Adaptation to seasonality and the winter freeze

Jill C. Preston1* and Simen R. Sandve2
1 Department of Plant Biology, University of Vermont, Burlington, VT USA
2 Norwegian University of Life Sciences, Ås, Norway

*Correspondence: Jill C. Preston, Department of Plant Biology, University of Vermont, 111 Jeffords Hall, 63 Carrigan Drive, Burlington, VT 05405, USA. E-mail: jill.preston@uvm.edu

INTRODUCTION

Since the late Eocene and Oligocene around 47.5 to 26 million years ago (mya) the Earth has experienced dramatic cooling events, resulting in an overall contraction of the tropics, and establishment of novel temperate zones in both northern and southern hemispheres (Zachos et al., 2001; Stickley et al., 2009). In response to this cooling, several ancestrally tropical lineages have successfully diversified outside their ecological zone of origin, becoming adapted to cooler and often more seasonal environments (Latham et al., 2010). However, the fact that less than half the families of modern angiosperms are represented in the temperate zones suggests that adaptations to cold seasonal climates might be difficult to evolve (Ricklefs and Rеннor, 1994; Donoghue, 2008).

Support for the hypothesis that adaptations to low or freezing seasonal temperatures are relatively hard and/or slow to evolve comes from the fact that climate cooling during the Eocene–Oligocene boundary was associated with large-scale extinctions of both animals and plants (Irby et al., 2000), and by the apparent complexity of physiological and morphological adaptations to cold (see later sections). However, as an alternative hypothesis, it has been postulated that, since climate cooling has been an ongoing process throughout the Cenozoic, the relatively recent expansions of cold temperate zones has meant that only a minority of plant families have been historically party to selection by cold winters (Pine and Ree, 2006). Thus, there is still much debate about whether different adaptations to extended periods of cold can evolve quickly enough to allow range expansions and/or local adaptation under gradual or rapid climate change conditions (Frankel et al., 2007; Cook et al., 2012). The focus of this review is to highlight the major ways in which plants have adapted physiologically to cold seasonal environments, and to synthesize some of the current available data on the genetic basis of these adaptations, with the general goal of understanding the evolutionary lability of cold-season traits.

PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS TO SEASONAL COLD

Flowering plants initially diversified during the Mesozoic era at least 140 million years ago in regions of the world where temperate seasonal environments were not encountered. Since then several cooling events resulted in the contraction of warm and wet environments and the establishment of novel temperate zones in both hemispheres. In response, less than half of modern angiosperm families have members that evolved specific adaptations to cold seasonal climates, including cold acclimation, freezing tolerance, endodormancy, and vernalization responsiveness. Despite compelling evidence for multiple independent origins, the level of genetic constraint on the evolution of adaptations to seasonal cold is not well understood. However, the recent increase in molecular genetic studies examining the response of model and crop species to seasonal cold offers new insight into the evolutionary lability of these traits. This insight has major implications for our understanding of complex trait evolution, and the potential role of local adaptation in response to past and future climate change. In this review, we discuss the biochemical, morphological, and developmental basis of adaptations to seasonal cold, and synthesize recent literature on the genetic basis of these traits in a phylogenomic context. We find evidence for multiple genetic links between distinct physiological responses to cold, possibly reinforcing the coordinated expression of these traits. Furthermore, repeated recruitment of the same or similar ancestral pathways suggests that land plants might be somewhat pre-adapted to dealing with temperature stress, perhaps making inducible cold traits relatively easy to evolve.

Keywords: cold acclimation, freezing tolerance, endodormancy, plant adaptation, seasonality, vernalization responsiveness

www.frontiern.org

June 2013 | Volume 4 | Article 167 | 5
to seasonal cold, i.e., adaptation to the coldest season of the year in temperate climates.

Unlike animals, individual plants are immobile. Thus, in order to reduce the negative effects of winter cold, many temperate plants must synchronize their sensitive reproductive output with favorable environmental conditions of the spring and summer (Bradshaw, 1972; King and Heide, 2009). In the case of spring annuals, germination, reproduction, and senescence occur during the warm seasons. However, rather than relying only on seed to produce the next generation, herbaceous perennials are capable of secondary rounds of vegetative growth from dormant underground meristems (e.g., rhizomes), which occurs at the conclusion of winter. By contrast, woody perennials such as trees, often delay their flowering for several years until a critical biomass is achieved (Rothde and Bhalerao, 2007). As in the case of winter annuals, temperate herbaceous perennials are often responsive to vernalization, and can tolerate chilling and frost. Furthermore, in addition to cold tolerance, many temperate and boreal trees are able to protect new growth from harsh winter conditions by becoming dormant prior to winter (endodormancy; Lang et al., 1987; Howe et al., 2003; Campoy and Egea, 2011). Recent studies on the genetic basis of these varied adaptations to winter cold offer exciting opportunities to understand constraints on plant transitions from the tropical to the temperate zone, and vice versa. This is particularly relevant in the face of current and projected changes to our climate. The following sections will focus on the evolution and genetic basis of three important physiological adaptations to seasonal cold: cold acclimation (i.e., the seasonal acquisition of constitutive freezing tolerance), endodormancy, and vernalization responsiveness. However, first we will consider what is currently known about the phylogenetic pattern of these traits across seed plant clades, and their relationships to climate.

PHENOTYPIC CORRELATIONS AND THE PHYLOGENETIC DISTRIBUTION OF COLD ADAPTIVE TRAITS

In temperate plants that experience prolonged cold to sub-zero winter temperatures, above ground tissues are susceptible to delayed growth and damage by frost. Thus, high latitude plants that undergo endodormancy (woody perennials), or are responsive to vernalization (herbaceous annuals and perennials), are often also able to induce cold tolerance through a process known as cold acclimation (Howe et al., 2003; see Cold Acclimation and Cold Tolerance). For example, non-vernalization responsive (spring) wheat varieties generally have lower freezing tolerance than vernalization responsive (winter) wheat, and in winter wheat length of vernalization requirement is positively correlated with speed of cold acclimation (Prasil et al., 2004). Furthermore, in temperate trees such as *Pinus contorta* and Douglas-fir (*Pseudotsuga menziesii*), elevation and distance from warmer ocean climates are strongly associated with the timing of growth cessation and endodormancy and the temperature required to induce cold acclimation and subsequent freezing tolerance (Campbell and Sugano, 1979; Howe et al., 2003). A similar trend has been found between length of vernalization needed to elicit flowering and continental-oceanic gradients in *A. thaliana* (Lewandowska-Sabat et al., 2012).

