SPP1530 Workshop :

Pleiotropic Effects of Flowering Time Genes and Impact on Adaptation and Speciation

January 21-23, 2013

Max Planck Institute for Plant Breeding Research
Carl-von-Linné-Weg 10
50829 Köln

Contents

I. Preface

In recent years, the discovery of pleiotropic effects of Flowering Time (FTi) genes has emerged as a field of research with significant potential to impact crop improvement. There is increasing evidence, that expression of FTi genes has global effects on plant performance.

We aim to bring together researchers focusing on this interesting field to promote cross species comparisons of flowering time regulators. The conference will take place in an inspiring environment at the Max Planck Institute for Plant Breeding Research in Cologne from January 21-23, 2013.

Session themes will cover pleiotropic aspects of FTi genes in model plants, cultivated species and their wild relatives. Evolutionary aspects of FTi genes and their roles in speciation and for species stability will be discussed. Additionally, contributions on the role of FTi genes for adaptation to changing environmental factors/climate conditions will also be highly welcomed.

II. Program Commitee

- George Coupland, MPIPZ Cologne
- Maria von Korff, MPIPZ Cologne
- Seth Davis, MPIPZ Cologne
- Maria Albani, MPIPZ Cologne
- Christian Jung, CAU Kiel
- Martina Blümel, CAU Kiel

III. Program

Monday, January 21

14.00-14.15	**Welcome:** **George Coupland** (Director Max-Planck Institute for Plant Breeding Research, Cologne) and **Christian Jung** (Coordinator SPP1530, Director Plant Breeding Institute, Christian-Albrechts-University, Kiel)	
Session 1:	**Comparative studies of flowering time genes across species, Chair: Maria Albani**	
14.15-15.00	**Keynote Lecture: Timo Hytönen** Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland	Regulation of flowering in Rosaceae – same genes in different context
15:00-15.30	**Yuan Guo** Plant Breeding Institute, Christian-Albrechts-University, Kiel	TILLING suggests pleiotropic effects related to EMS-generated alleles of flowering genes in the allopolyploid *Brassica napus*
15.30-16.00	**Maria von Korff** Max-Planck Institute for Plant Breeding Research, Cologne	Mutations in the circadian clock ortholog HvElf3 faciilitates short-season adaptation in barley.
16.00-16.30	Coffee break	
16.30-17.00	**Claire Perilleux** Université de Liége	Functional conservation of FLC activity between root chicory (*Cichorium intybus* var. *sativum*) and *Arabidopsis*
17.00-17.30	**Yiguo Hong** University Warwick	Florigen signalling in flowering and increased productivity
17.30-18.00	**Hans Hoenicka** vTI, Inst. for Forest Genetics, Grosshansdorf	Pleiotropic effects of „flowering“ genes in transgenic poplar
18.00-18.30	**Christina Kühn** (Humboldt-University Berlin)	The role of an Indeterminate1-like protein in floral induction and tuberization in potato plants

Tuesday, January 22

Session 2:	**Flowering time genes and their role in crop evolution, Chair: Maria von Korff**	
9.30-10.15	***Keynote Lecture: Robbie Waugh*** James Hutton Institute, Dundee, UK	Adaptation of barley to new environments
10.15-10.45	**Ana Casas** Department of Genetics and Plant Production, Aula Dei Experimental Station, EEAD-CSIC, Zaragoza	Barley adaptation. Lessons learned from landraces will help to cope with climate change
10.45-11.15	**Wiebke Sannemann** Rheinische Friedrich Wilhelms-University Bonn	Flowering time in a MAGIC population in barley
11.15-12.00	Coffee break	
12.00-12.30	**Nina Pfeiffer** (Plant Breeding Institute, Christian-Albrechts-University, Kiel)	Genetic and phenotypic characterization of bolting failure in *Beta vulgaris*
12.30-13.00	**Nadine Dally** (Plant Breeding Institute, Christian-Albrechts-University, Kiel)	New bolting genes from sugar beet (*B. vulgaris*) which control early bolting independent of BvBTC1
13.00-14.00	Lunch (DiPalma Kantine @MPIPZ)	

Tuesday, January 22 (continued)

Session 3: Pleiotropic Effects of Arabidopsis flowering pathways/genes, Chair: Christian Jung

14.00-14.45	***Keynote lecture Maarten Koornneef*** Max-Planck Institute for Plant Breeding Research, Cologne	*Arabidopsis* Natural Variation: Epistasis of Flowering Time Alleles Reveals A New Function For An Old Gene
14.45-15.15	**Fernando Andres** Max-Planck Institute for Plant Breeding Research, Cologne	Photoperiodic signals activate the gibberellin pathway to accelerate flowering in *Arabidopsis*
15.15-15.45	**Liangyu Liu** Max-Planck Institute for Plant Breeding Research, Cologne	A distant enhancer controls Flowering Locus T in *Arabidopsis*
15.45-16.15	Coffee break	
16.15-16.45	**Ute Höcker** University of Cologne	SPA-mediated protein degradation in flowering time control and photomorphogenesis
16.45-17.15	**Peter Huijser** Max-Planck Institute for Plant Breeding Research, Cologne	Redeployment of SPL genes beyond the vegetative-to-reproductive phase transition
17.15-18.00	**Poster Session**	
19.30-open end	joint in-town evening (Brauhaus Päffgen). Address: Friesenstraße 64, 50670 Cologne **Please be prepared to pay for drinks yourself.**	

Wednesday, January 23

Session 4: Flowering time genes and Adaptation to different environments, Chair: Seth Davis

