.8, RAV2, RELATED TO ABI3/VP1 2, RELATED TO AP2 8, TEM2, TEMPRANILLO 2	1801	489	chrUn_random	6'727'945
TFL1	AT5G03840	TERMINAL FLOWER 1, TFL-1, TFL1	1373	535	chrA10	16'767'191
TFL1	AT5G03840	TERMINAL FLOWER 1, TFL-1, TFL1	1373	543	chrC02	1'320'654
TFL1	AT5G03840	TERMINAL FLOWER 1, TFL-1, TFL1	1373	518	chrC03	673'244
TFL1	AT5G03840	TERMINAL FLOWER 1, TFL-1, TFL1	1373	420	chrUn_random	1'815'690
TFL1	AT5G03840	TERMINAL FLOWER 1, TFL-1, TFL1	1373	526	chrUn_random	16'225'985

TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1457	chrA02	111'472
TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1424	chrA10	15'036'480
TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	382	chrC02	45'804'623
TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1440	chrC02	232'006
TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	1427	chrC09	46'435'924
TGA4	AT5G10030	OBF4, OCS ELEMENT BINDING FACTOR 4, TGA4, TGACG MOTIF-BINDING FACTOR 4	3221	564	chrUn_random	13'452'360
TOC1	AT5G61380	APRR1, ATTOC1, PRR1, PSEUDO-RESPONSE REGULATOR 1, TIMING OF CAB EXPRESSION 1, TOC1	3588	1463	chrA03	20'054'213
TOC1	AT5G61380	APRR1, ATTOC1, PRR1, PSEUDO-RESPONSE REGULATOR 1, TIMING OF CAB EXPRESSION 1, TOC1	3588	1587	chrC09	3'082'975
TOC1	AT5G61380	APRR1, ATTOC1, PRR1, PSEUDO-RESPONSE REGULATOR 1, TIMING OF CAB EXPRESSION 1, TOC1	3588	1503	chrUn_random	63'439'741
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	2992	chrA02	11'693'928
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	520	chrA03	24'948'902
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	360	chrA06	5'957'732
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	613	chrA06	5'965'784
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	3238	chrA07	23'335'941
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	3196	chrC02	22'383'747
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	517	chrC05	7'582'765
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	3017	chrC06	36'340'198
TPS1	AT1G78580	ATTPS1, TPS1, TREHALOSE-6-PHOSPHATE SYNTHASE, TREHALOSE-6-PHOSPHATE SYNTHASE 1	7472	441	chrC07_random	2'539'028
TSF	AT4G20370	TSF, TWIN SISTER OF FT	2240	433	chrC02	20'907'410
TSF	AT4G20370	TSF, TWIN SISTER OF FT	2240	364	chrC02_random	996'303
TSF	AT4G20370	TSF, TWIN SISTER OF FT	2240	477	chrC04	12'434'938
VIN3	AT5G57380	VERNALIZATION INSENSITIVE 3, VIN3	3110	1223	chrA02	3'861'878
VIN3	AT5G57380	VERNALIZATION INSENSITIVE 3, VIN3	3110	1275	chrA03	4'638'707
VIN3	AT5G57380	VERNALIZATION INSENSITIVE 3, VIN3	3110	1273	chrC02	6'853'914
VIN3	AT5G57380	VERNALIZATION INSENSITIVE 3, VIN3	3110	1423	chrC03	6'232'095
VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	2005	chrA02	3'270'858
VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	1861	chrA03	4'183'369

VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	917	chrA10	10'370'384
VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	1965	chrC02_random	113'384
VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	1831	chrC03	5'661'606
VIP2	AT5G59710	ATVIP2, NEGATIVE ON TATA LESS2B, NOT2B, VIP2, VIRE2 INTERACTING PROTEIN 2	4705	578	chrC09	38'413'970
VIP3	AT4G29830	A. THALIANA HOMOLOG OF YEAST SKI8, SKI8, VERNALIZATION INDEPENDENCE 3, VIP3	1742	835	chrA01	3'359'928
VIP3	AT4G29830	A. THALIANA HOMOLOG OF YEAST SKI8, SKI8, VERNALIZATION INDEPENDENCE 3, VIP3	1742	826	chrA08	11'579'930
VIP3	AT4G29830	A. THALIANA HOMOLOG OF YEAST SKI8, SKI8, VERNALIZATION INDEPENDENCE 3, VIP3	1742	837	chrC01	4'729'569
VIP3	AT4G29830	A. THALIANA HOMOLOG OF YEAST SKI8, SKI8, VERNALIZATION INDEPENDENCE 3, VIP3	1742	906	chrC03	57'860'189
VIP4	AT5G61150	VERNALIZATION INDEPENDENCE 4, VIP4	4092	1755	chrA09	2'756'935
VIP4	AT5G61150	VERNALIZATION INDEPENDENCE 4, VIP4	4092	1204	chrC02	44'850'228
VIP4	AT5G61150	VERNALIZATION INDEPENDENCE 4, VIP4	4092	1761	chrC09	3'037'464
VIP4	AT5G61150	VERNALIZATION INDEPENDENCE 4, VIP4	4092	1331	chrUn_random	16'391'457
VIP5	AT1G61040	VERNALIZATION INDEPENDENCE 5, VIP5	2866	1332	chrA01_random	1'529'151
VIP5	AT1G61040	VERNALIZATION INDEPENDENCE 5, VIP5	2866	1496	chrC01	27'140'690
VIP5	AT1G61040	VERNALIZATION INDEPENDENCE 5, VIP5	2866	568	chrUn_random	93'468'159
VIP5	AT1G61040	VERNALIZATION INDEPENDENCE 5, VIP5	2866	1378	chrUn_random	11'162'551
VIP5	AT1G61040	VERNALIZATION INDEPENDENCE 5, VIP5	2866	1504	chrUn_random	28'798'416
VIP6	AT2G06210	EARLY FLOWERING 8, ELF8, VERNALIZATION INDEPENDENCE 6, VIP6	7785	3509	chrA03	18'986'657
VIP6	AT2G06210	EARLY FLOWERING 8, ELF8, VERNALIZATION INDEPENDENCE 6, VIP6	7785	3516	chrC03	30'081'336
VIP6	AT2G06210	EARLY FLOWERING 8, ELF8, VERNALIZATION INDEPENDENCE 6, VIP6	7785	369	chrC07_random	143'151
VOZ1	AT1G28520	ATVOZ1, VASCULAR PLANT ONE ZINC FINGER PROTEIN, VOZ1	2908	1202	chrA08	14'312'607
VOZ1	AT1G28520	ATVOZ1, VASCULAR PLANT ONE ZINC FINGER PROTEIN, VOZ1	2908	1283	chrA09	20'343'704
VOZ1	AT1G28520	ATVOZ1, VASCULAR PLANT ONE ZINC FINGER PROTEIN, VOZ1	2908	1154	chrC03	48'067'527
VOZ1	AT1G28520	ATVOZ1, VASCULAR PLANT ONE ZINC FINGER PROTEIN, VOZ1	2908	1336	chrC05	15'752'743
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	873	chrA04	18'434'276
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	702	chrA05	1'508'024
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	990	chrC04	46'956'755
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	825	chrC04_random	521'749
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	571	chrC09	8'247'318
VOZ2	AT2G42400	ATVOZ2, VASCULAR PLANT ONE ZINC FINGER PROTEIN 2, VOZ2	2694	576	chrC09	47'641'469
VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1357	chrA01	18'401'986

VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1113	chrA03	17'099'318
VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1229	chrA05	16'377'702
VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1199	chrC01	32'886'081
VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1095	chrC03	25'637'793
VRN1	AT3G18990	REDUCED VERNALIZATION RESPONSE 1, REM39, REPRODUCTIVE MERISTEM 39, VRN1	3291	1129	chrC05	33'573'914
VRN2	AT4G16845	REDUCED VERNALIZATION RESPONSE 2, VRN2	3810	472	chrA01	9'597'214
VRN2	AT4G16845	REDUCED VERNALIZATION RESPONSE 2, VRN2	3810	1028	chrA08	8'024'274
VRN2	AT4G16845	REDUCED VERNALIZATION RESPONSE 2, VRN2	3810	1027	chrC08_random	3'239'514
ZTL	AT5G57360	ADAGIO 1, ADO1, FKF1-LIKE PROTEIN 2, FKL2, LKP1, LOV KELCH PROTEIN 1, ZEITLUPE, ZTL	3164	381	chrA02	9'980'728

Appendix D: Phenotypic data from the freezing tolerance experiment for each DH line as well as parental genotypes and F1 as means over nine repetitions. DH lines were categoriesed by vernalization requirement (type) and SNP markers on A07 and C06.

				After Hardening					After Frost				After Regrowth		
Line	type	A07	C06	Vigor	Number of Leaves	Hypocotyl Length	Epicotyl Length	Stem Length	Number of Viable Leaves	Leaf Survival Rate	Leaf Damage Score	Stem Damage score	Number of Leaves	Death Rate	N° of Regrown Leaves
DH4079		A	A	5.4	4.6	2.9	1.7	4.7	1.8	0.37	6.6	5.0	2.6	0.49	0.8
Express617		B	B	6.2	5.3	2.1	1.1	3.2	3.0	0.57	4.6	2.6	5.1	0.22	2.1
F1		-	-	5.9	4.9	3.0	1.2	4.1	2.4	0.51	5.5	3.4	4.3	0.25	1.9
1	'winter' type	A	B	5.1	4.1	2.8	1.5	4.3	2.4	0.54	5.7	2.5	4.1	0.09	1.8
2	'winter' type	B	A	5.4	5.6	1.9	0.9	2.8	2.3	0.39	6.2	4.8	4.4	0.28	2.1
4	'winter' type	A	A	5.4	4.7	2.6	1.7	4.3	1.8	0.40	6.4	6.0	2.2	0.66	0.4
5	'winter' type	A	A	5.1	5.0	2.4	1.5	3.9	1.6	0.33	6.6	5.4	2.7	0.40	1.0
6	'winter' type	B	B	5.4	4.7	2.4	0.7	3.1	2.2	0.45	5.3	2.5	5.0	0.28	2.7
7	'winter' type	B	A	5.6	5.6	2.2	0.5	2.8	2.3	0.40	6.1	4.3	2.7	0.48	0.4
8	'winter' type	A	A	5.5	4.6	2.9	1.6	4.5	1.7	0.37	6.4	3.4	3.4	0.34	1.7
9	'spring' type	A	A	6.0	5.4	2.7	1.3	4.1	2.3	0.43	5.9	3.3	4.1	0.30	1.8
12	'spring' type	A	A	5.6	4.6	2.1	1.7	3.9	2.3	0.50	5.9	3.2	4.0	0.19	1.8
16	'spring' type	A	A	5.7	4.5	2.7	1.1	3.7	2.5	0.56	5.3	4.4	3.7	0.41	1.2
19	'spring' type	A	A	4.9	4.7	2.5	1.1	3.6	2.0	0.42	6.2	4.5	2.6	0.50	0.6
20	'winter' type	A	A	5.0	4.3	3.1	1.0	4.2	1.8	0.40	6.1	4.6	2.7	0.42	0.9
21	'winter' type	B	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
22	'spring' type	A	A	5.5	4.7	2.3	1.3	3.6	2.3	0.49	5.6	4.2	3.4	0.43	1.1
23	'spring' type	B	B	5.0	5.6	1.8	0.6	2.4	2.7	0.49	5.1	3.1	3.8	0.34	1.1
24	'spring' type	B	A	5.0	4.8	2.1	1.0	3.1	1.8	0.38	6.4	4.8	2.2	0.54	0.4
25	'spring' type	B	A	4.8	4.3	3.3	0.6	3.9	2.0	0.46	5.7	4.2	2.7	0.37	0.6
26	'spring' type	A	A	5.4	4.8	2.8	1.6	4.4	1.8	0.34	6.7	4.7	2.4	0.54	0.6
27	'spring' type	A	B	5.4	4.4	2.6	1.6	4.2	2.5	0.52	5.6	4.3	2.8	0.43	0.3
28	'winter' type	A	A	5.5	5.3	3.3	1.3	4.6	2.6	0.50	5.0	3.2	4.2	0.21	1.6
32	'winter' type	B	B	5.0	4.6	2.6	0.7	3.3	2.3	0.53	5.6	2.7	3.8	0.20	1.5
36	'spring' type	A	A	5.0	4.8	3.1	1.6	4.7	1.7	0.34	6.7	6.4	1.9	0.80	0.2
39	'winter' type	B	A	5.0	5.7	3.1	0.7	3.8	1.9	0.31	6.8	5.3	2.6	0.55	0.7
40	'winter' type	A	B	5.5	5.1	2.6	1.3	3.9	2.8	0.54	5.0	3.2	5.2	0.20	2.4
41	'winter' type	A	A	5.4	5.2	2.7	1.5	4.2	2.9	0.56	4.8	4.3	4.2	0.40	1.3
43	'spring' type	A	B	5.4	4.4	2.3	1.7	4.1	2.1	0.48	5.6	3.9	2.9	0.38	0.8
45	'winter' type	B	B	5.5	5.6	2.5	0.8	3.4	3.0	0.52	4.9	3.3	5.6	0.17	2.6
46	'winter' type	B	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
49	'winter' type	B	B	5.1	4.6	2.6	0.8	3.3	1.6	0.34	6.4	3.9	3.0	0.27	1.4
50	'spring' type	A	A	5.9	5.1	2.9	1.5	4.3	2.4	0.46	5.6	4.2	3.0	0.45	0.7
52	'winter' type	B	B	5.6	4.9	2.5	0.8	3.3	2.2	0.46	5.6	4.0	3.8	0.36	1.6
54	'spring' type	A	B	5.5	5.4	2.8	2.5	5.2	2.6	0.46	5.5	3.8	4.0	0.39	1.5
55	'spring' type	A	A	5.8	5.0	2.8	1.1	3.9	2.0	0.41	6.0	4.7	3.1	0.41	1.0
56	'spring' type	B	A	5.0	4.9	1.9	0.6	2.5	2.0	0.40	6.1	4.2	3.4	0.29	1.4
57	'spring' type	A	A	5.7	4.9	2.7	1.5	4.2	1.7	0.36	6.1	4.6	2.6	0.56	1.0
59	'spring' type	B	B	5.2	4.4	2.6	1.0	3.6	2.2	0.50	5.6	3.5	4.3	0.33	2.1
62	'winter' type	A	A	5.4	5.0	2.4	1.0	3.3	2.3	0.44	5.6	4.3	4.3	0.35	1.9
63	'winter' type	A	A	5.2	4.6	2.5	0.9	3.4	2.2	0.49	5.6	3.8	3.0	0.36	0.8
64	'winter' type	A	B	4.9	4.8	2.6	1.4	4.0	2.4	0.51	5.2	3.5	4.3	0.09	1.9