Despite the correlation between cold adaptive traits, there are examples of endodormant and vernalization responsive plants that cannot induce cold tolerance, and vice versa. For example, *Thuja plicata* and *Tsuga heterophylla* both acclimate to cold, but do not experience endodormancy (Silim and Lavender, 1994), several trees undergo endodormancy without acclimating to cold (Kramer and Kozlowski, 1979), and several vernalization-responsive cereals cultivars are considered cold-sensitive (Trister and Bucic, 2005). The lack of a strict association between endodormancy/vernalization responsiveness and cold acclimation might be explained by the fact that low non-freezing temperatures can be detrimental to young bud development without affecting growth of other plant structures. For example, in plants adapted to, or derived from, subtropical climates, synchronization of bud development with warm conditions might be enough to escape the negative effects of occasional low winter temperatures, without the additional need for cold/freezing tolerance. Alternatively, boreal plants that experience sub-zero temperatures for large parts of the year might benefit from constitutive freezing tolerance, negating the importance of cold acclimation.

As outlined in the introduction, angiosperm families containing temperate species are less common than families confined to the tropics (Ricklefs and Renner, 1994; Donoghue, 2008). However, temperate taxa are distributed throughout the seed plant phylogeny (Ricklefs, 2005; Figure 1). Thus, the timing of angiosperm diversification relative to global Eocene cooling events suggests numerous independent origins of temperate seed plants (Wang et al., 2009b). How many of these major lineages evolved physiological adaptations to seasonal cold? With the exception of early-diverging angiosperms and several tropical gymnosperms for which there are no or limited experimental data, a broad literature search suggests that cold acclimation, endodormancy, and vernalization responsiveness have evolved in all major seed plant clades (Figure 1). Thus, at a broad phylogenetic scale, adaptations to cold might be relatively easy to evolve. In the following sections, we review available genetic data to determine whether multiple independent origins of cold traits can be explained by the modification of pre-adapted pathways (e.g., exaptations, sensu Gould and Vrba, 1982), and/or represent novel evolutionary innovations. We also suggest future studies that could be carried out to determine the potential for evolution of seasonal cold traits on shorter timescales and in response to current global change.
FIGURE 1 | Evolution of cold adaptive traits in seed plants. Relationships among major seed plant orders are inferred using representative taxa from Smith et al. (2011) in phylogenetic scenes and Cronyn (2000). Orders are color-coded as primarily temperate (blue), broadly distributed, or primarily tropical (red), based on the APG website (Stevens, 2001 onward). Blue stars indicate orders where trees are primarily temperate based on Rickles (2005). Evidence for endodormancy (E), cold acclimation/freezing tolerance (A), and vernalization responsiveness (V) are denoted for each order with example species. Since most species have not been tested for cold adaptations, absence of data does not necessarily indicate absence of traits. However, since cold climates arose after major radiations in seed plants, presence data (based on Krug, 1991; De la Rosa et al., 2000; Kawamura et al., 2002; Wilson et al., 2002; Karlson et al., 2004; Steck and Schult, 2005; Loper and Runkle, 2006; Fausey and Cameron, 2010; Kalibrier et al., 2007; Mewes and Pank, 2007; Rohr and Heins, 2007; Swendsen et al., 2007; Padhye and Cameron, 2008, 2009; PiotTO et al., 2009; Zhou and Anderson, 2009; Bass et al., 2010; Byard et al., 2010; Ghirardi et al., 2010; Kaymak and Guzzen, 2010; Kubeta et al., 2010; Lesnahan et al., 2010; Rantasen and Palonen, 2010; Caffarra et al., 2011; Cave et al., 2011; Cherrier et al., 2011; Dogramaci et al., 2011; Lin et al., 2011; Ardhang et al., 2012; Andren et al., 2012; Bigler et al., 2012; Diao et al., 2012; Kessler et al., 2012; Sangha-Person et al., 2012; Whitman and Runkle, 2012; Alessandro et al., 2013; Guzy-Wrobelska et al., 2013; Jones et al., 2013; Mjafahed et al., 2013) indicates multiple origins of cold adaptive traits across the phylogeny.
COLD ACCLIMATION AND COLD TOLERANCE
Cold tolerance is a highly complex trait that encompasses both the ability to tolerate the direct effects of low temperatures on plant function and the indirect effects of ice formation in and surrounding the plant. Direct effects of cold conditions change biological thermodynamic processes, biomolecule stability and function, and alter normal cellular processes such as photosynthesis, inter- and intracellular transport, and the balance between production and neutralization of toxic reactive oxygen species (ROS; Thomashow, 1999; Figure 2). By contrast, indirect effects of ice formation that occur during sub-zero temperatures create a different kind of cellular stress. First, extracellular ice formation depletes available water in and around cells, affecting normal water dependent processes and inducing freezing dehydration with associated cell membrane disruption (Steponkus et al., 1998). Second, large ice crystals grow at the expense of the formation of small new crystals, a process referred to as ice recrystallization (Capicotti et al., 2012). This process generates large and potentially damaging expanding crystals in extracellular spaces. Although most species have some innate tolerance to a sudden exposure to cold, many temperate species have evolved the ability to gradually increase their freezing tolerance during extended periods of cold, but non-freezing, temperatures and changing photoperiod during autumn (Thomashow, 1999; Catalá et al., 2011). This inducible process is referred to as cold acclimation, and ultimately leads to healthy plants that can successfully reproduce the following spring (Figure 2).

MOLECULAR AND PHYSIOLOGICAL CHANGES ASSOCIATED WITH COLD ACCLIMATION AND COLD TOLERANCE
Cold acclimation involves major changes in the biochemical and physiological state of the plant, improving low temperature stress tolerance. In general, proteins and compounds with various protective functions are increased, while photosynthesis and several other metabolism-related biochemical pathways are suppressed (e.g., Fowler and Thomashow, 2002; Lee et al., 2005; Rudi et al., 2010; Winfield et al., 2010; Table 1). Although cold acclimation genes and genetic pathways can vary widely between species, some molecular and physiological changes seem to be similar across major angiosperm clades (reviewed in Sandve et al., 2011).