9.00-9.30	**Claus Schwechheimer** WissenschaftszentrumWeihenstephan, TU München	Cross-repressive interactions between SOC1 and the GATA factors GNC and GNL/CGA1 in the control of greening, cold tolerance and flowering time in Arabidopsis
9.30-10.00	**Benedikt Drosse** Max-Planck Institute for Plant Breeding Research, Cologne	Whole Transcriptome Profiling in Barley Shoot Apices During Floral Transition
10.00-10.30	**Susan Duncan** John Innes Centre, Norwich	An Increased Vernalization Temperature Optimum at the Northerly Limit of the *Arabidopsis* Range
10.30-11.00	**Amaury de Montaigue** Max-Planck Institute for Plant Breeding Research, Cologne	Phenotypic impact of natural variation in diurnal gene expression waveforms
11.00-11.30	Coffee break	
11.30-12.30	***Keynote lecture Cynthia Weinig*** Department of Botany, University of Wyoming	Characterizing the circadian clock in seasonal settings.
12.30-13.00	Closing Remarks, Comments	
13.00	Lunch (Sandwiches), End of Meeting	

IV. Keynote Lectures

Timo Hytonen	Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland	Regulation of flowering in Rosaceae -same genes in different context
Robbie Waugh	James Hutton Institute, Dundee, United Kingdom	Adaptation of barley to new environments
Maarten Koornneef	Max Planck Institute for Plant Breeding Research, Cologne, Germany	*Arabidopsis* natural variation: Epistasis of Flowering Time alleles reveals a new function for an old gene
Cynthia Weinig	Department of Botany, University of Wyoming, United States of America	Characterizing the circadian clock in seasonal settings.

V. Talks

TILLING suggests pleiotropic effects related to EMS-generated alleles of flowering genes in the allopolyploid *Brassica napus*

Yuan Guo (1), Ida Suppanz (2), Nicole Jedrusik (1), Carlos Molina (1)
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(2) Albert-Ludwigs-Universität Freiburg, Department of Functional Proteomics, Freiburg, Germany

Oilseed rape (*Brassica napus*) from different geographical regions of the world have different requirements for day length and vernalization. This inhibits the introgression of genes from non-adapted breeding lines in new environments. Thus, understanding the mechanisms governing flowering time (FTi) and vernalisation requirement in *B. napus* is of great interest. In Arabidopsis, the main regulatory pathways for flowering time have been uncovered. However, transfer of information is hindered by the allopolyploid nature of *B. napus. B. napus* is a young species that resulted from the hybridization (~10,000 years ago) of two closely related species: *B. rapa* and *B. oleracea*. These two species underwent genome triplication between the Brassica-Arabidopsis split (~13 MYA) and their actual divergence event (~2 MYA).

Here, we report on the characterization of similar copies of candidate FTi genes in *B. napus* via TILLING. For this, more than 3500 M3 plants (>2100 M1 plants) were screened for mutations in three target genes, starting from EMS-mutagenized seeds of the winter-type cultivar Express617. As an outcome, more than 117 new EMS-generated alleles of the Arabidopsis orthologs *FRIGIDA, FLOWERING LOCUS-T,* and *TERMINAL FLOWER-1* have been detected. After an initial in silico screening for protein function disruption, several M3 families carrying selected alleles were analyzed by their phenotype and genotype. Surprisingly, single loci mutations show effects in FTi delay/acceleration and vernalisation responses despite the existence of several gene-copies. Additionally, TILLING families carrying mutated gene copies showed other phenotypic effects non-related to FTi. As an exemplifying result, two *B.napus* orthologs from the Arabidopsis *FLOWERING LOCUS-T* were analyzed (*BnC6FTa* and *BnC6FTb*). Interestingly, strong FTi delay was observed in plant families carrying missense/nonsense *BnC6FTb* mutations, whereas *BnC6FTa* mutant families did not differ in FTi in relation to non-mutated donor plants. However, *BnC6FTa* TILLING-M3 families displayed significant changes on plant growth architecture.

The present results are an entry point towards understanding of the gene dosage effects and possible sub-functionalization of multiple similar copies on the oilseed rape genome. The generated TILLING-alleles profiles constitute a novel source of information for *B. napus* that can be extensively exploited in breeding approaches.

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Functional conservation of FLC activity between root chicory (*Cichorium intybus* var. *sativum*) and *Arabidopsis*

Périlleux C. (1), Pieltain A. (1), Jacquemin G. (2), D'Aloia M. (1), Bouché F. (1), Thiry L. (1), Aljochim P. (1), Delansnay1 M. (1), Mathieu A.-S. (2), Lutts S. (2), Tocquin, P. (1)

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Root chicory (*Cichorium intybus* var. *sativum*) is a biennial crop, but is harvested for root inulin at the end of the first growing season. Incidental exposure of seedlings to cold temperatures might induce undesired flowering and hence understanding the molecular basis of vernalization is important. Although *FLOWERING LOCUS C* (FLC) was identified in Arabidopsis as a key vernalization-responsive floral repressor, the presence of FLC genes outside the Brassicaceae is scarcely documented.

We isolated *FLC-LIKE 1* (*Ci*FL1) from chicory and phylogenetic analyses confirmed its orthology with AtFLC. Vernalization repressed *Ci*FL1 in seeds or plantlets of chicory, but repression was unstable whether the post-vernalization temperature was favorable to flowering or whether it devernalized the plants. When overexpressed in Arabidopsis, *Ci*FL1 acted like *At*FLC as a repressor of flowering and prevented activation of *FLOWERING LOCUS T* by photoperiod. These results show conserved biological and mechanistic effects of an FLC-like gene in chicory.