65	'winter' type	B	B	5.1	4.7	2.5	0.8	3.3	2.7	0.60	4.3	3.2	3.7	0.32	0.9
66	'winter' type	B	B	5.1	5.0	2.7	0.9	3.5	2.7	0.54	4.7	3.7	4.6	0.26	1.9
67	'spring' type	A	A	5.7	4.9	2.2	1.7	3.9	2.1	0.43	6.1	4.6	2.9	0.50	0.8
68	'winter' type	A	B	5.7	4.8	2.0	1.3	3.3	2.4	0.48	5.6	2.8	4.7	0.16	2.3
69	'spring' type	A	A	5.9	5.1	3.2	1.4	4.5	2.1	0.41	5.8	2.9	2.9	0.38	0.8
70	'spring' type	A	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
71	'winter' type	A	A	5.1	4.7	2.7	1.3	4.0	2.3	0.48	5.7	5.4	2.8	0.53	0.5
72	'spring' type	B	B	5.3	4.4	2.6	1.0	3.6	1.9	0.43	6.5	4.5	3.2	0.40	1.3
73	'winter' type	A	A	5.4	5.1	1.7	1.4	3.1	2.9	0.55	5.4	2.4	5.1	0.21	2.2
74	'spring' type	B	B	5.4	4.9	3.0	1.1	4.2	2.1	0.43	6.0	3.3	4.0	0.28	1.8
75	'spring' type	A	B	5.7	4.6	2.9	1.7	4.6	2.4	0.53	5.3	4.4	3.5	0.35	1.1
76	'spring' type	A	B	5.6	4.8	2.4	2.0	4.3	2.8	0.59	4.9	3.0	4.6	0.19	1.8
80	'spring' type	A	B	5.1	4.7	2.5	1.0	3.4	2.2	0.49	5.4	3.8	4.0	0.38	1.8
81	'winter' type	A	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
82	'winter' type	A	A	5.5	5.0	2.5	1.0	3.5	2.1	0.40	6.2	4.1	3.2	0.44	1.1
84	'spring' type	A	A	5.5	4.7	2.6	1.7	4.4	1.7	0.36	6.5	4.6	2.4	0.64	0.7
85	'winter' type	B	B	5.6	4.6	3.2	1.6	4.7	2.4	0.51	5.5	4.3	3.0	0.46	0.6
88	'winter' type	A	A	5.1	4.7	2.8	1.4	4.2	2.3	0.53	5.5	4.7	3.0	0.40	0.7
89	'spring' type	A	A	5.2	4.8	2.4	1.9	4.4	1.9	0.39	6.3	5.8	2.4	0.55	0.5
90	'spring' type	A	A	5.7	4.4	3.1	2.3	5.4	1.4	0.34	6.3	5.4	2.1	0.58	0.7
91	'spring' type	A	A	5.0	5.1	2.5	1.6	4.2	2.0	0.38	6.2	5.4	2.5	0.62	0.6
92	'spring' type	B	A	5.4	4.4	3.2	1.0	4.3	1.4	0.32	7.3	5.2	1.3	0.66	0.0
93	'winter' type	NA	A	4.7	4.6	3.1	0.8	3.9	1.6	0.37	6.8	5.0	1.9	0.57	0.2
94	'spring' type	A	A	5.7	4.5	2.7	1.1	3.7	1.8	0.37	6.7	4.6	2.4	0.53	0.6
95	'winter' type	A	B	4.9	4.5	2.2	1.3	3.5	2.2	0.51	5.3	3.6	3.5	0.25	1.3
96	'winter' type	A	A	5.2	4.7	2.6	1.4	4.0	2.5	0.52	5.0	3.2	3.7	0.24	1.1
97	'spring' type	A	A	5.1	4.4	3.1	1.7	4.9	1.1	0.24	7.4	6.8	1.3	0.79	0.2
98	'spring' type	B	B	5.0	5.2	2.2	0.8	2.9	2.2	0.42	5.9	4.4	3.4	0.49	1.2
99	'winter' type	A	A	5.6	4.8	3.0	1.2	4.3	2.3	0.44	5.9	5.1	3.1	0.50	0.8
100	'spring' type	B	B	5.6	5.0	2.3	1.0	3.3	2.2	0.43	5.8	3.6	3.5	0.33	1.3
101	'spring' type	A	A	5.7	5.5	2.2	2.4	4.5	2.3	0.43	6.0	4.4	3.6	0.36	1.3
103	'spring' type	A	A	5.4	4.8	3.4	1.4	4.8	1.9	0.39	6.3	4.3	3.2	0.47	1.2
104	'spring' type	A	A	4.6	4.2	2.3	1.6	3.9	1.6	0.37	6.7	6.1	2.1	0.52	0.5
105	'winter' type	B	B	5.3	5.3	2.0	0.8	2.8	2.8	0.54	4.8	2.6	4.5	0.18	1.7
106	'winter' type	A	A	4.6	4.5	2.3	1.5	3.8	1.4	0.31	7.0	6.2	1.1	0.87	-0.3
107	'spring' type	A	B	5.1	4.7	2.6	1.3	3.9	2.5	0.53	5.1	3.7	4.1	0.28	1.6
109	'spring' type	A	A	5.4	5.1	2.7	2.0	4.7	2.1	0.41	6.2	4.7	2.8	0.50	0.7
110	'winter' type	B	B	5.2	4.8	2.5	0.8	3.3	2.7	0.56	4.7	1.6	5.2	0.07	2.4
111	'spring' type	A	A	5.9	4.9	2.3	1.8	4.1	2.5	0.49	5.4	3.7	4.0	0.22	1.5
112	'winter' type	B	B	4.7	4.8	1.8	0.7	2.5	2.2	0.45	5.7	3.0	3.4	0.25	1.2
113	'spring' type	A	A	5.8	4.9	2.6	1.7	4.4	1.3	0.27	6.9	4.6	2.5	0.43	1.1
114	'spring' type	A	A	5.4	5.4	3.0	2.0	5.0	2.5	0.45	5.6	4.1	3.5	0.38	1.0
115	'spring' type	A	A	5.7	5.1	2.2	1.4	3.7	2.4	0.45	6.0	4.7	3.7	0.25	1.3
116	'spring' type	B	A	5.9	5.0	2.9	1.1	3.9	1.7	0.35	6.6	4.4	2.7	0.46	1.0
117	'winter' type	B	A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
118	'winter' type	B	B	4.8	4.7	1.9	0.7	2.6	2.2	0.45	5.6	3.9	3.4	0.34	1.2
119	'spring' type	A	B	5.6	5.0	2.4	1.7	4.0	2.5	0.50	5.4	4.2	4.3	0.32	1.8
120	'winter' type	B	A	4.4	4.2	3.0	1.0	4.1	0.8	0.18	7.7	7.5	1.2	0.79	0.4
121	'spring' type	A	A	5.4	5.0	2.9	2.2	5.1	1.6	0.31	7.0	5.2	2.8	0.40	1.1
123	'winter' type	NA	NA	5.5	4.6	2.7	1.1	3.8	2.9	0.65	4.4	3.1	4.1	0.24	1.2
124	'winter' type	A	A	5.3	4.5	3.1	1.6	4.7	1.8	0.37	6.4	4.2	3.1	0.39	1.4
125	'spring' type	A	A	5.3	4.3	2.8	1.8	4.6	1.4	0.33	6.9	4.7	2.4	0.30	0.9