The ability to manipulate ice formation has arisen multiple times throughout angiosperm evolution, and is achieved either by decreasing the freezing point (thermal hysteresis) or by inhibiting ice recrystallization (Griffith and Yaish, 2004; Byard et al., 2010; Figure 2). Although thermal hysteresis is commonly found in plants, it is not affected much by cold acclimation (Urrutia et al., 1992); ice recrystallization inhibition is believed to be more important for plant cold acclimation (Griffith and Yaish, 2004; Table 1). Ice recrystallization inhibition is found in species of many plant lineages (Doucet et al., 2000) and is caused by a range of factors.
of diverse proteins, including beta-1,3-glucanases, WRKY proteins, chitinases, and thaumatin-like proteins (Griffith and Y aish, 2004 and references therein). For example, in endocots the carrot (Daucus carota) polygalacturonase inhibitor protein inhibits ice recrystallization and decreases the freezing point; its expression in tobacco (Solomon tubscum) and A. thaliana results in inhibition of ice recrystallization and increased freezing tolerance (Worrall et al., 1998; Meyer et al., 1999). In monocots, a different Poaceae (Poaceae)-specific inhibitor of ice recrystallization-protein (IRIP) family shows strong inhibition of ice recrystallization (Sidebottom et al., 2000), which has been shown to increase freezing tolerance in planta (Zhang et al., 2010).

Freezing induced cell dehydration is another factor plants have to deal with during winter (Uemura et al., 1995; Figure 2). During cold acclimation plants gain the ability to modify membrane stability, which involves both changes to the cell membrane lipid content (Li et al., 2004; Moellering et al., 2010) and production of membrane-interacting protective compounds, such as proline and a diversity of carbohydrates (Fujikawa et al., 1999; Hussan et al., 2004; Vahuru and Van den Ende, 2006; Table 1). Manipulation of lipid metabolism and membrane lipid composition in transgenic plants has improved freezing and chilling tolerance in tobacco (Khodakovskaya et al., 2006), poplar (Populus sp.; Zhou et al., 2009), and tomato (S. lycopersicum; Domínguez et al., 2010).

In addition to proteins and compounds with direct protective action in cold, modulation of photosynthetic processes is a common cold acclimation response among angiosperms (Figure 2). During photosynthesis, light energy is absorbed and converted to chemical energy in thylakoid membranes of chloroplasts, and then used for CO2 fixation in the Calvin cycle. Absorption of light by photosystem II (PSII) normally leads to light-induced damage of the PSII, a process referred to as photoinhibition, which is counteracted by a PSII damage repair mechanism that restores PSII function (Hetherington et al., 1989; Aro et al., 1993, 2005; Melis, 1999; Bascuñán-Godoy et al., 2012). However, if the level of absorbed light energy greatly exceeds that of the consumed chemical energy this will impair PSII damage repair and accelerate photoinhibition (Takahashi and Murata, 2008), with potential detrimental consequences for plant growth (Melis, 1999). Low temperatures promote increased photoinhibition (Hetherington et al., 1989), and to minimize photoinhibition-associated damage, higher plants undergo photosynthetic acclimation during cold acclimation either by increasing the energy demand through increased carbon assimilation and carbon metabolism (Huner et al., 1993), dissipation of excess excitation energy as heat (Dall’Osto et al., 2005), or improving the PSII repair machinery (Bascuñán-Godoy et al., 2012; Table 1). Photoinhibition is also detrimental to the entire cell due to the associated increase of ROS (Krause, 1988). Photoinhibition has been shown to regulate the expression of genes in cold acclimation (Gray et al., 1997), hence, a plants’ freezing tolerance is inherently linked to temperature-induced photoinhibition. Variation in the capacity for photosynthetic acclimation during cold acclimation is correlated with genotypic differences in winter survival and freezing tolerance of grasses (Rapacz et al., 2004). Moreover, the C-REPEAT binding factor (CBF) pathway has been shown to alleviate photoinhibition in autumn conditions (Yang et al., 2010).

In woody species, freezing temperatures can disrupt whole-plant functioning by limiting long-distance water transport in the xylem (Sperry et al., 1994; Ambrošič, 2001). This is particularly true following xylem embolisms (Figure 2), which are often induced by freeze-thaw cycles in regions that experience freezing winter nights and above freezing winter days,

### Table 1 | Genes and pathways regulated during cold acclimation.

| Class                        | Subclass                   | Regulation | Function                                  | Reference                     |
|------------------------------|----------------------------|------------|--------------------------------------------|-------------------------------|
| Protective                   | Antioxidant                | Up         | Free oxygen radical regulation             | Winfield et al. (2010)        |
| Chaperones                   |                            | Up         | Biomolecule protection/stabilization       | Carvalho et al. (2011)        |
| Dihydroxylys/LEA             |                            | Up         | Unknown                                    | Hanin et al. (2011)           |
| Proline                      |                            | Up         | Osmoregulation                             | Janská et al. (2011)          |
| Cysara                       |                            | Up         | Osmoregulation                             | Janská et al. (2011)          |
| Ice interacting, e.g.,       |                            | Up         | Reduce freezing point, inhibit ice recrystallization | Sidebottom et al. (2000); Griffith and Y aish (2004), Zhang et al. (2010), Janská et al. (2011) |
| LipRF/1                      |                            | Up         | Non-bilayer formation, membrane stabilization | Moellering et al. (2010) |
| Protective/signaling         | Carbohydrate metabolism/  | Up         | Stabilize membranes, osmoregulation, signaling | Maryama et al. (2008), Janská et al. (2011) |
| Starch degradation           |                            |            |                                             |                               |
| Lipid membrane               | Lipid membrane remodeling, | Up/down    | Non-bilayer formation, membrane stabilization |                               |
| Metabolism                   | Homeostatic                | Down       | Metabolic and energetic control             | Huner et al. (1993); Fowler and Thomashow (2002), Li et al. (2004) |
At least 50–60 transcription factors are known to be important in Absence of the CG-1 element in promoters of cold responsive plant adaptations to winter. (2013) | Volume 4 | Article 167 | 6

such as North Africa, the Mediterranean region of Europe, and southern parts of North America (Cavendar-Bares et al., 2005; Mederos and Pockman, 2011). Although variation in resistance to embolism can be explained by differences in vessel diameter and architecture (Sperry et al., 1994; Améglio et al., 2001), cold acclimation has been found to reduce xylem embolisms in oak (Quercus) and several conifers (Hammel, 1967; Sperry et al., 1994; Cavendar-Bares et al., 2005). Furthermore, it is hypothesized that some woody plants can repair winter embolism; the mechanisms underlying repair and induced resistance are largely unknown (Cavendar-Bares et al., 2005).