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Florigen signalling in flowering and increased productivity

Cheng Qin (1), Chunyang Li (2), Jiajia Shen (1), Mark Smedley (3), Xian Zhang (1), Zhiming Yu (1), Stephen Jackson (2), Wendy Harwood (3), Yiguo Hong (1,2,3)

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FLOWERING LOCUS T (FT) plays a key role in the transition from vegetative to reproductive growth
and flowering. Here we report that ectopic expression of different alleles of the Arabidopsis FT gene uncovered differential regulation of flowering time, bolting, floral number and seed yield. Individual amino acids affecting the diverse functions of the FT protein in these developmental processes were mapped through systematic mutagenesis and a high-throughput floral induction assay. Using these approaches, we have identified novel FT alleles that cause a marked increase in flower numbers and seed yield in tobacco. Moreover, transgenic spring barley lines expressing one of these FT alleles produced significantly more grains, demonstrating its usefulness in increasing yield in monocot cereals. How the FT protein and RNA contribute to florigen signalling in flowering and increased productivity will be discussed.

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Pleiotropic effects of „flowering“ genes in transgenic poplar

Hans Hoenicka (1), Matthias Fladung (1), Denise Lehnhardt (1), Tobias Brügman (1)

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Thanks to the genome sequencing project of *Populus trichocarpa*, the number of annotated genes was determined to about 45.555. As in many other plant species, also in poplar many genes are believed to affect multiple traits. Therefore, it is not surprising that genetic transformation of poplar with some genes caused unexpected pleiotropic effects. For instance, the meristem identity gene *leafy* (LFY) from Arabidopsis induces precocious flowering in transgenic poplar. Additional side effects of this gene are dwarfism, single flowers (instead of catkins) and gender change. The homeobox gene *Bp*MADS4 (*FRUITFULL* [FUL]-homolog) induces early flowering in birch and apple but not in poplar. Instead, broad changes on senescence and winter dormancy were observed in 35S::BpMADS4 transgenic poplars which also maintain leaves under winter conditions. Third, the constitutive expression of the Arabidopsis *FLOWERING PROMOTING FACTOR 1* (*At*FPF1) gene in poplar revealed a strong effect on wood formation but no effect on flowering time. Wood density and lignin content was lower in FPF1 transgenic poplar than in wildtype poplar. Also, the SOC1/TM3 class gene PTM5 (POPTR_0014s07010), which has been related to wood formation and flowering time, showed a strong activity in stems of all transgenic lines studied.
Transcriptome analysis of hybrid poplar xylem revealed a high expression of known and unknown genes showing activity in both developing xylem and flowers. Some of these genes will be currently transformed into poplar. Phenotypic effects on resulting transgenic lines will be evaluated soon.

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The role of an Indeterminate1-like protein in floral induction and tuberization in potato plants

Marie Majaura (1), Izabela Chinscinska (2), Hongxia He (3), Christina Kühn (1)

(1) Humboldt University of Berlin, Berlin, Germany, (2) University of Gdansk, Gdnask, Poland, (3) University of Changchun, Changchun, China

The maize indeterminate1 (ID1) gene encodes a zinc-finger protein involved in the production of a transmissible signal that is generated in leaves and inducing flowering in the shoot apical meristem in a photoperiod-independent manner (Colasanti et al., 1998). Several potential homologs of the maize ID1 gene carrying an ID domain (IDD) are found in the Arabidopsis genome, but they differ from the maize homolog regarding their expression pattern and their corresponding mutant phenotype.

The role of Arabidopsis IDD transcription factor AtIDD8 in the regulation of the photoperiodic pathway of flower induction involves the modulation of sugar transport and metabolism. Flowering time of transgenic Arabidopsis plants with reduced or increased expression of AtIDD8 is affected in a photoperiod-dependent manner. IDD8 binds directly to the promoter of the SUS4 gene and promotes flowering suggesting that IDD genes link sugar metabolism to the photoperiodic flowering pathway (Seo et al., 2011).

The ID1 gene from maize shows high homology to the potato PCP1 gene, which was originally identified in a screen for sucrose transporter proteins since it complements a sucrose-uptake deficient yeast mutant strain (Kühn and Frommer, 1995). In order to analyze the impact of PCP1 on flowering in Solanaceous plants (*N. tabacum, S. tuberosum*), we generated transgenic plants with reduced or increased PCP1 expression. Both sets of plants showed alteration in flowering time and a link between photoperiod-dependent flowering control and regulation of sugar related genes by IDD proteins is suggested.

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Barley adaptation. Lessons learned from landraces will help to cope with climate change

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Adaptation of crops to temperate climates depends to a large extent on plants having the appropriate combination of genes to respond to environmental cues. Global warming poses new challenges to plant breeding. In many places, current cultivars will no longer be suited for cultivation. We present several findings on barley adaptation to Mediterranean climates, which resulted from the study of adaptations presented by local landraces.

Winter barley is widely grown in the Mediterranean region. We found that local winter landraces have some degree of vernalization requirement, tuned to respond to the winter temperatures typical for each region. Our results demonstrate that the allelic series of the main vernalization gene, VrnH1, is essential to determine the length of the cold period needed to promote flowering in barley.

The presence of photoperiod gene HvFT3 in most Mediterranean landraces is presented as a safety mechanism to promote flowering, which comes into play at least when vernalization conditions are not optimum (rather often in some areas). This mechanism is coordinated with the vernalization pathway through repression by VrnH2.