127	'spring' type	B	B	5.5	5.0	2.3	0.9	3.2	2.4	0.47	6.0	3.5	4.0	0.33	1.6
128	'winter' type	B	B	5.3	5.1	2.2	0.9	3.1	2.6	0.53	4.7	3.2	4.9	0.18	2.2
129	'winter' type	NA	B	5.4	4.9	2.2	0.9	3.1	2.4	0.49	5.4	3.8	3.2	0.25	0.8
130	'winter' type	A	A	5.5	5.4	2.7	1.3	4.0	2.9	0.52	5.1	3.2	4.8	0.24	1.8
131	'spring' type	A	A	5.2	4.8	3.9	2.3	6.2	1.6	0.32	6.8	6.2	1.5	0.76	-0.1
132	'winter' type	A	B	4.8	5.5	2.2	1.5	3.7	2.7	0.50	5.5	5.3	3.3	0.63	0.7
133	'winter' type	A	B	4.7	4.0	2.6	1.1	3.7	1.5	0.35	6.6	4.5	2.0	0.63	0.5
136	'spring' type	A	B	5.3	4.7	2.7	1.6	4.3	2.4	0.52	5.6	4.0	3.9	0.30	1.5
137	'spring' type	A	A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
138	'winter' type	A	A	5.5	4.4	2.2	1.3	3.6	2.6	0.57	5.3	3.9	3.1	0.36	0.5
139	'spring' type	B	B	5.7	5.3	2.6	0.9	3.5	2.3	0.42	5.2	3.9	4.4	0.22	2.1
140	'spring' type	A	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
141	'winter' type	B	B	5.9	5.2	2.5	1.0	3.5	2.7	0.51	5.2	2.8	3.7	0.37	1.0
144	'winter' type	B	B	5.0	5.0	1.7	0.7	2.4	2.7	0.53	4.9	3.0	4.8	0.22	2.1
145	'spring' type	A	A	5.1	4.0	3.8	1.1	4.9	1.4	0.37	6.4	4.5	1.9	0.66	0.4
146	'spring' type	B	B	5.3	4.7	3.2	1.1	4.3	2.3	0.51	5.3	3.5	4.0	0.35	1.7
147	'spring' type	A	A	5.3	5.2	2.7	1.7	4.4	1.7	0.35	6.6	5.2	2.7	0.54	1.0
148	'winter' type	A	A	5.4	4.4	3.0	1.6	4.6	2.1	0.47	5.9	5.2	3.2	0.40	1.1
149	'winter' type	NA	NA	5.3	4.1	2.9	1.1	4.0	1.8	0.41	5.9	4.4	2.5	0.52	0.7
150	'winter' type	A	B	4.9	4.6	2.2	1.3	3.5	2.3	0.48	5.5	3.8	3.3	0.45	1.0
151	'winter' type	B	A	5.8	5.7	2.4	0.8	3.1	2.1	0.37	6.1	4.4	2.9	0.53	0.8
152	'spring' type	A	A	5.4	5.0	2.2	1.5	3.6	1.7	0.35	6.4	3.9	2.8	0.50	1.1
153	'winter' type	A	A	5.4	5.0	2.5	2.0	4.5	1.9	0.37	6.4	4.1	3.3	0.27	1.4
155	'spring' type	A	A	5.6	5.5	2.8	1.4	4.2	2.3	0.42	6.4	4.6	2.7	0.45	0.4
156	'spring' type	A	A	5.3	4.5	3.1	1.7	4.7	1.3	0.28	7.1	6.5	1.8	0.69	0.5
157	'winter' type	A	B	5.8	4.7	2.6	2.3	4.9	2.8	0.60	4.8	3.8	4.1	0.38	1.3
158	'spring' type	A	A	5.8	4.6	2.7	1.3	4.0	2.3	0.49	5.7	4.5	3.5	0.51	1.2
161	'spring' type	A	A	5.6	5.2	2.9	1.3	4.2	1.8	0.35	6.5	5.9	2.7	0.58	0.9
162	'spring' type	A	A	5.6	4.8	2.7	1.4	4.2	2.2	0.46	5.8	4.3	3.3	0.43	1.1
163	'winter' type	B	B	5.3	5.3	2.2	1.0	3.2	2.3	0.41	6.0	4.0	3.0	0.41	0.8
164	'winter' type	B	B	5.0	4.3	1.9	0.7	2.6	2.5	0.59	4.8	3.2	3.3	0.38	0.8
165	'spring' type	A	A	5.8	4.9	3.1	2.2	5.2	1.8	0.37	6.4	5.6	2.4	0.57	0.7
169	'spring' type	NA	NA	5.0	4.7	2.3	0.9	3.2	2.5	0.51	5.4	4.0	3.3	0.39	0.8
176	'winter' type	A	A	5.5	5.0	2.7	1.4	4.1	3.0	0.61	4.6	3.8	4.5	0.22	1.5
177	'spring' type	B	A	5.1	4.9	2.6	0.7	3.4	1.6	0.33	6.5	4.8	2.8	0.65	1.2
178	'winter' type	B	B	5.5	4.6	2.4	0.7	3.1	2.5	0.55	5.2	2.6	3.2	0.37	0.7
179	'winter' type	B	B	5.1	4.8	2.5	0.8	3.2	2.8	0.55	4.9	2.3	5.3	0.08	2.5
181	'winter' type	B	B	5.4	5.5	2.6	0.7	3.4	2.7	0.50	5.4	3.9	4.1	0.45	1.4
183	'winter' type	B	B	4.9	4.6	2.1	0.4	2.5	2.7	0.58	5.2	3.2	4.4	0.24	1.7
184	'spring' type	A	A	5.2	4.7	2.6	1.6	4.2	2.1	0.47	6.4	4.6	3.0	0.47	1.0
187	'spring' type	B	B	5.3	4.7	2.9	0.7	3.6	1.8	0.40	6.2	3.6	3.4	0.21	1.6
188	'spring' type	B	B	6.1	6.1	3.8	1.2	5.0	3.0	0.48	5.4	4.3	4.2	0.45	1.2
193	'spring' type	B	B	5.3	4.8	2.5	1.8	4.2	2.4	0.48	5.9	4.2	2.7	0.51	0.3
195	'spring' type	A	B	4.7	4.0	2.6	1.3	4.0	2.7	0.65	4.5	3.6	3.9	0.39	1.2
196	'winter' type	A	B	5.7	5.4	2.0	1.4	3.4	3.7	0.64	4.2	2.6	4.8	0.16	1.1
197	'spring' type	B	A	5.7	5.7	3.3	1.0	4.4	2.5	0.45	5.7	5.5	2.8	0.57	0.3
199	'spring' type	B	B	5.5	4.7	3.0	1.5	4.5	1.9	0.41	6.3	5.0	2.9	0.51	0.9
200	'winter' type	A	A	5.5	5.3	2.9	1.3	4.2	2.3	0.41	6.4	4.8	2.6	0.55	0.3
204	'winter' type	A	A	5.4	4.6	2.2	1.6	3.9	2.9	0.62	5.1	3.9	4.3	0.33	1.5
205	'winter' type	B	A	5.5	5.3	2.4	0.9	3.3	1.8	0.33	6.6	5.8	2.4	0.54	0.7
206	'winter' type	NA	B	5.3	5.1	3.1	0.8	3.9	2.5	0.49	5.0	3.0	4.5	0.21	2.0
207	'winter' type	A	A	4.7	3.6	3.5	0.6	4.0	1.9	0.56	6.0	5.5	3.3	0.62	1.4

208	'winter' type	B	B	4.9	4.4	2.2	0.5	2.7	2.5	0.54	4.7	3.4	3.4	0.35	0.9
209	'spring' type	B	B	5.5	5.6	2.1	0.8	2.9	2.7	0.48	5.5	2.2	4.6	0.24	2.0
210	'winter' type	B	A	6.3	4.9	2.8	1.0	3.7	2.2	0.45	5.8	3.3	3.8	0.35	1.6
218	'spring' type	A	A	5.8	5.1	2.4	1.7	4.1	2.1	0.40	6.3	4.2	3.2	0.42	1.1
230	'spring' type	A	B	5.7	4.9	2.3	1.3	3.6	2.5	0.53	5.4	2.7	4.0	0.20	1.5
234	'winter' type	NA	NA	4.9	3.2	2.1	0.7	2.8	2.6	0.64	4.8	4.6	2.3	0.53	-0.3
237	'spring' type	B	B	5.4	5.0	3.1	1.0	4.1	3.2	0.65	4.9	3.6	3.8	0.31	0.6
238	'spring' type	B	A	5.8	4.6	3.4	1.1	4.5	2.0	0.41	6.1	4.5	2.7	0.35	0.7
239	'winter' type	B	A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
240	'spring' type	NA	NA	4.6	4.5	2.3	1.1	3.4	1.7	0.38	6.1	4.2	3.2	0.43	1.5
243	'spring' type	A	A	6.5	5.6	2.8	1.5	4.4	2.1	0.38	5.9	4.2	3.7	0.25	1.6
244	'spring' type	B	A	5.3	5.7	2.3	1.0	3.3	1.4	0.23	7.3	5.9	2.2	0.66	0.8
246	'spring' type	A	A	5.4	5.3	3.0	1.3	4.3	1.9	0.35	6.5	5.5	2.4	0.47	0.5
249	'spring' type	B	A	5.2	4.7	2.7	0.6	3.3	2.0	0.41	6.2	3.8	3.3	0.53	1.4
250	'spring' type	B	B	5.6	4.8	1.8	0.5	2.4	2.0	0.42	5.9	2.3	4.0	0.26	2.0
252	'winter' type	B	A	5.4	5.2	2.7	0.9	3.6	2.0	0.39	6.1	4.6	2.5	0.60	0.4
253	'winter' type	B	A	4.9	4.7	3.0	0.5	3.6	2.4	0.48	6.3	3.1	4.6	0.25	2.3
256	'spring' type	A	A	6.2	5.6	2.3	1.0	3.3	3.0	0.50	5.5	4.9	4.7	0.40	1.7
257	'winter' type	A	B	5.2	4.7	3.0	2.1	5.1	2.9	0.64	4.5	3.8	4.1	0.41	1.2
258	'winter' type	A	A	5.7	5.0	3.0	1.2	4.2	1.4	0.28	6.7	5.6	2.2	0.56	0.8
262	'spring' type	B	A	5.0	4.6	2.4	0.8	3.2	2.3	0.48	6.0	4.1	3.9	0.47	1.6
263	'winter' type	B	B	5.5	5.2	1.7	0.4	2.0	2.4	0.45	5.6	2.9	3.9	0.32	1.5
264	'winter' type	A	B	5.5	5.1	2.9	1.9	4.8	2.5	0.47	5.5	3.8	3.8	0.30	1.4
266	'spring' type	B	B	5.3	5.1	2.8	1.4	4.2	1.8	0.37	6.2	3.7	2.9	0.46	1.1
267	'winter' type	A	A	5.6	5.0	2.6	1.4	4.0	2.2	0.43	6.1	4.7	3.4	0.47	1.2
269	'winter' type	B	B	5.4	4.9	1.9	0.7	2.6	2.3	0.47	5.4	2.8	3.8	0.15	1.5
270	'winter' type	B	B	4.6	4.4	2.3	0.5	2.8	2.7	0.61	4.2	2.1	4.8	0.10	2.1
271	'spring' type	A	A	5.2	5.9	2.4	1.2	3.6	3.1	0.52	4.8	3.8	5.0	0.31	2.0
273	'spring' type	A	A	5.7	5.1	2.5	1.1	3.5	2.2	0.44	6.1	4.5	2.9	0.51	0.6
276	'spring' type	A	B	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
279	'winter' type	B	B	5.8	5.2	2.1	0.8	3.0	2.7	0.53	5.3	2.9	3.8	0.26	1.1
280	'winter' type	B	B	5.1	4.8	2.1	0.6	2.8	3.0	0.61	4.1	2.9	4.1	0.25	1.1
281	'winter' type	B	B	5.5	4.7	2.3	0.8	3.1	2.5	0.56	5.0	2.6	4.0	0.21	1.5
282	'winter' type	B	B	5.9	4.7	2.5	0.8	3.3	3.1	0.67	3.9	2.3	5.2	0.19	2.1
283	'winter' type	B	A	4.8	4.6	3.0	0.3	3.2	2.0	0.43	6.1	3.4	4.0	0.33	2.0
285	'winter' type	B	B	5.4	5.1	2.3	0.8	3.1	2.0	0.39	5.8	2.2	4.3	0.21	2.3
286	'winter' type	B	B	5.7	5.1	2.9	1.0	3.9	3.2	0.63	4.6	2.2	4.8	0.24	1.6
287	'winter' type	A	A	6.2	4.7	3.1	1.9	5.0	2.7	0.53	5.1	4.6	3.6	0.46	1.0
289	'spring' type	B	A	5.6	5.2	2.4	1.1	3.6	1.5	0.30	7.1	5.0	2.5	0.54	1.0
290	'winter' type	B	A	5.5	4.7	2.1	0.6	2.7	2.2	0.45	5.7	3.6	3.1	0.30	0.9
291	'spring' type	B	A	5.4	5.1	2.6	1.2	3.9	2.3	0.45	5.4	3.4	3.9	0.31	1.6
292	'spring' type	A	A	6.1	4.7	2.9	1.5	4.4	2.0	0.40	6.4	3.7	3.3	0.34	1.4
293	'spring' type	B	B	5.4	5.2	2.6	0.6	3.2	2.3	0.43	5.9	3.1	4.2	0.30	1.9
295	'spring' type	A	B	5.3	4.4	2.2	1.8	4.0	2.6	0.58	4.7	2.9	3.8	0.13	1.1
296	'winter' type	B	B	4.5	4.4	2.0	0.6	2.6	2.1	0.46	6.1	5.0	3.2	0.57	1.1
299	'winter' type	A	A	4.6	5.5	2.0	1.1	3.0	2.5	0.44	5.6	3.9	3.3	0.33	0.9
300	'winter' type	A	A	5.3	4.9	2.7	1.4	4.0	2.3	0.39	6.2	4.2	4.3	0.39	2.1
301	'winter' type	B	B	4.7	4.3	2.0	0.6	2.6	2.8	0.63	4.7	3.8	4.5	0.28	1.6
302	'spring' type	A	A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
303	'spring' type	B	A	5.3	4.6	2.1	0.7	2.8	1.9	0.38	6.0	3.7	2.9	0.40	1.1
304	'winter' type	B	B	5.7	5.0	1.5	0.8	2.3	2.3	0.46	5.4	3.4	3.6	0.20	1.3

Appendix E: Identification number of the DH lines denoted as the extreme genotype for minimum and maximum of each trait

	Number of Leaves	Vigor	Hypocotyl Length	Epicotyl Length	Stem Length	Number of Viable Leaves	Leaf Survival Rate	Leaf Damage Score	Stem Damage Score	Number of Leaves	Death Rate	Number of Regrown Leaves
DH line min	234	120	304	283	263	120	120	282	110	106	110	234
DH line max	188	243	131	54	131	196	282	120	120	45	106	6

Appendix F: Freezing tolerance candidate genes from Arabidopsis thaliana and homologous positions in reference genome of 'Damor-bzh'