SENSING AND SIGNALING COLD

How low temperature is sensed and then signaled to the cell nucleus is generally not well understood. The best-studied temperature sensing mechanism is membrane fluidity. Membranes surrounding cells, mitochondria, and chloroplasts consist of a lipid bilayer, and low temperatures causes lipid membranes to become more rigid (Alonso et al., 1997). Chemically induced membrane rigidity results in cytoskeleton changes, increased Ca$^{2+}$ influx to the cell, and changes in activity of certain protein kinases, which ultimately result in transcription of cold-induced genes that artifically mimic the process of cold acclimation and improve freezing tolerance of plants (Orrus et al., 2000; Sangoun et al., 2001). In addition to cell membrane changes, abscisic acid (ABA; Llorente et al., 2000; Xiong and Li, 2001) and ROS (Lee et al., 2002) accumulation in warm conditions has been shown to initiate processes similar to cold acclimation, resulting in increased freezing tolerance.

Recently, a molecular model of cold signaling, linking cold sensing and transcription, has been put forward (Doherty et al., 2009). The model includes four components: Ca$^{2+}$; calcium modulated proteins (calmodulins), calmodulin binding transcriptional activators (CAMTAs), and cold responsive transcription factors. Low temperatures increase the Ca$^{2+}$ influx (probably as an indirect response to more rigid membranes) and activate calmodulin proteins, which subsequently activate other Ca$^{2+}$-unresponsive CAMTA proteins essential for cold acclimation. The A. thaliana genome contains six CAMTA genes with calmodulin binding- and DNA binding CG-1 (CCGG) domains (Bouché et al., 2007). Absence of the CG-1 element in promoters of cold responsive transcription factors (both CBF and non-CBF), leads to a decrease in their transcript levels of up to 40–50% (Doherty et al., 2009). Loss-of-function CAMTA gene mutants are unable to acclimate to cold and drought, and so are sensitive to freezing (Doherty et al., 2009; Pandy et al., 2013). It should be noted that the validity of this model with respect to the role of calmodulin as Ca$^{2+}$ signal sensors has not been experimentally tested.

TRANSCRIPTIONAL REGULATION OF THE COLD ACCLIMATION PROCESS

At least 50–60 transcription factors are known to be important in initiation of cold acclimation in A. thaliana, including members of the AP2, MYB, MYC, IZIP, and Zn-FINGER transcription factor families, but relatively little is known about their downstream targets (Fowler and Thomashow, 2002; Lee et al., 2005; Vogel et al., 2005; Knight et al., 2009). The only well characterized cold acclimation pathway in plants is the INDUCER OF CBF EXPRESSION (ICE)-CBF-COLD-RESPONSIVE (COR) cold response pathway (Gilmour et al., 1988; Chinnusamy et al., 2003; Stockinger et al., 2007). During plant chilling, expression of ICE genes triggers rapid (~15 min) transient up-regulation of CBFs (Chinnusamy et al., 2003; Dong et al., 2006), which together directly or indirectly regulate approximately 30% of all cold-induced transcriptional changes (Vogel et al., 2005; Swenson et al., 2006; Van Buskirk and Thomashow, 2006; Table 1). The initial ICE-CBF regulatory switch was described in A. thaliana, but data suggest it is functionally conserved in apple (Malus domestica, Rosaceae), and (at least partially) in grasses, subfamily Pooidaeae (Chinnusamy et al., 2003; Badawi et al., 2008; Feng et al., 2012). Cold-induced CBFs are found in species across all land plant lineages (e.g., Skinner et al., 2005; Xiong and Li, 2006; Penneycooke et al., 2008), and their protein products bind to CCGAC core motifs in the promoters of diverse cold and dehydration responsive genes, including themselves (Liu et al., 1998; Novillo et al., 2004; Stockinger et al., 2007).

In addition to cold, CBF transcription is affected by photoperiod. Expression of A. thaliana CBFs fluctuates on a diurnal basis, peaking around 8 h after the dawn zeitgeber (Fowler et al., 2005). Under long day conditions, CBF gene expression is repressed by the action of PHYTOCHROME B (PHYB), PHYTOCHROME-INTERACTING FACTOR 4 (PIF4) and PIF7 (Lee and Thomashow, 2012). By contrast, under short days, reduced mRNA levels and stability of PHYB, PIF4, PIF7 and their protein products, respectively, result in the derepression of CBF transcription (Lee and Thomashow, 2012). Although the circadian regulation of CBFs is not well understood, the differential regulation of CBFs under short versus long days provides a secondary mechanism by which freezing tolerance can be timed to coincide with winter.

The plant hormone ABA is a major player in regulating genes involved in plant stress response through the transcriptional activation of ABA-dependent transcription factors (Shinozaki and Yamaguchi-Shinozaki, 2000). The importance of ABA in freezing tolerance is debated (Gusta et al., 2005), but much evidence supports a role for ABA in cold acclimation under natural conditions. First, endogenous ABA-levels increase in A. thaliana and wheat (Triticum aestivum) during low temperature exposure (Curvas et al., 2008; Shikavka et al., 2009). Second, application of exogenous ABA enhances freezing tolerance in whole plants (Chen and Gusta, 1983; Mantyla et al., 1995) and calli (Dallaire et al., 1994). Third, many genes expressed during cold acclimation are regulated by ABA, including the CBF genes (Khoth et al., 2002; Knight et al., 2004; Curvas et al., 2008; Kobayashi et al., 2008; Shikavka et al., 2009; Agarwal and Jha, 2010). Involvement of ABA in cold transcriptional regulation is observed in bryophytes (Bhyan et al., 2012), monocots, and eudicots (reviewed in Gusta et al., 2005).

CONSERVATION AND DIVERSIFICATION OF COLD ACCLIMATION AND COLD TOLERANCE

Despite independent evolution over hundreds of millions of years, some pathways and mechanisms involved in cold acclimation are similar among species of bryophytes, monocots, and eudicots (see above). This could be interpreted as evidence for conservation of ancestral cold response pathways from the earliest land
An alternative interpretation is that similarities in cold responses across land plant lineages are due to genetic parallelisms. The latter could occur if an ancient stress response pathway was recruited to cold acclimation and cold/freezing tolerance multiple times independently. Predictions of this hypothesis include substantial overlap between the cold acclimation/tolerance and other stress pathways. One potential pathway that might have been recruited for cold acclimation and cold/freezing tolerance is the drought tolerance pathway. All land plants are constantly battling to minimize water loss at the atmosphere-plant boundary and prevent cellular dehydration. Adaptations to withstand dehydration were probably some of the main evolutionary innovations when plants moved from aquatic to terrestrial life ~500 mya; hence basic molecular responses to dehydration can be assumed to have a common ancestry in all land plants. Interestingly, many key cold acclimation responses are tightly linked to dehydration. For example, in A. thaliana, gene expression correlations of 0.15–0.30 are found between response to dehydration stresses (drought, salt, and osmotic stress) and cold stress (Swindell, 2006). This strong molecular connection between dehydration-like stress responses and cold can only be explained by the control of these responses through non-specific stress triggers, perhaps by cellular redox states, or some other shared signaling mechanisms.