A latitudinal pattern of distribution of HvFT1 in Spanish barleys suggests a role in adaptation. This gene integrates the photoperiod and vernalization pathways in barley, and seems to present an allelic series of at least five functionally different alleles. We present evidences from several independent sets of materials that demonstrate the effect of three of these alelles, in accordance with the latitudinal distribution observed.

A combination of these three mechanisms optimizes the growth cycle of Mediterranean landraces. These mechanisms have a wider interest in a climate change scenario, as temperatures in most of Europe will increase, and may become beneficial in higher latitudes. Cultivars with new combinations of vernalization, photoperiod and frost tolerance alleles will have to be bred for the upcoming conditions.

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Flowering time in a MAGIC population in barley

Wiebke Sannemann (1), Boby Mathew (1), Emma Huang (2), Rohan Shah (2), Jens Léon (1)

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QTL mapping was employed in the first Multiparent Advanced Generation InterCross (MAGIC) population of barley. The DH-lines were derived from an eight parent intercross of Hordeum vulgare ssp. vulgare; comprising of seven so called 'founders' of German barley breeding and 'Barke' as an outstanding variety used for genetic research. The approach of utilising MAGIC populations is derived from mouse genetics and was applied for the first time in plants by Kover in Arabidopsis thaliana. The large number of parental accessions in a MAGIC population increases the allelic and phenotypic diversity compared to bi-parental crosses and the number QTLs segregating in the cross. The high rate of recombination events increases the mapping accuracy of the detected QTL.

A set of 534 DH-lines from the MAGIC population were phenotyped under controlled environmental conditions with two watering levels (well watered and terminal drought) for traits concerning yield and yield components. The DH-lines and parents were genotyped using the Illumina 9K iSelect chip at TraitGenetics. QTL-analysis (SAS 9.2) was performed based on haplotype blocks ("R/mpMap") and single SNPs analysis.

Analysis of variance (SAS 9.2) for flowering time confirmed significant difference within the genotypes, but not between the treatment and genotype*treatment interaction. Significant QTLs were detected on chromosome 3H, 4H, 5H and 7H for single SNP marker analysis. Epistatic effects were calculated and will be reported**.**

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Genetic and phenotypic characterization of bolting failure in *Beta vulgaris*

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In cool temperate climates, sugar beets are currently grown as a spring crop. They are sown in spring and harvested in autumn. Growing sugar beet as a winter crop with an extended vegetation period fails due to bolting after winter. To control this we are aiming to identify genes underlying bolting failure. Previously, we had identified a sugar beet accession which segregates for bolting failure. Fifty percent of the plants from this accession did not bolt after vernalization under field conditions. We hypothesized an oligogenic gene model responsible for the observed bolting failure. The respective sugar beet accession was crossed with a biennial sugar beet with regular bolting behavior to develop a structured mapping population. F2 and F3 generations were grown in consecutive years in the greenhouse and transplanted to the field after artificial vernalization at 5°C for 16 weeks. Bolting was recorded twice a week from mid of May until end of October. At the end of the experiment we observed non bolting plants in each generation. The statistical analysis of the replicated experiment with F3 families showed a significant genetic variation for bolting rate ($p < 0.0001$). Linkage mapping resulted in a first QTL termed nb1 (non bolting after vernalization 1) showing a LOD score of 15.46 and explained 34.2 % of the phenotypic variation of bolting failure.

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New bolting genes from sugar beet (*B. vulgaris*) which control early bolting independent of *BvBTC1*

Dally N (1), Minoche AE (2,3), Dohm JC (2,3), Himmelbauer H (2,3), Holtgräwe D, (4), Weisshaar B (4), Müller AE (1,5), Jung C (1)

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The species *Beta vulgaris* includes annual and biennial accessions. Annual accessions such as sea beet (*B. vulgaris* L. ssp. *maritima*) flower under long day conditions (LD) within one season, whereas induction of flowering in biennial accessions such as sugar beet requires prolonged exposure to cold temperatures (vernalization) followed by LD for induction of flowering. The recently isolated pseudo-response regulator gene BTC1 at the bolting locus B encodes a master switch distinguishing annual from biennial beets. Besides BTC1, two additional loci B2 and B4 have been identified in populations derived from crosses between an annual sea beet accession and biennial genotypes, isolated after EMS mutagenesis. Dominant alleles at these loci promote annual bolting. While BTC1 and B4 were mapped on chromosome II, the locus B2 was mapped on chromosome IX. We cloned the B2 gene from its position on chromosome IX using a large F2 population of 6000 plants segregating for early bolting. To improve the quality and resolution of the map, phenotypic data from F3 families were recorded. Sequence comparison of molecular markers to the draft sugar beet genome sequence identified one sequence scaffold of ~1.5 Mb. Based on this scaffold we generated new markers flanking and tightly linked to B2. Within this region, we identified a putative candidate gene which is completely linked to B2. We analysed its expression together with the expression of putative up- and downstream regulators in beet. A model is suggested how B2 is involved in the flowering time pathway in biennial Beta species.