Arabidopsis thaliana (TAIR)				Reference genome (genoscope)		
Gene name	Locus name	Synonyms	gene size [bp]	BLAT score	Chromosome	Postion [bp]
AHK2	AT5G35750	AHK2, HISTIDINE KINASE 2, HK2	5523	949	chrA03	18'857'498
AHK2	AT5G35750	AHK2, HISTIDINE KINASE 2, HK2	5523	3047	chrA04	6'487'453
AHK2	AT5G35750	AHK2, HISTIDINE KINASE 2, HK2	5523	1214	chrC03	30'045'315
AHK2	AT5G35750	AHK2, HISTIDINE KINASE 2, HK2	5523	2970	chrC04	31'447'348
AHK3	AT1G27320	AHK3, HISTIDINE KINASE 3, HK3	5744	2907	chrA07	8'918'537
AHK3	AT1G27320	AHK3, HISTIDINE KINASE 3, HK3	5744	395	chrA09	20'969'604
AHK3	AT1G27320	AHK3, HISTIDINE KINASE 3, HK3	5744	2844	chrC07	16'998'940
AHP2	AT3G29350	AHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2	1437	472	chrA06	20'847'124
AHP2	AT3G29350	AHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2	1437	483	chrA09	1'325'403
AHP2	AT3G29350	AHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2	1437	417	chrC07	31'786'270
AHP2	AT3G29350	AHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2	1437	431	chrC09	1'123'908
AHP3	AT5G39340	AHP3, ARABIDOPSIS THALIANA HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2, ATHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 3	2017	648	chrA04	8'231'754
AHP3	AT5G39340	AHP3, ARABIDOPSIS THALIANA HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 2, ATHP2, HISTIDINE-CONTAINING PHOSPHOTRANSMITTER 3	2017	540	chrC04	33'287'091
AHP5	AT1G03430	AHP5, HISTIDINE-CONTAINING PHOSPHOTRANSFER FACTOR 5	1829	552	chrA10	954'254
ARR15	AT1G74890	ARR15, RESPONSE REGULATOR 15	1579	655	chrA07	22'127'026
ARR15	AT1G74890	ARR15, RESPONSE REGULATOR 15	1579	603	chrA07	16'915'407
ARR15	AT1G74890	ARR15, RESPONSE REGULATOR 15	1579	646	chrC06	24'713'575
ARR15	AT1G74890	ARR15, RESPONSE REGULATOR 15	1579	580	chrC06	34'557'022
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE	2524	551	chrA01	12'163'237

		REGULATOR 5, RR5				
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	963	chrA06	9'534'791
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	924	chrA06	14'285'459
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	950	chrC01_random	2'181'181
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	416	chrC03	35'898'935
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	948	chrUn_random	51'492'264
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	862	chrUn_random	108'860'986
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	847	chrUn_random	90'871'766
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	597	chrUn_random	108'861'146
ARR5	AT3G48100	ARABIDOPSIS THALIANA RESPONSE REGULATOR 2, ARR5, ATRR2, IBC6, INDUCED BY CYTOKININ 6, RESPONSE REGULATOR 5, RR5	2524	416	chrUn_random	136'146'657
ARR7	AT1G19050	ARR7, RESPONSE REGULATOR 7	1482	653	chrA06	6'903'047
ARR7	AT1G19050	ARR7, RESPONSE REGULATOR 7	1482	566	chrA08	16'235'656
ARR7	AT1G19050	ARR7, RESPONSE REGULATOR 7	1482	660	chrC05	8'682'199
ARR7	AT1G19050	ARR7, RESPONSE REGULATOR 7	1482	654	chrC08	21'668'032
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	696	chrA01	18'143'456
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	564	chrA03	17'244'893
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	676	chrA05	15'858'446
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	644	chrC01	32'449'774
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	719	chrC03_random	1'919'902
AZF2	AT3G19580	AZF2, ZF2, ZINC-FINGER PROTEIN 2	1701	712	chrC05	32'661'769
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	927	chrA06	7'067'281
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	866	chrA06	7'210'543
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	594	chrA06	7'067'870
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	610	chrA07	16'876'981
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	839	chrA08	16'162'369
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	772	chrA09	30'386'980
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	493	chrC06	34'620'858
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	793	chrC08	21'799'024

BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	772	chrC08	33'857'703
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	574	chrUn_random	50'449'934
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	551	chrUn_random	106'720'763
BES1	AT1G19350	BES1, BRASSINAZOLE-RESISTANT 2, BRI1-EMS-SUPPRESSOR 1, BZR2	1877	491	chrUn_random	12'885'356
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1256	chrA01	4'679'229
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	897	chrA03_random	1'654'911
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1456	chrC01	6'943'708
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1268	chrC03	52'102'784
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	704	chrC03	52'105'904
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1170	chrC07_random	2'470'993
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1175	chrUn_random	115'451'760
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	1060	chrUn_random	104'125'619
BIN2	AT4G18710	ATSK21, BIN2, BRASSINOSTEROID-INSENSITIVE 2, DWARF 12, DWF12, SHAGGY-LIKE KINASE 21, SK21, UCU1, ULTRACURVATA 1	2787	367	chrUn_random	80'290'405
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2934	chrA01	2'554'186
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2900	chrA06_random	2'122'319
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	847	chrA06_random	2'122'485
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2291	chrA08	13'431'253
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	395	chrA08	13'435'588
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2812	chrC01_random	15'392
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2367	chrC03	49'687'650
BRI1	AT4G39400	ATBRI1, BIN1, BR INSENSITIVE 1, BRASSINOSTEROID INSENSITIVE 1, BRI1, CABBAGE 2, CBB2, DWARF 2, DWF2	4375	2887	chrC07	44'557'961

BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	592	chrA06	6'262'958
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	381	chrA07	17'283'443
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	352	chrA07	21'669'650
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	511	chrA08	16'486'655
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	572	chrA09	30'716'195
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	366	chrC02	18'901'453
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	621	chrC05	7'987'179
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	353	chrC06	33'742'958
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	627	chrC08	21'149'478
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	554	chrC08	34'258'547
BTF3	AT1G17880	ATBTF3, BASIC TRANSCRIPTION FACTOR 3, BTF3	1599	385	chrUn_random	67'713'775
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	606	chrA02	10'272'138
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	522	chrA06	7'210'577
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	502	chrA06	7'067'415
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	919	chrA07	16'876'781
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	563	chrA08	16'162'173
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	362	chrA09	30'386'840
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	711	chrC06	34'620'840
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	572	chrC08	21'798'968
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	945	chrUn_random	50'449'918
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	839	chrUn_random	12'885'371
BZR1	AT1G75080	BRASSINAZOLE-RESISTANT 1, BZR1	2687	751	chrUn_random	106'720'469
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	2457	chrA09	3'297'704
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	1415	chrA10	15'173'543
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	1186	chrA10	11'752'105
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	384	chrC02	32'299'290
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	361	chrC02	13'543'997
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	581	chrC05	34'281'912
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	2617	chrC09	3'766'455
CAMTA2	AT5G64220	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA2	5970	1346	chrC09	46'651'435
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	969	chrA05	17'453'023
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	2471	chrA08	6'008'214
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	1040	chrC05	35'683'235
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	2431	chrC08_random	2'585'692
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	918	chrC08_random	2'586'221
CAMTA5	AT4G16150	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 2, CAMTA5	5234	755	chrC08_random	3'219'901

CAMTA6	AT3G16940	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 6, CAMTA6	4892	699	chrA04	12'784'358
CAMTA6	AT3G16940	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 6, CAMTA6	4892	2011	chrA05	17'452'368
CAMTA6	AT3G16940	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 6, CAMTA6	4892	1173	chrA08	6'008'448
CAMTA6	AT3G16940	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 6, CAMTA6	4892	1865	chrC05	35'683'072
CAMTA6	AT3G16940	CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR 6, CAMTA6	4892	1058	chrC08_random	2'586'180
CBF1	AT4G25490	ATCBF1, C-REPEAT/DRE BINDING FACTOR 1, CBF1, DRE BINDING PROTEIN 1B, DREB1B	1217	395	chrC03_random	417'518
CBF1	AT4G25490	ATCBF1, C-REPEAT/DRE BINDING FACTOR 1, CBF1, DRE BINDING PROTEIN 1B, DREB1B	1217	455	chrC07	40'421'372
CBF1	AT4G25490	ATCBF1, C-REPEAT/DRE BINDING FACTOR 1, CBF1, DRE BINDING PROTEIN 1B, DREB1B	1217	453	chrUn_random	112'735'608
CBF1	AT4G25490	ATCBF1, C-REPEAT/DRE BINDING FACTOR 1, CBF1, DRE BINDING PROTEIN 1B, DREB1B	1217	415	chrUn_random	73'706'517
CBF2	AT4G25470	ATCBF2, C-REPEAT/DRE BINDING FACTOR 2, CBF2, DRE/CRT-BINDING PROTEIN 1C, DREB1C, FREEZING TOLERANCE QTL 4, FTQ4	986	361	chrA03	6'228'338
CBF2	AT4G25470	ATCBF2, C-REPEAT/DRE BINDING FACTOR 2, CBF2, DRE/CRT-BINDING PROTEIN 1C, DREB1C, FREEZING TOLERANCE QTL 4, FTQ4	986	353	chrA08_random	1'768'312
CBF2	AT4G25470	ATCBF2, C-REPEAT/DRE BINDING FACTOR 2, CBF2, DRE/CRT-BINDING PROTEIN 1C, DREB1C, FREEZING TOLERANCE QTL 4, FTQ4	986	385	chrC03_random	417'583
CBF2	AT4G25470	ATCBF2, C-REPEAT/DRE BINDING FACTOR 2, CBF2, DRE/CRT-BINDING PROTEIN 1C, DREB1C, FREEZING TOLERANCE QTL 4, FTQ4	986	362	chrC07	40'421'337
CBF2	AT4G25470	ATCBF2, C-REPEAT/DRE BINDING FACTOR 2, CBF2, DRE/CRT-BINDING PROTEIN 1C, DREB1C, FREEZING TOLERANCE QTL 4, FTQ4	986	402	chrUn_random	112'735'619
CBF3	AT4G25480	ATCBF3, C-REPEAT BINDING FACTOR 3, CBF3, DEHYDRATION RESPONSE ELEMENT B1A, DREB1A	1391	404	chrA08_random	1'768'070
CBF3	AT4G25480	ATCBF3, C-REPEAT BINDING FACTOR 3, CBF3, DEHYDRATION RESPONSE ELEMENT B1A, DREB1A	1391	418	chrC03_random	417'591
CBF3	AT4G25480	ATCBF3, C-REPEAT BINDING FACTOR 3, CBF3, DEHYDRATION RESPONSE ELEMENT B1A, DREB1A	1391	370	chrC07	40'421'342
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	955	chrA01	4'073'183
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	554	chrA02	18'357'257
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	810	chrA03	21'656'574
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	1012	chrC01	6'006'771
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN	3035	497	chrC02	35'642'278

		B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5				
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	878	chrC07	37'207'352
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	493	chrC09	17'083'178
CBL1	AT4G17615	ARABIDOPSIS THALIANA CALCINEURIN B-LIKE PROTEIN, ATCBL1, CALCINEURIN B-LIKE PROTEIN 1, CBL1, SCABP5, SOS3-LIKE CALCIUM BINDING PROTEIN 5	3035	483	chrUn_random	106'009'431
CCA1	AT2G46830	ATCCA1, CCA1, CIRCADIAN CLOCK ASSOCIATED 1	3325	1196	chrA05	582'475
CCA1	AT2G46830	ATCCA1, CCA1, CIRCADIAN CLOCK ASSOCIATED 1	3325	1218	chrC04	480'022
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1636	chrA06	6'842'565
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1036	chrA07	22'079'076
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	386	chrA08	16'264'361
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1563	chrA09	30'503'516
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1648	chrC05	8'590'207
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1128	chrC06	34'500'245
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	1759	chrC08	33'959'628
CDPK1	AT1G18890	ATCDPK1, ATCPK10, CALCIUM-DEPENDENT PROTEIN KINASE 1, CDPK1, CPK10	3312	390	chrC08	21'604'237
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1650	chrA02	1'894'130
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1625	chrA10	12'093'510
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1094	chrA10_random	2'013'073
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1669	chrC02	4'875'587
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1582	chrC09	41'185'367
CDPK19	AT5G19450	CALCIUM-DEPENDENT PROTEIN KINASE 19, CDPK19, CPK8	3375	1116	chrC09	45'146'575
CDPK6	AT4G23650	ATCDPK6, CALCIUM DEPENDENT PROTEIN KINASE 3, CALCIUM-DEPENDENT PROTEIN KINASE 6, CDPK6, CPK3	2894	1479	chrA01	6'736'110
CDPK6	AT4G23650	ATCDPK6, CALCIUM DEPENDENT PROTEIN KINASE 3, CALCIUM-DEPENDENT PROTEIN KINASE 6, CDPK6, CPK3	2894	1062	chrA03	23'628'031
CDPK6	AT4G23650	ATCDPK6, CALCIUM DEPENDENT PROTEIN KINASE 3, CALCIUM-DEPENDENT PROTEIN KINASE 6, CDPK6, CPK3	2894	1448	chrC01	10'567'898
CDPK6	AT4G23650	ATCDPK6, CALCIUM DEPENDENT	2894	1387	chrC07_r	2'511'723

		PROTEIN KINASE 3, CALCIUM-DEPENDENT PROTEIN KINASE 6, CDPK6, CPK3			andom	
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1227	chrA02	23'562'466
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1227	chrA02	23'562'466
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1029	chrA02	23'566'174
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1029	chrA02	23'566'174
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	718	chrA02	23'563'225
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	718	chrA02	23'563'225
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1287	chrA06	18'105'147
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1287	chrA06	18'105'147
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1275	chrA09	2'568'066
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1275	chrA09	2'568'066
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN	2418	1165	chrA10	11'687'004