Following this logic, distantly related cold or freezing tolerant species are predicted to have adapted to cold through changes in partially overlapping molecular pathways, resulting in the recurring recruitment of (a few) similar pathways. If this hypothesis holds, we would expect relatively similar initial transcriptional responses and more diverse downstream molecular changes between species with independent adaptations to cold. Comparative transcriptome analyses have shown conserved expression profiles during cold acclimation in potato (S. tuberosum) and A. thaliana, despite over 100 mya of independent evolution (Carvallo et al., 2011). However, more comprehensive comparative studies of stress responses among species are needed to better understand the patterns of transcriptional conservation over macro-evolutionary time scales.

Interestingly, cold acclimation has also been demonstrated in green algae (Nagao et al., 2008), but the algal process does not respond to ABA as many land plants do, suggesting involvement of different pathways. Algae do contain AP2 domain encoding genes like the CBF transcription factors, but it is not clear if these transcription factors are involved in cold acclimation. More detailed studies in algae will enable us to understand if the basic molecular modules of plant cold acclimation evolved as early as in an aquatic land plant ancestor.

**ENDODORMANCY**

Meristem dormancy is a common phenomenon in plants and has been linked to variation in a number of developmental genes (reviewed in Doust, 2007; Domagalska and Leyser, 2011). The most common type of meristem dormancy derives from the inability of the main axis to suppress the outgrowth of axillary meristems (apical dominance or paradormancy), and is a major determinant of architecture and growth habit across higher plants (Lang et al., 1987). By contrast, endodormancy is specific to temperate woody perennials, being shaped by both internal factors and seasonal fluctuations in both temperature and photoperiod (Chaine et al., 2001; reviewed in Campoy and Egea, 2011; Figures 2 and 3). Although closely linked to cold acclimation, endodormancy is a distinct physiological process that is sensitive to, but does not require, cold or other external factors to be induced (Faust et al., 1995). Endodormancy can be defined as dormancy under conditions that are conducive to growth (Dogramaci et al., 2011). By contrast, bud flush, which is induced after endodormancy is broken and mitotic division reinitiated, relies on a particular regime of cold followed by warm temperatures, the duration and timing of which is cultivar/species specific, and is often correlated with latitude (Saure, 1985; Erez and Couvillon, 1987; Naor et al., 2003; Campoy et al., 2011).

Despite inherent difficulties in working with woody species, research on both temperate gymnosperms and angiosperms, such as apple (M. domestica), apricot (Prunus armeniaca), poplar (Populus trichocarpa), hybrid aspen (Populus tremula x Populus tremuloides), and woody spurge (Euphorbia esula), have revealed many genes and gene networks underlying endodormancy and bud break (Dogramaci et al., 2011; Hisi et al., 2011; Karberg et al., 2011; reviewed in Campoy and Egea, 2011; Figure 3). Available data suggest a complex interplay between the circadian clock and ABA (autonomous), gibberellic acid, photoperiod, and temperature pathways (reviewed in Campoy and Egea, 2011). In species such as poplar and grape (Vitis vinifera), photoperiod and temperature appear to be major determinants of the timing of bud set (defined as bud formation and growth cessation) and endodormancy (Howe et al., 2003; Rohde et al., 2011). By contrast, species such as Pinus contorta that can become endormant as early as late summer use alternative cues such as drought and/or node number (Chaine et al., 2001; Howe et al., 2003). The endodormancy model presented below takes into account the former; future work is required to determine the genetic basis for summer onset endodormancy.

**GENETIC MODEL FOR BUD SET AND ENDODORMANCY**

Although not all aspects of autumn endodormancy have been worked out, the most plausible genetic model is that bud set and endodormancy are controlled largely through the differential regulation of FLOWER LOCUS T (FT) by photoperiod and/or temperature (Figure 3). According to research on poplar and A. thaliana, long summer days stabilize the CONSTANS (CO) protein through the action of the light-absorbing protein complex GIGANIA (GI)/FLAVIN KELCH F BOX (FKF1); Sawa et al., 2007; Song et al., 2012). Late in the day, GIGEFE also acts to degrade CYCLING DOF FACTORS (CDFs), which are transcriptional repressors of CO, and CO protein levels are stabilized through the action of another light-absorbing protein PHYTOCHROME A (PHIA; Yanofsky and Kay, 2002; Fornara et al., 2009; Andres and Coupland, 2012). In turn CO up-regulates the major flowering pathway integrator FT, resulting in meristem outgrowth and the development of leaf and branch initials (bud set; Samach et al., 2006). It is postulated that FT-regulated summer growth is mediated by the action of...
AINTEGUMENTLIKE (AIL) genes that are the direct targets of FT. Unlike A. thaliana, AIL genes in poplar and hybrid aspen positively control growth regulators such as D-type cyclins, suggesting that these genes have been recruited to the endodormancy pathway (Karlborg et al., 2011).

In contrast to the summer growth model, the poplar endodormancy model posits that as temperatures become cooler with the onset of autumn, expression of circadian clock genes, such as TIMING OF CAB EXPRESSION (TOC1) and PSEUDO-RESPONSE REGULATORS (PRRs), is repressed so that CO expression is no longer induced (Mas et al., 2003; reviewed in Inamumi, 2010; Figure 3). The ability of temperature to regulate circadian clock gene expression is still being investigated. However, evidence suggests that diurnal hot/cold cycles can replace photoperiod cycles for entrainment of the circadian clock (Salomé and McClung, 2005; Yamashino et al., 2008; Zuther et al., 2012). Furthermore, the reduced day length of autumn means that PHVA is no longer able to repress the expression of dark-regulated genes that reduce the reduced day length of autumn means that PHYA is no longer able to repress the expression of dark-regulated genes that reduce

**GENETIC MODEL FOR ENDODORMANCY RELEASE AND BUD FLUSH**

Endodormancy occurs either in the absence of cold or with intermittent cold, whereas release of endodormancy occurs in response to continuous above-freezing temperatures of the late autumn and winter (Vegis, 1964). As outlined above, levels of the growth activator/floral pathway integrator FT are reduced under short days from autumn onward due to low levels of CO (Joon Seo et al., 2013). However, during chilling conditions of the late autumn and early winter, repression of the FT inhibitor SVP is also reduced, resulting in a potentially moderate increase of FT during winter (Lee et al., 2007; Figure 3). In addition to A. thaliana SVP repression in response to prolonged cold was recently demonstrated for the SVP-like DAM6 genes in Japanese apricot (Prunus mume; Saiki et al., 2011). Moreover, SVP-like genes have been implicated in induction of endodormancy in leafy spurge (Euphorbia esula; Hurvath et al., 2008). Thus, temperature regulation of SVP-like genes could be a common mechanism for endodormancy release during the winter through the negative regulation of FT-like genes.