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Photoperiodic signals activate the gibberellin pathway to accelerate flowering in Arabidopsis

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In plants the transition from vegetative growth to flowering is regulated by several environmental and endogenous stimuli and by the age of the individual. In Arabidopsis, these pathways include the photoperiodic pathway that promotes flowering in response to long days (LDs) characteristic of summer, and the response pathway to the growth regulator gibberellin, which has its strongest effect under short days (SDs). LDs promote the transcription of *FLOWERING LOCUS T* (FT) in the leaf vascular tissue. Then, FT protein moves through the phloem to the shoot apex, where it causes changes in gene expression and promotes flowering. Interestingly, recent studies have shown that gibberellins also induce flowering by affecting the expression of floral promoter genes at the shoot apex under LDs. However, how the gibberellin pathway is activated in response to photoperiod to promote flowering is still unclear. Mutations in the MADS box transcription factor encoding gene *SHORT VEGETATIVE PHASE* (SVP) cause a number of pleiotropic developmental effects, such as early flowering and floral homeotic changes. These pleiotropic phenotypes suggest that SVP is involved in different genetic pathways. In order to identify the pathways affected by SVP we have performed several phenotypic, genetic and genomic studies. Surprisingly, our results show that SVP represses a key gene of the gibberellin biosynthetic pathway. In addition, we found that SVP transcription is repressed by the photoperiodic signals, mainly represented by FT protein, so that inductive LD conditions contribute to the reduction of SVP expression in the shoot apex. In turn, SVP reduction allows the de-repression of the gibberellin pathway and therefore accelerates the floral transition process. Taking our results together, we propose a model to explain how the floral transition is accelerated by the accumulation of gibberellins in the shoot apex in response to inductive photoperiods.

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A distal enhancer controls Flowering Locus T in Arabidopsis

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Control of flowering time is critical for reproductive development. In *Arabidopsis thaliana*, the integrator gene FLOWERING LOCUS T (FT) encodes part of florigen, which moves from leaves to the shoot apex to induce the floral transition. A 5.7kb long FT promoter containing phylogenetically conserved Blocks A, B and C is sufficient to mediate spatial and temporal control of FT transcription in inductive long days (LDs). Our aim is to characterize novel cis-elements at the FT promoter.

Complementation assays showed that Block C (400bp region from 5.2 to 5.6 kb upstream of the transcriptional start site) is necessary for FT expression in LDs, and mutation of a conserved CCAAT box in Block C reduces the efficiency of a full length FT promoter. In addition, mutagenesis of four conserved domains in Block C dramatically impacted promoter function. Surprisingly, deletion of middle region DNA between Block C and A does not affect FT expression in LDs, whereas several transgenic lines with T-DNAs inserted into the regions between Block C and A only show slightly delayed flowering.

In order to figure out whether a chromatin looping formed between block C and A, Chromosome conformation capture (3C) was carried out at FT locus. However, due to a few cells expressing FT in the whole leaves, we are adapting new cell-sorting system called INTACT (isolation of nuclei tagged in specific cell types) to isolate the nuclei from companion cells to study the chromatin state of FT.

In sum, our data indicates that Block C acts as a distal enhancer that is essential for FT transcription in LDs, and the chromatin state of Block C is under investigating.

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SPA-mediated protein degradation in flowering time control and photomorphogenesis

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In dark-grown Arabidopsis plants, light signal transduction is suppressed by the activities of the COP1/SPA ubiquitin ligase complex which ubiquitinates transcriptional activators of the light response and thereby targets them for degradation in the proteasome. One of the substrates of the COP1/SPA complex is the transcription factor CO, a key positive regulator of photoperiodic flowering. Genetic and biochemical analysis shows that SPA proteins - in concert with COP1 - suppress the induction of flowering in non-inductive short-day conditions. Flowering is also accelerated by a low red/far-red ratio (R/FR) in the incident light. This is part of the shade avoidance syndrome in vegetation-dense canopies. We have shown that the COP1/SPA complex is not required for flowering-time response to low R/FR, while it is required for other shade avoidance syndrome-related responses, such as enhanced seedling elongation and the expression of auxin biosynthesis genes. These results indicate that the different facets of the shade avoidance syndrome are genetically separable and, furthermore, suggest that phytochrome B-mediated effects on flowering time are independent of COP1/SPA.

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Cross-repressive interactions between SOC1 and the GATA factors GNC and GNL/CGA1 in the control of greening, cold tolerance and flowering time in Arabidopsis

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The paralogous and functionally redundant GATA transcription factors GNC (GATA, NITRATE-INDUCIBLE, CARBON-METABOLISM INVOLVED) and GNL/CGA1 (GNC-LIKE/CYTOKININ-RESPONSIVE GATA FACTOR1) from Arabidopsis thaliana promote greening and repress flowering downstream from the phytohormone gibberellin (GA). The target genes of GNC and GNL with regard to flowering time control have not been identified as yet. Here, we show by genetic and molecular analysis that the two GATA factors act upstream from the flowering time regulator SUPPRESSOR-OF-OVEREXPRESSION-OF-CONSTANS1 (SOC1) to directly repress SOC1 expression and thereby repress flowering. Interestingly, our genetic analysis inversely also reveals that the MADS box transcription factor SOC1 directly represses GNC and GNL expression to control cold tolerance and greening, two further physiological processes that are under control of SOC1. In summary, these findings support the case of a cross-repressive interaction between the GATA factors GNC and GNL and the MADS-box transcription factor SOC1 in flowering time control on the one side and greening and cold tolerance on the other that may be governed by the various signaling inputs that are integrated at the level of SOC1 expression.

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Whole Transcriptome Profiling in Barley Shoot Apices During Floral Transition

Benedikt Drosse (1), Maria von Korff (1)

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Genetic studies for flowering time in cereals focused on the duration of the whole pre-anthesis development. However, in cereals very little is known about how genetic variation at flowering time genes affect the timing of the different phases of inflorescence meristem development:i.) the vegetative phase, ii.) the spikelet initiation and iii.) the spikelet growth phase.