		KINASE 9, CDPK9, CPK12				
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1165	chrA10	11'687'004
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1216	chrC02	44'412'483
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1216	chrC02	44'412'483
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1114	chrC02	44'415'536
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1114	chrC02	44'415'536
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	840	chrC02	44'419'931
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	840	chrC02	44'419'931
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1264	chrC07	35'048'989
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1264	chrC07	35'048'989
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1315	chrC09	2'783'418
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1315	chrC09	2'783'418

CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1115	chrC09	40'522'860
CDPK9	AT5G23580	ARABIDOPSIS THALIANA CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, ATCDPK9, ATCPK12, CALCIUM-DEPENDENT PROTEIN KINASE 12, CALMODULIN-LIKE DOMAIN PROTEIN KINASE 9, CDPK9, CPK12	2418	1115	chrC09	40'522'860
CESTA	AT1G25330	CES, CESTA, HAF, HALF FILLED	1834	726	chrA08	14'940'485
CESTA	AT1G25330	CES, CESTA, HAF, HALF FILLED	1834	748	chrUn_random	6'804'871
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	1432	chrA03	16'805'245
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	1596	chrA05	17'234'038
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	506	chrA06	2'382'591
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	392	chrA08	2'780'604
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	1560	chrC03	25'000'268
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	1629	chrC05	35'200'638
CIPK1	AT3G17510	CBL-INTERACTING PROTEIN KINASE 1, CIPK1, SNF1-RELATED PROTEIN KINASE 3.16, SNRK3.16	4078	446	chrC08	3'755'263
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	856	chrA02	3'660'923
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	1194	chrA10_random	1'856'208
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	941	chrC02	6'250'038
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	485	chrC02	757'981
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	1014	chrC09	37'083'547
CIPK10	AT5G58380	CBL-INTERACTING PROTEIN KINASE 10, CIPK10, PKS2, SIP1, SNF1-RELATED PROTEIN KINASE 3.8, SNRK3.8, SOS3-INTERACTING PROTEIN 1	2392	368	chrUn_random	2'260'833
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4	1867	758	chrA03	6'364'344
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN	1867	855	chrA04	14'758'472

		KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4				
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4	1867	799	chrC03	8'563'262
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4	1867	834	chrC04	11'732'946
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4	1867	909	chrUn_random	38'275'048
CIPK11	AT2G30360	CBL-INTERACTING PROTEIN KINASE 11, CIPK11, PKS5, PROTEIN KINASE SOS2-LIKE 5, SIP4, SNF1-RELATED PROTEIN KINASE 3.22, SNRK3.22, SOS3-INTERACTING PROTEIN 4	1867	863	chrUn_random	90'471'840
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	969	chrA01	4'672'364
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	500	chrA04	16'071'156
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	423	chrA05	5'288'893
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	436	chrA08	14'220'576
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	726	chrC01	6'928'274
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	411	chrC02	14'796'825
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	1129	chrC03	52'086'678
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	1130	chrUn_random	106'372'880
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	534	chrUn_random	87'125'354
CIPK12	AT4G18700	ATWL4, CBL-INTERACTING PROTEIN KINASE 12, CIPK12, PKS8, PROTEIN KINASE 8, SNF1-RELATED PROTEIN KINASE 3.9, SNRK3.9, WL4, WPL4-LIKE 4	2261	418	chrUn_random	111'582'560
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	1100	chrA04	16'071'076
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED	1722	979	chrA05	5'288'660

		PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2				
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	537	chrA08	14'220'552
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	637	chrC03	48'215'985
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	533	chrC03	52'086'986
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	1026	chrC04	44'410'418
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	1129	chrUn_random	94'887'062
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	1066	chrUn_random	96'693'566
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	976	chrUn_random	60'601'246
CIPK13	AT2G34180	ATWL2, CBL-INTERACTING PROTEIN KINASE 13, CIPK13, SNF1-RELATED PROTEIN KINASE 3.7, SNRK3.7, WL2, WPL4-LIKE 2	1722	426	chrUn_random	106'373'195
CIPK14	AT5G01820	ATCIPK14, ATSR1, CBL-INTERACTING PROTEIN KINASE 14, CIPK14, PKS24, SERINE/THREONINE PROTEIN KINASE 1, SNF1-RELATED PROTEIN KINASE 3.15, SNRK3.15, SOS2-LIKE PROTEIN KINASE 24, SR1	2216	618	chrUn_random	1'338'939
CIPK15	AT5G01810	ATPK10, CBL-INTERACTING PROTEIN KINASE 15, CIPK15, PKS3, PROTEIN KINASE 10, SIP2, SNF1-RELATED PROTEIN KINASE 3.1, SNRK3.1, SOS3-INTERACTING PROTEIN 2	2724	872	chrUn_random	1'343'062
CIPK16	AT2G25090	ATCIPK16, CBL-INTERACTING PROTEIN KINASE 16, CIPK16, SNF1-RELATED PROTEIN KINASE 3.18, SNRK3.18	2483	1029	chrA04_random	667'320
CIPK16	AT2G25090	ATCIPK16, CBL-INTERACTING PROTEIN KINASE 16, CIPK16, SNF1-RELATED PROTEIN KINASE 3.18, SNRK3.18	2483	981	chrC04	38'854'187
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	514	chrA01	4'672'748
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	619	chrA04	16'071'117
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	634	chrA05	5'288'806
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	1209	chrA08	14'220'183
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING	1883	463	chrC01	6'928'659

		PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1				
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	1257	chrC03	48'215'873
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	561	chrC03	52'086'986
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	701	chrC04	44'410'459
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	633	chrUn_random	60'601'598
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	586	chrUn_random	94'887'091
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	576	chrUn_random	106'373'195
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	452	chrUn_random	96'694'000
CIPK18	AT1G29230	ATCIPK18, ATWL1, CBL-INTERACTING PROTEIN KINASE 18, CIPK18, SNF1-RELATED PROTEIN KINASE 3.20, SNRK3.20, WL1, WPL4-LIKE 1	1883	366	chrUn_random	87'125'378
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	448	chrA05	5'288'829
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	484	chrC01	6'928'660
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	448	chrC03	52'087'111
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	1022	chrUn_random	111'582'472
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	991	chrUn_random	87'124'849
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	648	chrUn_random	106'373'170
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	560	chrUn_random	121'619'527
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	428	chrUn_random	14'431'969
CIPK19	AT5G45810	CBL-INTERACTING PROTEIN KINASE 19, CIPK19, SNF1-RELATED PROTEIN KINASE 3.5, SNRK3.5	1915	383	chrUn_random	60'601'534
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	566	chrA02	3'661'336
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	725	chrA10	15'535'257

CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	551	chrA10	15'535'500
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	753	chrA10_random	1'856'645
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	599	chrC02	6'250'359
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	572	chrC02	758'039
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	697	chrC09	37'083'563
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	619	chrC09	47'157'336
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	437	chrC09	47'159'612
CIPK2	AT5G07070	CBL-INTERACTING PROTEIN KINASE 2, CIPK2, SNF1-RELATED PROTEIN KINASE 3.2, SNRK3.2	2112	575	chrUn_random	2'260'345
CIPK20	AT5G45820	CBL-INTERACTING PROTEIN KINASE 20, CIPK20, PKS18, PROTEIN KINASE 18, SNF1-RELATED PROTEIN KINASE 3.6, SNRK3.6	1923	1050	chrA02	17'447'591
CIPK20	AT5G45820	CBL-INTERACTING PROTEIN KINASE 20, CIPK20, PKS18, PROTEIN KINASE 18, SNF1-RELATED PROTEIN KINASE 3.6, SNRK3.6	1923	1009	chrC02	34'260'519
CIPK20	AT5G45820	CBL-INTERACTING PROTEIN KINASE 20, CIPK20, PKS18, PROTEIN KINASE 18, SNF1-RELATED PROTEIN KINASE 3.6, SNRK3.6	1923	940	chrUn_random	87'122'850
CIPK20	AT5G45820	CBL-INTERACTING PROTEIN KINASE 20, CIPK20, PKS18, PROTEIN KINASE 18, SNF1-RELATED PROTEIN KINASE 3.6, SNRK3.6	1923	511	chrUn_random	121'621'252
CIPK22	AT2G38490	CBL-INTERACTING PROTEIN KINASE 22, CIPK22, SNF1-RELATED PROTEIN KINASE 3.19, SNRK3.19	1296	743	chrA03	8'420'150
CIPK22	AT2G38490	CBL-INTERACTING PROTEIN KINASE 22, CIPK22, SNF1-RELATED PROTEIN KINASE 3.19, SNRK3.19	1296	776	chrA05_random	366'939
CIPK22	AT2G38490	CBL-INTERACTING PROTEIN KINASE 22, CIPK22, SNF1-RELATED PROTEIN KINASE 3.19, SNRK3.19	1296	761	chrC03	11'547'763
CIPK22	AT2G38490	CBL-INTERACTING PROTEIN KINASE 22, CIPK22, SNF1-RELATED PROTEIN KINASE 3.19, SNRK3.19	1296	816	chrC04	4'908'083
CIPK22	AT2G38490	CBL-INTERACTING PROTEIN KINASE 22, CIPK22, SNF1-RELATED PROTEIN KINASE 3.19, SNRK3.19	1296	460	chrC07_random	1'907'033
CIPK25	AT5G25110	CBL-INTERACTING PROTEIN KINASE 25, CIPK25, SNF1-RELATED PROTEIN KINASE 3.25, SNRK3.25	1749	662	chrA06_random	1'535'800
CIPK25	AT5G25110	CBL-INTERACTING PROTEIN KINASE 25, CIPK25, SNF1-RELATED PROTEIN KINASE 3.25, SNRK3.25	1749	581	chrA10	14'762'006
CIPK25	AT5G25110	CBL-INTERACTING PROTEIN KINASE 25, CIPK25, SNF1-RELATED PROTEIN KINASE 3.25, SNRK3.25	1749	666	chrC07	34'302'304
CIPK3	AT2G26980	CBL-INTERACTING PROTEIN KINASE 3, CIPK3, SNF1-RELATED PROTEIN KINASE 3.17, SNRK3.17	3990	1437	chrA04	13'428'385
CIPK3	AT2G26980	CBL-INTERACTING PROTEIN KINASE 3,	3990	1443	chrC04	39'727'563

		CIPK3, SNF1-RELATED PROTEIN KINASE 3.17, SNRK3.17				
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	795	chrA01	10'761'618
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	622	chrA01	10'774'419
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	355	chrA01	16'656'978
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	458	chrA05	11'401'674
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	781	chrC01	16'794'713
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	502	chrC01	16'815'650
CIPK4	AT4G14580	CBL-INTERACTING PROTEIN KINASE 4, CIPK4, SNF1-RELATED PROTEIN KINASE 3.3, SNRK3.3	1650	371	chrC01	29'990'564
CIPK5	AT5G10930	CBL-INTERACTING PROTEIN KINASE 5, CIPK5, SNF1-RELATED PROTEIN KINASE 3.24, SNRK3.24	2250	505	chrA06_random	1'535'582
CIPK5	AT5G10930	CBL-INTERACTING PROTEIN KINASE 5, CIPK5, SNF1-RELATED PROTEIN KINASE 3.24, SNRK3.24	2250	859	chrA10	14'762'002
CIPK5	AT5G10930	CBL-INTERACTING PROTEIN KINASE 5, CIPK5, SNF1-RELATED PROTEIN KINASE 3.24, SNRK3.24	2250	469	chrC07	34'302'303
CIPK5	AT5G10930	CBL-INTERACTING PROTEIN KINASE 5, CIPK5, SNF1-RELATED PROTEIN KINASE 3.24, SNRK3.24	2250	926	chrC09	45'864'926
CIPK7	AT3G23000	ATSR2, ATSRPK1, CBL-INTERACTING PROTEIN KINASE 7, CIPK7, PKS7, SNF1-RELATED PROTEIN KINASE 3.10, SNRK3.10	1664	677	chrA01	16'656'463
CIPK7	AT3G23000	ATSR2, ATSRPK1, CBL-INTERACTING PROTEIN KINASE 7, CIPK7, PKS7, SNF1-RELATED PROTEIN KINASE 3.10, SNRK3.10	1664	759	chrA05	11'401'665
CIPK7	AT3G23000	ATSR2, ATSRPK1, CBL-INTERACTING PROTEIN KINASE 7, CIPK7, PKS7, SNF1-RELATED PROTEIN KINASE 3.10, SNRK3.10	1664	818	chrC01	29'990'151
CIPK7	AT3G23000	ATSR2, ATSRPK1, CBL-INTERACTING PROTEIN KINASE 7, CIPK7, PKS7, SNF1-RELATED PROTEIN KINASE 3.10, SNRK3.10	1664	727	chrC05	28'176'858
CIPK8	AT4G24400	ATCIPK8, CBL-INTERACTING PROTEIN KINASE 8, CIPK8, PKS11, PROTEIN KINASE 11, SNF1-RELATED PROTEIN KINASE 3.13, SNRK3.13	3736	1565	chrA01_random	398'399
CIPK8	AT4G24400	ATCIPK8, CBL-INTERACTING PROTEIN KINASE 8, CIPK8, PKS11, PROTEIN KINASE 11, SNF1-RELATED PROTEIN KINASE 3.13, SNRK3.13	3736	1582	chrC01	11'219'385
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9, CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12	3459	1444	chrA09	33'834'415
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9, CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12	3459	1013	chrA09	33'834'415
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9,	3459	1440	chrA10	341'212

		CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12				
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9, CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12	3459	1409	chrC05	398'232
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9, CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12	3459	1282	chrUn_random	13'770'924
CIPK9	AT1G01140	CBL-INTERACTING PROTEIN KINASE 9, CIPK9, PKS6, PROTEIN KINASE 6, SNF1-RELATED PROTEIN KINASE 3.12, SNRK3.12	3459	822	chrUn_random	92'147'069
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	1100	chrA03_random	784'652
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	859	chrA04	17'593'989
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	693	chrA04	17'597'284
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	1235	chrA05	2'958'602
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	1172	chrC03	12'251'924
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	1283	chrC04	3'852'082
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	917	chrC04	45'932'042
COI1	AT2G39940	COI1, CORONATINE INSENSITIVE 1	3372	732	chrC04	45'932'217
CPK4	AT4G09570	ATCPK4, CALCIUM-DEPENDENT PROTEIN KINASE 4, CPK4	2940	1334	chrA03	11'562'041
CPK4	AT4G09570	ATCPK4, CALCIUM-DEPENDENT PROTEIN KINASE 4, CPK4	2940	1422	chrC03	16'912'734
CPK4	AT4G09570	ATCPK4, CALCIUM-DEPENDENT PROTEIN KINASE 4, CPK4	2940	1107	chrC05	24'871'214
CPK4	AT4G09570	ATCPK4, CALCIUM-DEPENDENT PROTEIN KINASE 4, CPK4	2940	1080	chrUn_random	12'644'015
CRF2	AT4G23750	CRF2, CYTOKININ RESPONSE FACTOR 2, TARGET OF MONOPTEROS 3, TMO3	1911	783	chrA01	6'829'640
CRF2	AT4G23750	CRF2, CYTOKININ RESPONSE FACTOR 2, TARGET OF MONOPTEROS 3, TMO3	1911	673	chrA03	23'699'611
CRF2	AT4G23750	CRF2, CYTOKININ RESPONSE FACTOR 2, TARGET OF MONOPTEROS 3, TMO3	1911	860	chrC01	10'708'790
CRF2	AT4G23750	CRF2, CYTOKININ RESPONSE FACTOR 2, TARGET OF MONOPTEROS 3, TMO3	1911	691	chrC07	39'822'694
CRF3	AT5G53290	CRF3, CYTOKININ RESPONSE FACTOR 3	1568	772	chrA02	5'285'232
CRF3	AT5G53290	CRF3, CYTOKININ RESPONSE FACTOR 3	1568	729	chrA03	5'606'970
CRF3	AT5G53290	CRF3, CYTOKININ RESPONSE FACTOR 3	1568	781	chrC02	9'852'778
CRF3	AT5G53290	CRF3, CYTOKININ RESPONSE FACTOR 3	1568	676	chrC03	7'314'501
CRF3	AT5G53290	CRF3, CYTOKININ RESPONSE FACTOR 3	1568	776	chrUn_random	55'581'259
CRLK1	AT5G54590	CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1, CRLK1	3129	1167	chrA03	5'311'948
CRLK1	AT5G54590	CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1, CRLK1	3129	997	chrA10	7'152'111
CRLK1	AT5G54590	CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1, CRLK1	3129	1064	chrC02	8'871'204
CRLK1	AT5G54590	CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1, CRLK1	3129	1040	chrC03	6'979'982
CRLK1	AT5G54590	CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1, CRLK1	3129	1010	chrC09	33'929'663
CRLK2	AT5G15730	ATCRLK2, CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 2, CRLK2	2819	1145	chrA10	13'402'287
CRLK2	AT5G15730	ATCRLK2, CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 2, CRLK2	2819	1101	chrC09	43'814'569
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1,	2655	1010	chrA06	5'868'134

		CRPK1				
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	1001	chrA08	16'729'358
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	1132	chrA09_random	3'641'645
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	936	chrA09_random	3'646'259
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	1062	chrC05	7'442'590
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	1204	chrC08	34'649'133
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	939	chrC08	34'656'992
CRPK1	AT1G16670	COLD-RESPONSIVE PROTEIN KINASE 1, CRPK1	2655	929	chrC08	20'746'867
CTR1	AT5G03730	ATCTR1, CONSTITUTIVE TRIPLE RESPONSE 1, CTR1, SIS1, SUGAR-INSENSITIVE 1	5490	2656	chrA03	446'322
CTR1	AT5G03730	ATCTR1, CONSTITUTIVE TRIPLE RESPONSE 1, CTR1, SIS1, SUGAR-INSENSITIVE 1	5490	2648	chrA10	16'821'104
CTR1	AT5G03730	ATCTR1, CONSTITUTIVE TRIPLE RESPONSE 1, CTR1, SIS1, SUGAR-INSENSITIVE 1	5490	2529	chrC03	629'908
CTR1	AT5G03730	ATCTR1, CONSTITUTIVE TRIPLE RESPONSE 1, CTR1, SIS1, SUGAR-INSENSITIVE 1	5490	2706	chrUn_random	3'310'924
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	1145	chrA03	8'924'424
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	544	chrA05	20'270'603
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	1306	chrA05_random	193'217
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	1112	chrC03	12'402'674
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	980	chrC03	12'402'674
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	785	chrC04	7'748'559
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	606	chrC08	28'128'712
CZF1	AT2G40140	SALT-INDUCIBLE ZINC FINGER 2, ATSZF2, CZF1, SZF2, TANDEM ZINC FINGER 10, TZF10, ZFAR1	2738	1276	chrUn_random	41'269'276
CZF2	AT5G04340	ATZAT6, C2H2, COLD INDUCED ZINC FINGER PROTEIN 2, CZF2, ZAT6, ZINC FINGER OF ARABIDOPSIS THALIANA 6	1305	551	chrA10	16'572'614
CZF2	AT5G04340	ATZAT6, C2H2, COLD INDUCED ZINC FINGER PROTEIN 2, CZF2, ZAT6, ZINC FINGER OF ARABIDOPSIS THALIANA 6	1305	535	chrUn_random	31'103'297
EBF2	AT5G25350	EBF2, EIN3-BINDING F BOX PROTEIN 2	3098	1504	chrA06	18'977'638
EBF2	AT5G25350	EBF2, EIN3-BINDING F BOX PROTEIN 2	3098	1177	chrA09	2'264'912
EBF2	AT5G25350	EBF2, EIN3-BINDING F BOX PROTEIN 2	3098	1498	chrC07	34'178'273
EBF2	AT5G25350	EBF2, EIN3-BINDING F BOX PROTEIN 2	3098	1453	chrC09	2'296'331
EBF2	AT5G25350	EBF2, EIN3-BINDING F BOX PROTEIN 2	3098	507	chrC09	2'298'102
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	538	chrA01_random	2'307'994
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-	2638	1254	chrA03	10'717'382

		LIKE 1				
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	622	chrA03	17'575'556
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	682	chrA05	15'578'895
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	561	chrC01	31'744'964
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	1353	chrC03	15'143'027
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	534	chrC03	26'641'786
EIL1	AT2G27050	ATEIL1, EIL1, ETHYLENE-INSENSITIVE3-LIKE 1	2638	522	chrC05	30'890'839
EIN2	AT5G03280	ATEIN2, CKR1, CYTOKININ RESISTANT 1, EIN2, ENHANCED RESPONSE TO ABA3, ERA3, ETHYLENE INSENSITIVE 2, ORE2, ORE3, ORESARA 2, ORESARA 3, PIR2	5977	3203	chrA10	16'952'942
EIN2	AT5G03280	ATEIN2, CKR1, CYTOKININ RESISTANT 1, EIN2, ENHANCED RESPONSE TO ABA3, ERA3, ETHYLENE INSENSITIVE 2, ORE2, ORE3, ORESARA 2, ORESARA 3, PIR2	5977	3211	chrUn_random	3'498'442
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1184	chrA01_random	2'308'147
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1270	chrA03	17'574'803
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	581	chrA03	10'717'818
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1501	chrA05	15'578'137
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1200	chrC01	31'744'965
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1241	chrC03	26'640'739
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	632	chrC03	15'143'307
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	1552	chrC05	30'890'092
EIN3	AT3G20770	ATEIN3, EIN3, ETHYLENE-INSENSITIVE3	2956	374	chrC05	30'897'188
EPF1	AT2G20875	ATEPF1, EPF1, EPIDERMAL PATTERNING FACTOR 1	952	497	chrA09	30'139'498
EPF1	AT2G20875	ATEPF1, EPF1, EPIDERMAL PATTERNING FACTOR 1	952	491	chrC08	33'585'436
ETR1	AT1G66340	ATETR1, EIN1, ETHYLENE INSENSITIVE 1, ETHYLENE RESPONSE, ETHYLENE RESPONSE 1, ETR, ETR1	3595	1705	chrA07	19'050'440
ETR1	AT1G66340	ATETR1, EIN1, ETHYLENE INSENSITIVE 1, ETHYLENE RESPONSE, ETHYLENE RESPONSE 1, ETR, ETR1	3595	1755	chrUn_random	28'005'771
ETR1	AT1G66340	ATETR1, EIN1, ETHYLENE INSENSITIVE 1, ETHYLENE RESPONSE, ETHYLENE RESPONSE 1, ETR, ETR1	3595	386	chrUn_random	77'665'915
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	1214	chrA04	19'635'510
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	1396	chrA05	209'320
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	1367	chrC04	48'588'544
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	1389	chrC04_random	82'500
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	723	chrC04_random	26'069
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	1109	chrUn_random	37'544'019
FUM2	AT5G50950	FUM2, FUMARASE 2	3959	578	chrUn_random	37'550'754
GID1A	AT3G05120	ATGID1A, GA INSENSITIVE DWARF1A, GID1A	2482	639	chrA05	22'026'356
GID1A	AT3G05120	ATGID1A, GA INSENSITIVE DWARF1A, GID1A	2482	633	chrA09	13'480'326
GID1A	AT3G05120	ATGID1A, GA INSENSITIVE DWARF1A, GID1A	2482	675	chrC05	42'053'548
GID1A	AT3G05120	ATGID1A, GA INSENSITIVE DWARF1A, GID1A	2482	628	chrC07	33'179'108

GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	888	chrA04	113'838
GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	901	chrA07	15'590'257
GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	959	chrA09_random	3'325'028
GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	909	chrC04	21'974'834
GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	882	chrUn_random	85'676'770
GID1B	AT3G63010	ATGID1B, GA INSENSITIVE DWARF1B, GID1B	2244	864	chrUn_random	113'504'940
GID1C	AT5G27320	ATGID1C, GA INSENSITIVE DWARF1C, GID1C	2302	537	chrA05	22'026'438
GID1C	AT5G27320	ATGID1C, GA INSENSITIVE DWARF1C, GID1C	2302	642	chrA06	19'762'369
GID1C	AT5G27320	ATGID1C, GA INSENSITIVE DWARF1C, GID1C	2302	1068	chrA09	13'480'177
GID1C	AT5G27320	ATGID1C, GA INSENSITIVE DWARF1C, GID1C	2302	416	chrC05	42'053'682
GID1C	AT5G27320	ATGID1C, GA INSENSITIVE DWARF1C, GID1C	2302	1193	chrC07	33'178'683
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	1420	chrA01	22'780'817
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	984	chrA10	16'703'932
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	1464	chrC01	38'520'411
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	627	chrC06_random	1'704'211
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	364	chrC06_random	1'704'391
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	958	chrUn_random	5'241'671
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	813	chrUn_random	16'070'713
GLR1.1	AT3G04110	ATGLR1.1, GLR1, GLR1.1, GLUTAMATE RECEPTOR 1, GLUTAMATE RECEPTOR 1.1	3269	756	chrUn_random	16'070'847
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1494	chrA02	21'861'167
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1206	chrA02	21'866'708
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1141	chrA02	21'871'666
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1534	chrA06	20'469'416
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1584	chrA09	1'502'687
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1577	chrA09	1'518'230
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1262	chrA09	1'518'680
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1429	chrC02	41'509'261
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1344	chrC02	41'514'050
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1236	chrC02	41'488'750
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1635	chrC07	32'420'358

GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1581	chrC09	1'345'266
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1497	chrC09	1'362'199
GLR1.2	AT5G48400	ATGLR1.2, GLR1.2, GLUTAMATE RECEPTOR 1.2	3443	1290	chrC09	1'362'592
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1585	chrA02	21'871'367
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1152	chrA02	21'861'167
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	969	chrA02	21'866'531
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1585	chrA06	20'469'562
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1449	chrA09	1'502'792
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1394	chrA09	1'525'224
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1155	chrA09	1'518'683
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1603	chrC02	41'509'250
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1401	chrC02	41'496'295
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1277	chrC02	41'513'892
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1672	chrC07	32'420'457
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1526	chrC09	1'370'197
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1440	chrC09	1'345'263
GLR1.3	AT5G48410	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 1.3, ATGLR1.3, GLR1.3, GLUTAMATE RECEPTOR 1.3	3159	1201	chrC09	1'362'350
GLR1.4	AT3G07520	ATGLR1.4, GLR1.4, GLUTAMATE RECEPTOR 1.4	3401	352	chrA09	1'502'874
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	1915	chrA03	26'854'910
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	372	chrA04_random	693'432
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	1921	chrC04	24'846'028
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	2068	chrC07	42'514'699
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	953	chrC07	42'507'283
GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	815	chrC07_random	2'807'335

GLR2.1	AT5G27100	ARABIDOPSIS THALIANA GLUTAMATE RECEPTOR 2.1, ATGLR2.1, GLR2.1, GLUTAMATE RECEPTOR 2.1	3386	2010	chrUn_random	45'379'624
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	817	chrA03	26'855'228
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	1295	chrA04	12'862'660
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	1542	chrA04_random	692'235
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	1302	chrC04	38'658'240
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	1101	chrC04	38'490'950
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	560	chrC04	24'847'128
GLR2.2	AT2G24720	ATGLR2.2, GLR2.2, GLUTAMATE RECEPTOR 2.2	3512	709	chrC07	42'515'076
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	545	chrA04	14'398'885
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	500	chrA04	14'366'747
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	525	chrA05	7'684'734
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	733	chrC04	41'289'392
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	555	chrC04	13'062'832
GLR2.7	AT2G29120	ATGLR2.7, GLR2.7, GLUTAMATE RECEPTOR 2.7, GLUTAMATE RECEPTOR 2.7	2310	470	chrC04	41'277'877
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	710	chrA01	1'045'569
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	2323	chrA07	2'124'311
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	1002	chrA08	9'905'607
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	589	chrC01	1'672'496
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	2280	chrUn_random	33'847'038
GLR3.1	AT2G17260	ATGLR2, ATGLR3.1, GLR2, GLR3.1, GLUTAMATE RECEPTOR 2	3647	1368	chrUn_random	71'139'901
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	1506	chrA03	6'882'807
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	1566	chrA05	5'937'883
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	2136	chrA09	33'337'887
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	2056	chrA10	1'638'811
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	1487	chrC04	9'666'636
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	2144	chrC05	1'567'287
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	719	chrC05	1'567'959
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	2211	chrC08	37'504'765
GLR3.4	AT1G05200	ATGLR3.4, GLR3.4, GLUR3, GLUTAMATE RECEPTOR 3.4	3967	1539	chrUn_random	78'676'363
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	2527	chrA03	6'887'171

GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	391	chrA04	15'445'377
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	2605	chrA05	5'941'679
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	2441	chrC04	9'661'924
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	1712	chrC04	43'353'361
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	2594	chrUn_random	78'680'180
GLR3.7	AT2G32400	ATGLR3.7, GLR3.7, GLR5, GLUTAMATE RECEPTOR 3.7, GLUTAMATE RECEPTOR 5	4631	370	chrUn_random	127'215'230
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1079	chrA02	4'162'564
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1054	chrA03	4'766'252
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1182	chrA10	9'264'610
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1046	chrC02_random	268'762
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1146	chrC09	36'593'520
GNC	AT5G56860	GATA TRANSCRIPTION FACTOR 21, GATA, NITRATE-INDUCIBLE, CARBON METABOLISM-INVOLVED, GATA21, GNC	2315	1101	chrUn_random	69'861'795
GNL	AT4G26150	CGA1, CYTOKININ-RESPONSIVE GATA FACTOR 1, GATA TRANSCRIPTION FACTOR 22, GATA22, GNC-LIKE, GNL	2023	652	chrA01	7'847'697
GNL	AT4G26150	CGA1, CYTOKININ-RESPONSIVE GATA FACTOR 1, GATA TRANSCRIPTION FACTOR 22, GATA22, GNC-LIKE, GNL	2023	798	chrA03	24'595'913
GNL	AT4G26150	CGA1, CYTOKININ-RESPONSIVE GATA FACTOR 1, GATA TRANSCRIPTION FACTOR 22, GATA22, GNC-LIKE, GNL	2023	747	chrA03	24'590'333
GNL	AT4G26150	CGA1, CYTOKININ-RESPONSIVE GATA FACTOR 1, GATA TRANSCRIPTION FACTOR 22, GATA22, GNC-LIKE, GNL	2023	558	chrC01	12'640'495
GNL	AT4G26150	CGA1, CYTOKININ-RESPONSIVE GATA FACTOR 1, GATA TRANSCRIPTION FACTOR 22, GATA22, GNC-LIKE, GNL	2023	787	chrUn_random	86'462'259
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	1025	chrA01	2'902'154
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	852	chrA03	26'496'607
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	572	chrA03	10'970'195
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	542	chrA09	29'038'801
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	1008	chrC01	3'948'491
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	570	chrC03	15'622'419
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	895	chrC07	42'216'030
HHP2	AT4G30850	HEPTAHELICAL TRANSMEMBRANE PROTEIN2, HHP2	2091	522	chrC08	32'349'795
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	381	chrA01	2'903'497

HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	668	chrA03	10'970'174
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	483	chrA03	26'496'687
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	646	chrA09	29'038'936
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	524	chrC01	3'948'788
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	751	chrC03	15'622'368
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	480	chrC07	42'216'154
HHP3	AT2G24150	HEPTAHELICAL PROTEIN 3, HHP3	2337	798	chrC08	32'349'677
HOS1	AT2G39810	EARLY IN SHORT DAYS 6, ESD6, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1, HOS1	5346	2438	chrA04	17'623'424
HOS1	AT2G39810	EARLY IN SHORT DAYS 6, ESD6, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1, HOS1	5346	2456	chrC03_random	882'625
HOS1	AT2G39810	EARLY IN SHORT DAYS 6, ESD6, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1, HOS1	5346	2401	chrC04	45'899'462
HOS1	AT2G39810	EARLY IN SHORT DAYS 6, ESD6, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1, HOS1	5346	1993	chrC04	3'955'282
HSFC1	AT3G24520	AT-HSFC1, HEAT SHOCK TRANSCRIPTION FACTOR C1, HSFC1	1809	840	chrA03	18'569'051
HSFC1	AT3G24520	AT-HSFC1, HEAT SHOCK TRANSCRIPTION FACTOR C1, HSFC1	1809	976	chrA07	5'882'253
HSFC1	AT3G24520	AT-HSFC1, HEAT SHOCK TRANSCRIPTION FACTOR C1, HSFC1	1809	786	chrC03	29'055'461
HSFC1	AT3G24520	AT-HSFC1, HEAT SHOCK TRANSCRIPTION FACTOR C1, HSFC1	1809	830	chrC07	11'406'047
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	1014	chrA02	20'794'873
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	1251	chrA06	21'711'327
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	402	chrA06	4'186'945
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	372	chrA08	17'126'239
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	714	chrA09_random	341'489
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	1074	chrC02	39'384'711
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	519	chrC02	37'365'648
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	470	chrC02	9'205'522
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	440	chrC05	4'995'022
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	487	chrC06	6'549'417
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	355	chrC06_random	2'693'223
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	1189	chrC07	30'242'549
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER	2591	749	chrC09	692'244

		OF CBF EXPRESSION 1, SCREAM, SCRM				
ICE1	AT3G26744	A. THALIANA INDUCER OF CBP EXPRESSION 1, ATICE1, ICE1, INDUCER OF CBF EXPRESSION 1, SCREAM, SCRM	2591	554	chrUn_random	35'951'989
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	427	chrA02	20'795'135
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	797	chrA06	4'186'590
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	354	chrA06	21'712'606
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	863	chrA08	17'126'102
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	404	chrA09_random	341'705
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	431	chrC02	39'384'972
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	789	chrC03	46'198'708
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	757	chrC05	4'994'886
ICE2	AT1G12860	ICE2, INDUCER OF CBF EXPRESSION 2, SCREAM 2, SCRM2	2348	409	chrC07	30'242'746
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	697	chrA06	6'945'943
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	744	chrA08	16'213'613
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	734	chrA09	30'447'490
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	620	chrC05	8'732'496
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	545	chrC05	25'772'112
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	704	chrC08	33'906'055
JAZ1	AT1G19180	ATJAZ1, JASMONATE-ZIM-DOMAIN PROTEIN 1, JAZ1, TIFY10A	1844	609	chrC08	21'708'952
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	663	chrA02_random	1'447'529
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	1128	chrA06	4'975'893
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	836	chrA06	4'969'847
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	741	chrA06	22'518'956
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	1025	chrA09_random	4'037'104
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	513	chrC02	37'403'641
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	943	chrC05	6'093'525
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	788	chrC05	6'093'554
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	651	chrC07	28'449'656
KIN1	AT1G14370	APK2A, KIN1, KINASE 1, PBL2, PBS1-LIKE 2, PROTEIN KINASE 2A	2648	1213	chrC08	35'265'703
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	1250	chrA02_random	1'447'286
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	1059	chrA06	22'519'200
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	553	chrA06	4'976'017
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	486	chrA09_random	4'038'030
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	1260	chrC02	37'402'697
KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	1056	chrC07	28'449'644

KIN2	AT2G02800	APK2B, KIN2, KINASE 2, PBL3, PBS1-LIKE 3, PROTEIN KINASE 2B	2912	518	chrC08	35'266'702
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1385	chrA03	7'826'027
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1489	chrA05	4'212'484
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1252	chrC03	10'578'418
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1037	chrC03	10'578'801
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1409	chrC04	6'548'029
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	809	chrC08	26'207'387
LOS2	AT2G36530	ENO2, ENOLASE 2, LOS2, LOW EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 2	3374	1498	chrUn_random	72'788'403
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	17	chrA01	4268153
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1403	chrA02	19470063
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	376	chrA02	19470063
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	235	chrA02	19465176
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1467	chrA06	22586359
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	27	chrA07	4385237
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1368	chrA09	11992291
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	51	chrA09	7918195
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1461	chrC02	37120970

LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	26	chrC03	9667240
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	19	chrC03	13411280
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1450	chrC07	28357438
LOV1	AT2G02450	ANAC034, ANAC035, ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 34, ATLOV1, LONG VEGETATIVE PHASE 1, LOV1, NAC DOMAIN CONTAINING PROTEIN 35, NAC035	3283	1196	chrC09	18287985
MBP1	AT4G38630	ATMCB1, MBP1, MCB1, MULTIUBIQUITIN CHAIN BINDING PROTEIN 1, MULTIUBIQUITIN-CHAIN-BINDING PROTEIN 1, REGULATORY PARTICLE NON-ATPASE 10, RPN10	2611	1118	chrA06	24'370'181
MBP1	AT4G38630	ATMCB1, MBP1, MCB1, MULTIUBIQUITIN CHAIN BINDING PROTEIN 1, MULTIUBIQUITIN-CHAIN-BINDING PROTEIN 1, REGULATORY PARTICLE NON-ATPASE 10, RPN10	2611	1186	chrA08	13'638'212
MBP1	AT4G38630	ATMCB1, MBP1, MCB1, MULTIUBIQUITIN CHAIN BINDING PROTEIN 1, MULTIUBIQUITIN-CHAIN-BINDING PROTEIN 1, REGULATORY PARTICLE NON-ATPASE 10, RPN10	2611	1163	chrC03	49'281'598
MBP1	AT4G38630	ATMCB1, MBP1, MCB1, MULTIUBIQUITIN CHAIN BINDING PROTEIN 1, MULTIUBIQUITIN-CHAIN-BINDING PROTEIN 1, REGULATORY PARTICLE NON-ATPASE 10, RPN10	2611	1193	chrC07	44'732'179
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	642	chrA01	16'382'829
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	798	chrA03	18'255'385
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	683	chrA07	7'018'310
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	573	chrC01	29'546'630
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	505	chrC03_random	2'484'609
MYB15	AT3G23250	ATMYB15, ATY19, MYB DOMAIN PROTEIN 15, MYB15	1702	730	chrC07	13'206'131
MYB96	AT5G62470	ATMYB96, MYB DOMAIN PROTEIN 96, MYB96, MYBCOV1	2151	1138	chrA02	23'963'064
MYB96	AT5G62470	ATMYB96, MYB DOMAIN PROTEIN 96, MYB96, MYBCOV1	2151	1167	chrA06	15'304'777
MYB96	AT5G62470	ATMYB96, MYB DOMAIN PROTEIN 96, MYB96, MYBCOV1	2151	1233	chrA09	2'951'202
MYB96	AT5G62470	ATMYB96, MYB DOMAIN PROTEIN 96, MYB96, MYBCOV1	2151	1224	chrC09	3'301'182
MYB96	AT5G62470	ATMYB96, MYB DOMAIN PROTEIN 96, MYB96, MYBCOV1	2151	1044	chrUn_random	100'458'523
OST1	AT4G33950	ATOST1, OPEN STOMATA 1, OST1, P44, SNF1-RELATED PROTEIN KINASE 2.6, SNRK2-6, SNRK2.6, SRK2E, SUCROSE NONFERMENTING 1-RELATED PROTEIN KINASE 2-6	2294	1089	chrA01	1'504'947
OST1	AT4G33950	ATOST1, OPEN STOMATA 1, OST1, P44,	2294	1054	chrC01	2'290'843