Rinne et al. (2011) recently suggested a potential complicating factor regarding the involvement of FT in endodormancy release in temperate and boreal trees. During cool autumn temperatures, mobile signals are potentially blocked from entering hybrid aspen shoot apices due to the presence of callus plugs (Rinne et al., 2011). However, during winter freezing temperatures, callus plugs are gradually removed through the activation of gibberellic acid responsive genes that regulate GH17 proteins, the latter being associated with lipid bodies that help to breakdown callus (Rinne et al., 2011). Since FT in A. thaliana is a mobile protein that travels from leaves to shoot apices, the formation of callus plugs is one mechanism that might delay FT signaling in the shoot apex during autumn. An explicit test of this hypothesis will be required to determine whether FT is mobile in hybrid aspen and other
temperate trees. Furthermore, if FT levels do gradually increase in the shoot apex during the winter it will be interesting to determine whether this influences the timing of endodormancy release, bud flush, or both.

**BUD FLUSH**

Endodormancy affects both vegetative and reproductive meristems through the negative regulation of FT. However, since FT is a positive regulator of inflorescence meristem genes, it has been unclear how vegetative meristems maintain their identity during bud flush. As a possible solution to this puzzle, Heu et al. (2011) recently demonstrated that poplar contains two FT paralogs, FT1 and FT2, that are differentially expressed both spatially and temporally in response to temperature (both genes) and daylength (FT2; Figure 3). Whereas expression of FT1 peaks during winter in leaves, shoots, vegetative buds, and reproductive buds, FT2 expression is highest during spring, and is confined to leaves and reproductive buds (Hsu et al., 2011). The sequential action of FT1 and FT2 on axillary meristems in winter and spring, respectively, results in discrete zones of floral growth and vegetative growth along lateral shoots. A similar partitioning of FT-like gene function has been described for the vernalization response of sugar beet (Beta vulgaris; Pin et al., 2010; see later section).

**EVOLUTION OF ENDO DORMANCY**

Like tree habit, endodormancy has multiple independent evolutionary origins, being found in diverse lineages of both gymnosperms and angiosperms (Figure 1). Recent studies in poplar suggest that duplication and diversification of FT-like genes has been important for the periodic growth of vegetative and inflorescence structures along the shoot axis (Hsu et al., 2011). However, it is unclear whether diversification of FT-like genes contributed to the evolution of endodormancy per se. Intriguingly, functional analyses of the closest FT homologs in spruces (Picea sp.) and pines (Pinus sp.) suggest that the positive role of FT in flowering time evolved after the split of gymnosperms and angiosperms (Klintenäs et al., 2012). Constitutive expression of spruce FT-like genes in Arabidopsis results in late flowering phenotypes, suggesting that the gymnosperm FT-like genes repress flowering similar to the A. thaliana FT paralog, TFL1 (Klintenäs et al., 2012). In Norway spruce (Picea abies), PaFTL1 and PaFTL2 are up-regulated under short days and spring conditions, respectively (Gyllenstrand et al., 2007; Asante et al., 2011; Karlgren et al., 2011). Together these studies suggest independent recruitment of FT-like genes in angiosperm and gymnosperm bud set and bud burst. Similar studies in other plants will be required to determine the prevalence of FT-like gene involvement in the evolution of endodormancy. Furthermore, future research is needed to determine the nature of regulatory evolution in the FT gene family.

**VERNALIZATION RESPONSIVENESS**

Vernalization is the process by which an extended period of cold makes plants competent to flower (Chouard, 1960). In other words, vernalization responsive individuals will flower earlier under inductive conditions (long days and warm temperatures) when those conditions are preceded by a prolonged exposure to cold. This allows plants to synchronize flowering with favorable conditions of the spring (Amasino, 2010). Unlike endodormancy, shoot apices of vernalized plants continue to undergo some level of mitotic division, so that vegetative growth is maintained. In addition, vernalization is distinct from seed stratification, the latter being the release of seed dormancy through chilling (reviewed in Finch-Savage and Leubner-Metzger, 2006).

Extensive variation for vernalization responsiveness is found within many lineages of angiosperms, and is associated with both latitudinal clines and temperature/precipitation variables (Briggs and Walters, 1997; Stinchcombe et al., 2004; Franks et al., 2007; Samis et al., 2008; Kim et al., 2009; Méndez-Vigo et al., 2011; Figure 1). Thus, vernalization responsiveness appears to have evolved multiple times in response to selection by cold seasonal climates, and is hypothesized to have allowed expansion of clades within temperate zones (Preston and Kellogg, 2008; Kim et al., 2009; Edwards and Smith, 2010). For example, at least 3 out of 17 rosids, 5 out of 16 asterids, 1 out of 9 early-diverging eudicot, and 4 out of 10 monocot orders contain species that respond to vernalization. This conservative estimate suggests that vernalization responsiveness is a relatively evolvable trait at higher taxonomic levels. Whether this can be explained by relatively simple changes to pre-existing pathways is discussed below.