Natural allelic variation for PPD-H1 has been shown to affect flowering time under long photoperiods. We have phenotyped the pre-anthesis development of an European spring barley cultivar "Scarlett" (*Hordeum vulgare* ssp. *vulgare*), carrying the recessive allele for ppd-H1, and an introgression line for the dominant allele of PPD-H1, derived from the wild barley accession"ISR42-8" (Hordeum vulgare ssp. spontaneum) under long (16h light) and short (8h light) photoperiods.

Floral transition, from a vegetative to a reproductive inflorescence meristem, occurred under long and short photoperiods in both genotypes. However, long photoperiods accelerated floral transition in the introgression line (PPD-H1) more strongly than in Scarlett (ppd-H1). Whole transcriptome profiling of inflorescence meristems during floral transition pointed to a role for the AP1-/FUL-like gene family of MADS-box transcription factors in establishing floral meristem identity. Here we present a comparison of expression profiles between a set of candidate genes for the induction of floral primordia in barley and their homologous genes in Arabidopsis, known to be essential for the establishment of floral meristem identity.

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An Increased Vernalization Temperature Optimum at the Northerly Limit of the *Arabidopsis* Range

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Arabidopsis thaliana has adapted to growth across a wide latitudinal range. Many natural accessions that grow in northern Europe require exposure to prolonged cold during winter to align their flowering to optimal conditions in spring. This cold induced acceleration of flowering, known as vernalization, involves epigenetic silencing of the major floral repressor *FLOWERING LOCUS C* (FLC). Natural variation exists in the length of cold required to fully trigger this epigenetic silencing and much of this variation maps to cis elements at FLC itself. Little is known, however, about the vernalization response of natural accessions at temperatures other than 4oC. In an attempt to reveal potential adaptation to extreme latitudes, we determined the temperature optimum for vernalization in Lov-1, an accession collected from the most northerly limit of the Arabidopsis range – Lövvik (62.5oN). Contrary to expectations, we found a pronounced temperature optimum of 8oC for Lov-1. This prompted us to set up a field experiment in Sweden to test whether Lov-1 vernalizes during autumn (Sep-Nov). Our results support the hypothesis that a higher optimal vernalizing temperature has evolved in Lov-1 to ensure complete vernalization before the sub-zero temperatures of winter.

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Phenotypic impact of natural variation in diurnal gene expression waveforms

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Temporal regulation of biological processes at defined times of the day provides an adaptive advantage to most organisms. Many plant genes are diurnally regulated and show peaks of expression around the time at which their function is required to regulate downstream pathways. However, the mechanisms that confer diurnal patterns of gene expression in natural accessions grown in ecologically relevant day/night cycles, and how precise these patterns must be to optimally regulate downstream pathways is not known. We first explored the natural diversity of the timing of expression of *GIGANTEA* (*GI*), an evening expressed gene, at high resolution and throughout diurnal cycles. Natural variation of this trait existed specifically in long days, and was mediated by changes in light signaling that influence *GI* transcription in the evening. Precise changes in the diurnal waveform of *GI* transcription altered *PHYTOCHROME INTERACTING FACTOR 4* (*PIF4*) expression and reprogrammed growth. These findings demonstrate that diurnal expression patterns are precisely modified by natural genetic variants at specific times of the day and that these changes in diurnal rhythms modify the activity of downstream processes leading to phenotypic diversity.

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VI. Posters

P/1

Flowering Time Regulation in Maize

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Flowering time is an important agronomical trait of relevance for harvest date, biomass yield and crop rotation schemes.

The regulation of flowering time and associated transition from vegetative to inflorescence meristems in the very important crop maize seems to be dominated by small additive QTLs with few genetic or environmental interactions [1]. Mutants do not promise as much insight into the pathways regulating flowering time as in Arabidopsis, since only three late flowering mutants are known to date: indeterminate 1 (id1), delayed flowering 1 (dlf1) and leafy [2]. ID1 encodes a zinc-finger transcription factor absent in Arabidopsis and DLF1 a bZIP transcription factor homologous to the Arabidopsis floral integrator *FLOWERING LOCUS D* (FD) [3]. *LEAFY* has not yet been cloned to date. In order to gain new insights into the processes regulating flowering time in maize we analyzed the transcriptome of leaves before, during and after the switch from vegetative to reproductive development of the shoot apical meristem (SAM). Two pairs of genetically related maize inbred lines were initially identified differing significantly in flowering time. By obtaining and analyzing transcriptome data from these 4 lines we identified genes that are putatively components of the flowering time regulating machinery in maize.

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P/2

Effects of viral-mediated expression of Arabidopsis FT gene in tomato

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This poster will describe the effects of viral-mediated transient expression of the Arabidopsis FT gene in tomato plants. Expression of the Arabidopsis FT gene from the PVX virus was detected in systemic non-inoculated leaves of inoculated plants showing that the FT gene was being expressed throughout the plant. PVX is not a seed transmissible virus and we confirmed that no PVX or Arabidopsis FT RNA could be detected in seed harvested from inoculated plants. Viral-mediated expression of the Arabidopsis FT gene did not have much effect on flowering time, but did have a significant effect on fruit weight, seed number, and branching in tomato plants**.**

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P/3

Approaches to Integrate Nitrogen Signals into the Flowering Network

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Nitrogen (N) is an essential nutrient for plants, typically representing 2-5% of the plant dry weight. The N supply often limits plant growth and development. Next to developmental processes like germination, shoot-root allocation, lateral root growth, senescence, the concentration of nitrate as the major source of N in the soil has been known for almost a century to modify the timing of flowering in plants. Marin and coworkers suggested in a recent publication that N influences flowering via a novel signaling pathway that includes nitrate or a substance that is metabolized from nitrate (Marín et al., 2010). At which point the N signal, which is thought to act in a separate pathway, interacts with the known floral induction pathways is not known to date. In the work presented here, we aim at getting a better insight into how the N signal is to be integrated into the existing flowering network.