		SNF1-RELATED PROTEIN KINASE 2.6, SNRK2-6, SNRK2.6, SRK2E, SUCROSE NONFERMENTING 1-RELATED PROTEIN KINASE 2-6				
OST1	AT4G33950	ATOST1, OPEN STOMATA 1, OST1, P44, SNF1-RELATED PROTEIN KINASE 2.6, SNRK2-6, SNRK2.6, SRK2E, SUCROSE NONFERMENTING 1-RELATED PROTEIN KINASE 2-6	2294	857	chrUn_random	135'231'295
PHYB	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	649	chrA03	16'746'223
PHYB	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2627	chrA05	17'432'648
PHYB	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2125	chrC03	24'846'334
PHYB	AT2G18790	HY3, OOP1, OUT OF PHASE 1, PHYB, PHYTOCHROME B	4699	2686	chrC05	35'604'638
PIF3	AT1G09530	PAP3, PHOTOCURRENT 1, PHYTOCHROME INTERACTING FACTOR 3, PHYTOCHROME-ASSOCIATED PROTEIN 3, PIF3, POC1	3887	1390	chrA06_random	199'215
PIF3	AT1G09530	PAP3, PHOTOCURRENT 1, PHYTOCHROME INTERACTING FACTOR 3, PHYTOCHROME-ASSOCIATED PROTEIN 3, PIF3, POC1	3887	1462	chrA09	32'454'014
PIF3	AT1G09530	PAP3, PHOTOCURRENT 1, PHYTOCHROME INTERACTING FACTOR 3, PHYTOCHROME-ASSOCIATED PROTEIN 3, PIF3, POC1	3887	1394	chrC05	3'493'141
PIF3	AT1G09530	PAP3, PHOTOCURRENT 1, PHYTOCHROME INTERACTING FACTOR 3, PHYTOCHROME-ASSOCIATED PROTEIN 3, PIF3, POC1	3887	1333	chrC08	36'766'160
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1356	chrA03	9'501'931
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1300	chrA04	18'575'801
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	842	chrC01	38'735'396
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1330	chrC03	13'424'755
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	972	chrC03	2'586'906
PIF4	AT2G43010	ATPIF4, PHYTOCHROME INTERACTING FACTOR 4, PIF4, SRL2	2981	1260	chrC04	47'145'131
PIF7	AT5G61270	PHYTOCHROME-INTERACTING FACTOR7, PIF7	2275	1200	chrA03	20'017'787
PIF7	AT5G61270	PHYTOCHROME-INTERACTING FACTOR7, PIF7	2275	1212	chrC07	35'327'714
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	601	chrA03	9'003'216
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	659	chrA04_random	1'302'892
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	654	chrA05	2'798'775
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	659	chrC03	12'499'219
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	732	chrC04	46'155'287
PYL6	AT2G40330	PYL6, PYR1-LIKE 6, RCAR9, REGULATORY COMPONENTS OF ABA RECEPTOR 9	1607	665	chrC04	3'526'021
PYL9	AT1G01360	PYL9, PYRABACTIN RESISTANCE 1-LIKE	1392	459	chrA10	269'950

		9, RCAR1, REGULATORY COMPONENT OF ABA RECEPTOR 1				
PYL9	AT1G01360	PYL9, PYRABACTIN RESISTANCE 1-LIKE 9, RCAR1, REGULATORY COMPONENT OF ABA RECEPTOR 1	1392	489	chrC05	331'752
PYL9	AT1G01360	PYL9, PYRABACTIN RESISTANCE 1-LIKE 9, RCAR1, REGULATORY COMPONENT OF ABA RECEPTOR 1	1392	469	chrC05	10'921'594
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	2549	chrA02	3'037'633
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	1331	chrA02	3'037'633
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	832	chrA06_random	902'150
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	362	chrA06_random	904'198
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	2851	chrA10	10'712'940
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	1211	chrC03	44'209'443
SIZ1	AT5G60410	ATSIZ1, SIZ1	6388	2784	chrUn_random	56'588'462
YODA	AT1G63700	EMB71, EMBRYO DEFECTIVE 71, MAP KINASE KINASE KINASE 4, MAPKKK4, YDA, YODA	5447	2678	chrA09	6'505'462
YODA	AT1G63700	EMB71, EMBRYO DEFECTIVE 71, MAP KINASE KINASE KINASE 4, MAPKKK4, YDA, YODA	5447	2904	chrC09	9'266'270
ZAT10	AT1G27730	SALT TOLERANCE ZINC FINGER, STZ, ZAT10	1303	591	chrA08	14'611'932
ZAT10	AT1G27730	SALT TOLERANCE ZINC FINGER, STZ, ZAT10	1303	443	chrA09	20'844'301
ZAT10	AT1G27730	SALT TOLERANCE ZINC FINGER, STZ, ZAT10	1303	630	chrC03	47'491'428
ZAT10	AT1G27730	SALT TOLERANCE ZINC FINGER, STZ, ZAT10	1303	461	chrC05	15'206'590
ZAT10	AT1G27730	SALT TOLERANCE ZINC FINGER, STZ, ZAT10	1303	595	chrC07	17'224'546
ZAT12	AT5G59820	ATZAT12, RESPONSIVE TO HIGH LIGHT 41, RHL41, ZAT12	981	477	chrA02	3'227'663
ZAT12	AT5G59820	ATZAT12, RESPONSIVE TO HIGH LIGHT 41, RHL41, ZAT12	981	538	chrA03	4'154'580

Appendix G: Non-significant (n.s.) peaks from the QTL analyses which collocate with significant QTL (sign., gray).

Chrom.	Pos.[cM]	Trait	sign	LOD	R^2 [%]	Additive effect
A01	69.60	Stem Length	sign	4.8	5.4	-0.17
	70.60	Hypocotyl Length	sign	5.4	8.7	-0.13
	58.86	Stem Damage Score	n.s.	1.8	2.3	-0.16
	73.47	Death Rate	n.s.	1.9	3.1	-0.03
A02	36.61	Leaf Damage Score	sign	6.7	8.1	-0.20
	49.01	Leaf Survival Rate	sign	4.6	6.6	-0.02
	53.70	Stem Length	sign	3.2	3.5	-0.14
	54.70	Stem Damage Score	n.s.	1.8	2.5	-0.17
A03	113.80	Hypocotyl Length	sign	3.0	4.2	-0.09
	103.62	Stem Damage Score	n.s.	1.4	1.7	-0.14
A09	33.91	Hypocotyl Length	sign	3.6	5.4	0.10
	22.43	Stem Damage Score	n.s.	1.2	1.7	-0.13
C02	100.41	Stem Damage Score	sign	6.2	8.7	-0.32
	100.41	Death Rate	sign	4.8	7.6	-0.05
	100.43	Leaf Damage Score	n.s.	2.1	2.2	-0.11
	100.43	Leaf Survival Rate	n.s.	1.4	1.7	0.01
C08	65.58	Leaf Damage Score	n.s.	2.3	2.6	0.11
	71.28	Stem Damage Score	n.s.	1.9	2.6	0.17
	80.52	Epicotyl Length	n.s.	2.4	1.9	-0.06
C09	81.11	Death Rate	sign	3.3	5.1	0.04
	74.90	Leaf Survival Rate	n.s.	1.9	2.4	-0.01
	78.03	Leaf Damage Score	n.s.	1.4	1.5	0.09
	81.10	Stem Damage Score	n.s.	1.8	2.4	0.17

Appendix H Phenotypic data presented in Markowski and Rapacz (1994) for 14 rapeseed DH lines with new correlations done with Excel. GDC is definded by the autors as the ratio of the percentage of flowering plants to numbers of days to flowering.

GDC	*flowering plants [%]*	*leaf area injuries [%]*	*Dead plants [%]*
1.2	*71.9*	*28.3*	*8.62*
1.14	*68.6*	*54.5*	*35.6*
0.95	*62.4*	*32.7*	*20.8*
0.76	*44.8*	*39.9*	*25.5*
0.74	*43.3*	*43.3*	*21.9*
0.74	*43.8*	*52.9*	*41.5*
0.73	*42.9*	*55.8*	*44.4*
0.73	*43.3*	*48.7*	*29.5*
0.73	*43.3*	*32.6*	*19.4*
0.73	*42.9*	*39.2*	*22.8*
0.72	*43.3*	*55.1*	*38.7*
0.68	*43.3*	*57.6*	*44*
0.53	*35.2*	*65.1*	*58.6*
0.04	*2.89*	*3.6*	*4.2*
GDC	0.99	0.31	0.03
flowering		0.32	0.05
leaf area			0.93

8 Curriculum vitae

Personal Data

Name:	Eva Heinrich
Birth:	30. Mai 1987, Bad Salzungen
Nationality:	Deutsch

Education and Scientific Career

2005	Secondary School Diploma (Abitur), Herzog-Georg-Gymnasium Bad Liebenstein
01.10.2005 – 30.08.2006	Freiwilliges Ökologisches Jahr (Voluntary ecological year), Landschaftspflegeverband „Thüringer Wald“ e.V. Included landscape conservation and environmental education
01.10.2006 – 30.07.2014	Ernst-Moritz-Arndt University Greifswald, degree in biology (Diplom Biologie); Thesis topic: „Molekulare und Morphologische Charakterisierung der Myxomycetengattung *Meriderma*“; major subject: botany, minor subjects: genetic and biochemistry
01.06. – 30.09.2013	Student research assistant, Institute for Botany and Landscape Ecology, Ernst-Moritz-Arndt-Universität Greifswald Building a database and supporting foreign exchange students
15.10. – 30.11.2014	Research assistant in the project „FloraGREIF, the Virtual Guide to the Flora of Mongolia“ Expanding the function of the eKey by entering more traits
1.5.2015 – 30.4.2018	Scientific researcher in the Department of Crop Sciences. Project: “Quantitative effects of vernalization requirement, day length and temperature on flowering time of oilseed rape” in the DFG Priority Program 1530: Flowering Time Control – from Natural Variation to Crop improvement
1.5.2015 – present	PhD Programm for Agricultural Science (PAG), Georg-August-University Göttingen

Poster presentations:

Eva Heinrich and Christian Möllers: „Homeologous regions regulate flowering time of oilseed rape (*Brassica napus* L.) under short days." , CiBreed Week, 11. – 14. April 2022, Göttingen, Germany

Eva Heinrich and Christian Möllers: „Quantitative effects of vernalization requirement on flowering time of oilseed rape", 4th International Symposium on Genomics of Plant Genetic Resources, 3. – 7. Spetember 2017 Giessen. Germany

Eva Heinrich and Christian Möllers: „Inheritance of vernalization requirement and frost tolerance in oilseed rape (Brassica napus L.)", VII International Symposium on Brassicas, 22. – 25. May 2017, Pontevedra, Spain

Eva Heinrich and Christian Möllers: „Quantitative effects of vernalization requirement, day length and temperature on flowering time of oilseed rape", German Plant Breeding Conference, 8. – 10. March 2016, Bonn, Gemany

Publications in preparation:

Eva Heinrich and Christian Möllers: „QTL clusters in three genomic regions explain flowering time variation in a Brassica napus L. winter × spring-type DH population regarding day length and temperature" (rewrite after rejection)

Antje Schierholt, Thomas Alcock, Christian Flügge, Wolfgang Ecke, **Eva Heinrich**, Renate Schmidt, Nicolaus von Wirén, Astrid Junker, Thomas Altmann, Gerd Patrick Bienert: „Identification of novel major QTL controlling shoot performance of oilseed rape (*Brassica napus L.*) in response to boron starvation by an automated plant phenotyping system approach"

9 Declaration

I, Eva Heinrich, hereby declare that

1. this dissertation was conducted independently and without unauthorized references and assistance
2. this dissertation has not been presented to any other examining body either in its present or a similar form
3. I have not applied for a doctoral degree at any other universities.