**GENETIC MODELS OF VERNALIZATION RESPONSIVENESS**

In Arabidopsis, vernalization responsiveness is mediated through epigenetic silencing of the flowering repressor gene FLC, and possibly its five MADS AFFECTING FLOWERING (MAF) paralogs, by the Plant-HomeoDomain-Polycomb Repressive Complex 2- (PHD-PRC2) complex (Batcliffe et al., 2003; Kim et al., 2009). The PHD-PRC2 complex initiates trimethylation of histone 2 lysine 27 (H3K27me3) and becomes progressively localized to the first intron of FLC during exposure to cold (Shindo et al., 2006; Angel et al., 2011; Strange et al., 2011). Recent evidence suggests that the mechanism for PHD-PRC2 recruitment to FLC is associated with the FLC locus itself (Heo and Sung, 2010). Two non-coding transcripts that initiate from the first intron (COOL ASSISTED INTRONIC NONCODING RNA (COLDAIR)) and 3′-UTR (COOLAIR) of FLC are up-regulated in response to cold, and negatively regulate the transcription of FLC through recruitment of PRC2 (Heo and Sung, 2010; reviewed in Leitwaert et al., 2012). Reduction of FLC transcription in response to vernalization results in the release of FT and SOC1 from negative regulation, permitting the shoot apex to respond to inductive flowering signals (Sealle et al., 2006). Following cold treatment, warm temperatures and long days promote the expression of FT through the photoperiod, temperature-, and age-dependent pathways. This results in an FT-mediated morphological shift in the shoot apex from vegetative to inflorescence identity, via induction of MADS-box genes such as FRUITFULL (FUL) and APEXALAL1 (API), and the eventual production of flowers, fruits (siliques), and seeds (reviewed in Adrian et al., 2009; Amasino, 2010).

Several members of the temperate grass subfamily Pooidae also respond to vernalization. However, since the ancestor of grasses was likely tropical, vernalization responsiveness in posids is inferred to have evolved independently from vernalization
responsiveness in the Brassicaceae (Clayton and Remoive, 1986; Davis and Soreng, 2008; Preston and Kellogg, 2008; Edwards and Smith, 2010). In the closely related crop species wheat and barley (Poaceae), differences in vernalization responsiveness are largely a result of variation at three major loci: VERNALIZATION1 (VRN1), VRN2, and VRN3 (reviewed in Trevaskis et al., 2007a; Distelfeld et al., 2009). However several other genes are implicated in the pathway (Greenup et al., 2011). VRN1 is homologous to the flower development genes APAI, CAUDDLOWER (CAL), and FUL in A. thaliana, and its expression is progressively induced during long durations of cold in response to vernalization-induced changes to chromatin at the VRN1 locus (Oliver et al., 2009; Alonso-Perel et al., 2011). In wheat and barley cultivars that respond to vernalization, VRN1 expression is repressed prior to winter by chromatin modifications mediated by proteins that interact with regulatory sites within the promoter or first intron. Simultaneously, the long day induction of VRN1 is repressed by the zinc-finger CO-like gene VRN2 (Hemming et al., 2009). Independent of VRN1 expression, another MADS-box gene, ODDSOC2, is repressed during exposure to cold, resulting in the loss of transcriptional inhibition of downstream flowering genes (Greenup et al., 2010). Expression of VRN1 is required for long-term repression of ODDSOC2 and VRN2 (Trevaskis et al., 2006; Hemming et al., 2008), ODDSOC2 negatively regulates the flower development gene FLOWERING PROMOTING FACTOR 1 (FPP1; Greenup et al., 2010), and VRN2 negatively regulates the temperate cereal FT ortholog VRN3 above a certain threshold (Yan et al., 2004, 2008).

EVOLUTION OF VERNALIZATION RESPONSIVENESS

Vernalization responsiveness has evolved independently in several plant lineages, presumably in response to climate cooling events over the past 47.5 million years. Comparative genetic studies in a range of different angiosperm species suggest that vernalization responsiveness has evolved primarily through the neo-functionalization of ancient photoperiod pathway genes, including CO-like (i.e., VRN2), FT-like, FUL-like (i.e., grass VRN1), and SOC1-like (i.e., FLC), following their duplication (Figure 4). For example, phylogenetic analyses suggest that the FLC-like gene clade of A. thaliana is restricted to the Brassicaceae (Becker and Theissen, 2003; Ballerini and Kramer, 2011; Figure 4). Furthermore, although FLC/MAP-like genes are found in other core eudicots, gene expression tends to be positively rather than negatively regulated by cold. This is the case for Arabidopsis MAFS, the Texas bluebell (Eustoma grandiflorum, Gentianaceae) EgFLCL, and trifoliate orange (Poncirus trifoliate, Rutaceae) PtiFLC (Zhang et al., 2009; Nakano et al., 2011). In A. thaliana, natural variation in vernalization responsiveness has been linked to variation in the promoter, first exon, and first intron of FLC, and within the positive regulator of FLC, FRIGIDA (FRI; Michaels and Amasino, 1999, 2001; El-Din El-Assal et al., 2001; Werner et al., 2005; Balasubramanian et al., 2006; Angel et al., 2011; Bond et al., 2011; Crouchman et al., 2012; Wollenberg and Amasino, 2012). A similar role has been afforded to the FLC ortholog PERFETUAL FLOWERING 1 (PEP1) in the Brassicaceae species Arabis alpina. However, since Arabis alpina is a perennial species, cold-induced chromatin modification of PEP1 is only transient, being reset every growing season (Wang et al., 2009a).

In sugar beet (Beta vulgaris, Amaranthaceae, Caryophyllales) recruitment of a lineage-specific FT-like gene duplication has been implicated in the independent origin of vernalization responsiveness (Pin et al., 2010; Mutasa-Gottgens et al., 2012). Under warm conditions, the FT homolog BvFT1 represses its paralog BvFT2, resulting in a block to flowering. By contrast, under cold conditions, BvFT1 is down-regulated, causing derepression of BvFT2 and promoting flowering (Pin et al., 2010). It was recently discovered that down-regulation of BvFT1 during winter is due to the repressive action of ROTATING TIME CONTROL 1 (BvBTC1), which is related to the circadian clock FBR genes in A. thaliana (Pin et al., 2012). Moreover, variation in the response of BvBTC1 allelic to vernalization has been linked to growth habit differences in domesticated sugar beet (Pin et al., 2012). Together with the fact that VRN1 and VRN2 are inferred to have evolved somewhere at the base of (Preston and Kellogg, 2006) or within (Yan et al., 2004) the Poaceae, respectively, these data suggest that lineage-specific flowering gene duplications have been important for independent origins of vernalization responsiveness, either through subtle switches from flowering inductors to repressors (e.g., VRN2, FLC, and BvFT1) or more dramatic changes in regulation and downstream targeting (e.g., VRN1 and BvBTC1; Figure 3).