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P/4

Allele mining in wild barley: finding new exotic genes which control flowering time in the barley nested association mapping (NAM) population HEB-25

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Flowering time of crop plants is crucial in practical agriculture, especially for handling the consequences of climate change. Plant breeders have to deal with this problem and take it into account in upcoming breeding programs. A known way of controlling flowering time is the use of genetic resources from wild species. Therefore we have developed the barley NAM population HEB-25, consisting of 1,500 BC1S3 lines originating from crosses of the German elite barley cultivar Barke (C) with 25 highly divergent exotic barley accessions (E).

The aim of the present project is to find new genes or new alleles of known genes that influence flowering time. We expect to find new flowering time loci with a high probability as there is a high level of genetic diversity present among the 1,500 BC1S3 lines. The identification of flowering time associated genome regions is performed through a genome wide association study (GWAS). Genotype data for this study were derived from the Infinium 9k iSelect HD chip for barley, which consists of 7,864 SNPs (5,737 are polymorphic). Phenotype data have been collected in two field trials in 2011 and 2012. To determine which loci influence plant development five different traits (days to shooting, days to flowering, days to maturity, days from shooting to flowering, days from flowering to maturity) are evaluated.

After identifying BC1S3 lines that show interesting effects (for example new flowering time loci or extremely strong effects on flowering time) verification experiments with individual lines will be conducted in field trials and greenhouse or climate chamber experiments, respectively. The identified heterozygous NAM lines for a candidate gene are an ideal starting point for high resolution mapping. Finally, in a further step we plan to embark on cloning and characterizing newly identified flowering genes.

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P/5

Regulation of Flowering by Trehalose-6-phosphate Signaling in Arabidopsis thaliana

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Plants integrate diverse environmental and endogenous signals to ensure the timely transition to flowering.
This determines to a large extent the reproductive success of plants. The carbohydrate status is implicated in linking flowering to the metabolic and energy status of the plant. Trehalose-6-phosphate (T6P) has been suggested to function as a proxy for the carbohydrate status in plants. The loss of *TREHALOSE-6-PHOSPHATE SYNTHASE 1* (TPS1) causes *Arabidopsis thaliana* to flower late. In the leaves, TPS1 activity is absolutely required for the induction of FT, even under long days. Thus the plant is able to integrate an environmental signal, increasing day length, with an endogenous signal, the presence of high carbohydrate levels. Additionally, TPS1 is expressed in the shoot apical meristem. We found that T6P levels rise in the shoot apex over time, increasing more than two-fold during the floral transition in long day conditions as well as in short days. Interestingly, increasing TPS1 expression in the stem cells alone is sufficient to induce precocious flowering, while reducing T6P content by *TREHALOSE 6-PHOSPHATE PHOSPHATASE* (TPP) over-expression in the stem cells delays flowering. In addition, the T6P pathway affects the expression of important flowering time and flower patterning genes via the age pathway at the shoot meristem independently of the photoperiod pathway. Our results demonstrate that TPS1 is required for the timely initiation of flowering and that the T6P pathway regulates flowering at two sites in the plant, in the leaves and at the shoot meristem. In addition, we have placed the T6P pathway into the existing genetic framework of flowering time control.

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P/6

Identification of target genes of the Arabidopsis GATA transcription factor GNL

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The orthologous Arabidopsis GATA transcription factors GNC (*GATA NITRATE INDUCIBLE CARBON METABOLISM INVOLVED*) and GNL (*GNC-LIKE*) control a range of biological processes throughout plant development downstream from the DELLA proteins of the gibberellin (GA) pathway and the PIF transcription regulators, such as germination, greening, floral organ formation and flowering time. In addition, GNL integrates and transduces information from environmental stimuli such as nitrogen availability or light. In order to elucidate the molecular function of GNC and GNL, we decided to identify the target genes of these GATA factors in a genome wide analysis using chromatin immunoprecipitation combined with next generation sequencing. To this end, we generated transgenic plants with p GNL::GNL:HA in a double mutant gnc gnl background and performed ChIP-seq from 2 weeks-old plants. Our preliminary analysis of the putative GNL transgenes will be presented.

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P/7

Dissecting the CONSTANS promoter by Phylogenetic Shadowing

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Flowering of *Arabidopsis thaliana* is tightly regulated by genetic and environmental factors. The photoperiodic flowering pathway promotes transition from vegetative to reproductive phase through day length perception in the leaf leading to subsequent signal transduction to the apex. In this pathway FLOWERING LOCUS T (FT) is directly positively regulated by CONSTANS (CO) under long day conditions and the FT protein then moves from the leaf to the apex. CO is regulated both transcriptionally and post-translationally by light and the circadian clock. Its mRNA is low in the first light hours and starts to rise around ZT8 and peaks at night. Under LD conditions an additional peak around ZT14 forms which is important for FT induction. CO is efficiently switched off by a class of redundant, repressive and clock regulated DOF transcription factors (CDFs) in the morning. The evening expressed blue light and GIGANTEA stabilized F-Box protein FKF1 removes these TFs from CO locus towards the end of a Long Day. Recently identified Flowering bHLH transcription factors bind CO locus and promote expression. We found that key features of CO expression such as low expression in the morning and Long Day inducibility are conserved in the Brassicaceae family. Additionally, comparison of CO promoters from ten Brassicaceae species revealed highly conserved regions in the promoter. One conserved region around 2.1kb upstream of the TS of CO mediates a significant flowering time difference in a complementation assay. The same piece shows clock and light regulation similar to endogenous CO in a gain of function promoter LUCIFERASE assay. It contains a combination of TF binding sites that are both conserved between species and can be found in a prominent position close to the TS. It is a combination of DOF binding sites, light induced G-Box and putatively clock regulated LUX binding sites, which could mediate the features needed for tight regulation of CO in different day length.

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P/8

Characterization of a barley early flowering mutant

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Genetic variation in flowering time is important for the successful adaptation of crops to different environments. Barley is a long day responsive plant; mutations to the major barley photoperiodic response gene, Ppd-H1, orthologous to the Arabidopsis clock gene PRR7, confer earlier flowering under inductive condition, indicating that in barley, as in other plant species, is conserved the tight link between photoperiodic flowering and circadian clock.

We have identified and characterized an early flowering mutant in barley. The mutation leads to earliness under both long and short day growing conditions. We demonstrate that this mutation accelerates the transition from vegetative to reproductive growth and inflorescence development. We show that this mutant is impaired in the expression profile of a number of clock genes. We propose, then, that this mutation, through a defect in the clock, anticipate flowering time irrespective of the daylength.

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P/9

The Role of HvFT3 in Flowering of Barley under Different Photoperiods

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With the increasing demand for food, focus is directed at improving cereal productivity by breeding highly adapted germplasm to target environments. One key trait in plant adaptation is the control of flowering time. Barley flowering time is controlled by vernalization (VRN) and photoperiod (PPD) genes. HvFT3, a Flowering Locus T-like gene, is the candidate gene for the photoperiod response locus (Ppd-H2), which is yet to be fully characterized. We have over-expressed HvFT3 in a spring barley background, crossed it with a winter barley, then used the F2 population to investigate HvFT3 interactions with major flowering genes under long and short days.

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P/10

Investigating Flowering Time Control (FTC) Genes in Grapevine

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The control of flowering and timing of flowering seems to differ between grapevine (*Vitis vinifera*) and well-studied model organisms. Grapevine is a diploid (2n=38), woody perennial crop plant with a reproduction time of about three years. The genome is highly heterozygous, and the plant displays a strong inbreeding depression. In grapevine, neither vernalisation nor photoperiodism has an impact on the promotion of flowering. The plant hormone gibberellic acid, which induces flowering in *Arabidopsis thaliana*, seems to inhibit flowering in grapevine.

We would like to identify determinants or genes which are involved in the control of early or late flowering in grapevine. More than 150 candidate genes with a putative function in FTC have been identified based on functional data mainly from the model organism *Arabidopsis thaliana*. Several genes in a QTL for flowering time on Chromosome 1 have been chosen for expression analysis to associate gene expression patterns and phenotypes. Inflorescences (German: "Gescheine") of plants from a mapping population of Villard blanc (late flowering female mother) X Gf.Ga-47-42 (early flowering hermaphroditic father) were used. Material from the parents and four F1-members (two early flowering, two late flowering) was collected at different developmental stages, and expression levels of the candidate genes were determined by qRT-PCR. We detected clear and reproducible differences, but so far no significant correlation of candidate gene expression level and flowering time phenotype.

In order to define the haplotypes of candidate genes and to develop genetic markers for QTL fine mapping, a panel of 18 genotypes is currently in processing for NGS amplicon-sequencing. Primer design has been performed and verified. The Sanger sequencing has confirmed haplotype-specific SNPs in the first generated amplicons.

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P/11

Natural variation of gibberellin-regulated flowering in *Arabidopsis thaliana*

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Gibberellins (GAs) control a number of developmental processes in higher plants and act as mediators of environmental signals. In the frame of a natural variation analysis for altered GA responsiveness we identified Killean-0 (Kil-0) out of a collection of 250 *Arabidopsis thaliana* accessions that displays phenotypic changes in GA-dependent traits like hypocotyl elongation, chlorophyll accumulation, leaf size and flowering time in comparison to the reference accession Columbia-0 (Col-0). These differences were observed in different developmental stages as well as in different growth conditions (temperature, photoperiod, etc.). Interestingly, most phenotypic differences are increased when the plants are grown under cold (15°C) temperature, especially flowering time. Expression analyses that several GA-catabolic genes (GA2ox) but not metabolic genes are tissue-specifically down-regulated why we propose that plant development in Kil-0 might be controlled by a modified GA catabolism. Through the analysis of flowering time of F1 individuals and a F2 population derived from a cross of Col-0 and Kil-0 we found out that this phenotype segregates approximately in a monogenic manner. Rough mapping using F2 individuals with extreme phenotypes revealed that this trait might be controlled by a major effect locus which maps to a 2 Mb region of chromosome one. Different approaches will be combined to identify a candidate gene.

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VIII. Addresses and Phone Numbers

a) Addresses

Meeting Venue

Max Planck Institute for Plant Breeding Research
Carl-von-Linné-Weg 10
50829 Köln
Getting there…
please visit:
http://www.mpipz.mpg.de/2530/contact

Brauhaus Päffgen (joint in-town evening Tuesday, 19.30 – open end)

Friesenstraße 64, 50670 Köln

b) Phone numbers

Emergencies

Police Department	110
Fire Department	112
Emergency call	112

Taxi/Cab Service

Taxi Ruf Köln eG	+ 49 (0) 221 28 82
PÄFFGEN TAXI & BUS	+ 49 (0) 221 31 13 11