GENETIC LINKS BETWEEN SEASONAL ADAPTATIONS TO COLD

Given the temporal overlap between endodormancy and cold acclimation, an interesting question is whether these two processes are linked at the genetic level. Presently, such links can be tentatively formed by combining data from cold acclimating but not endodormant A. thaliana, and endodormant trees. In the case of A. thaliana, CO is a regulator of both FT and SOCI. Similar to FT, SOCI positively regulates the expression of meristem identity genes, such as FUL and LPP. However, SOCI also negatively regulates the cold responsive CBF genes (See et al., 2009; Figure 3). Thus, although it needs to be explicitly tested in endodormant species, these data suggest a mechanism by which the break of endodormancy can influence the loss of cold acclimation.

Similar genetic associations can also be postulated for cold acclimation and vernalization responsiveness. Recent studies have shown that wheat VRN1 has CBF-binding sites in its promoter, and that VRN1 negatively regulates CBF genes (Alonso-Perel et al., 2011). This suggests a negative feedback loop between cold acclimation and vernalization. However, it remains to be tested whether CBF proteins actually bind to the VRN1 promoter, and if so, whether this interaction is positive or negative. Interestingly, in A. thaliana genetic evidence suggests that CBF proteins positively regulate FLC in the autumn, accentuating the repression of flowering over winter (See et al., 2009; Figures 2 and 3). If this connection also exists in pooid grasses we would predict that CBF proteins positively regulate repressors of flowering such as VRN2 and homologs of SVP. Consistent with this, it has been demonstrated that the barley SVP-like genes Barley MAD51 (BM1, BM10), and Vegetative to Reproductive Transition gene 2 (VRT2), and wheat VRT2 are up-regulated by cold (Trevaskis et al., 2007b; Sutton et al., 2009, but see Kane et al., 2005). Alternatively, CBF proteins could directly repress flowering by negatively regulating VRN1 or VRN3.
CONCLUSIONS AND FUTURE PROSPECTS

Low to freezing temperatures are major determinants of latitudinal and altitudinal ranges of plants (Cavendar-Bares et al., 2003), and less than half of angiosperm plant families are distributed in regions with seasonally low temperatures (Ricklefs and Renner, 1994; Larcher, 2005). In the next 80 years it is predicted that global temperatures will increase by 1.1–6.4 °C, and that there will be an increase in the frequency and/or severity of warm spells during winter months (USGCRP, 2009; National Research Council, 2010). Both these escalating intermittent temperature fluctuations and long-term climate changes have the potential to affect the physiology of cold temperate adapted species that rely on an extended period of cold for timely flowering (Leik et al., 2004; Oﬀred, 2011). However, flowering time will ultimately result from the interaction of different genetic pathways in response to environmental factors such as photoperiod, cold, heat, water-stress, and developmental age (Cook et al., 2012). These interactions are only starting to be worked out.

Contrary to the hypothesis that cold-induced traits are hard to evolve, phylogenetic analyses in combination with past climate and trait data suggest multiple independent origins of cold acclimation, endodormancy, and vernalization responsiveness, at least in angiosperms. Furthermore, although often correlated, cold acclimation/endodormancy/vernalization responsiveness can be uncoupled at the physiological level, potentially allowing increased ﬂexibility in species-speciﬁc responses to seasonal cold. Does this imply parallel evolution of the same ancestral genes and/or pre-adapted genetic pathways?

Available data support the hypothesis that cold-induced traits have evolved multiple times independently through the modulation of the same genetic pathways. This suggests that these pathways are somewhat pre-adapted to providing avoidance of or to tolerance to cold stress. However, the exact genes and proteins that have been recruited to cold adaptive traits differ from clade to clade. Many of the known key regulators of cold-induced physiological traits are members of large gene families that have broadly conserved roles in stress responses (e.g., dehydrin proteins) and/or developmental transitions (e.g., VRN1/FUL-like genes).

In Poaceae, Brassicaceae, and poplar several genes involved in cold acclimation (e.g., CBP/DRE genes and CBF/DRE-containing genes), vernalization responsiveness (CO-like and FLC), and endodormancy (FT-like genes) have evolved from lineage-speciﬁc duplications (Recker and Theissen, 2003; Yan et al., 2004; Sandve et al., 2008; Sandve and Fjellheim, 2010; Figure 4). Loss of vernalization responsiveness has been documented for multiple cultivars of wheat and barley under artiﬁcial selection either through the loss of VRN2, or the loss of cis-acting regulatory elements in VRN1 and VRN3 (Yan et al., 2003, 2004; Fu et al., 2005; Andersen et al., 2006; Szucs et al., 2007; Schwartz et al., 2010; Abouz-Peral et al., 2011). Whether these changes can happen rapidly enough in natural populations to combat human-induced climate change is a hot topic of debate.

Despite an unfolding picture at the broad phylogenetic scale that suggests multiple evolutionary origins of cold adaptive traits (Figure 1), relatively little physiological, developmental, or genomic data are available for understanding the evolutionary lability of seasonal cold adaptations at the family level and below. This is particularly true for species that might have retained cold adaptive traits following secondary shifts to the tropics, thus hampering our understanding of adaptation on relatively short timescales. Nonetheless, exciting recent and ongoing experimental and phylogenomic studies in both tropical and temperate taxa of the Brassicaceae (Brassicals), Poaceae (Poaales), Pinaceae (Pinales), and Phrymaceae (Lamiales) are providing novel insights into the tempo, ancestral selection pressures, and potential constraints related to the evolution of cold acclimation/tolerance, endodormancy, and vernalization responsiveness (e.g., Lin et al., 2005; Preston and Kellogg, 2008; Sandve and Fjellheim, 2010; Méndez-Vigo et al., 2011; Sandve et al., 2011; Friedman and Willis, 2013; Humphreys and Linder, 2013). Successful studies will need to combine physiological observations with ancestral state reconstruction and
ACKNOWLEDGMENTS

We would like to thank Toby Kellogg and three anonymous reviewers for helpful suggestions on an earlier version of the manuscript. This work was funded by a United States Department of Agriculture (USDA) Hatch grant to Jill C. Preston.

REFERENCES

Andreini, L., Viti, R., Bartolini, S., Amasino, R. (2010). Arabidopsis Frontiers in Plant Science | Volume 4 | Article 167 | “fpls-04-00167” — 2013/5/31 — 12:03 — page 12 — #12

genetic/genomic analyses to determine the direction of trait shifts, and any prerequisites for their evolution. Finally, population-level studies will continue to provide insight into evolution- related responses to more subtle (both temporal and quantitative) seasonal variation in temperature across species’ ranges.

seasonal variation in temperature across species’ ranges. 

and the role in the development and evolution of flowering traits. Mol. 

Physiol. 39, 464–489. doi: 10.1016/S0026- 

30120005000018 

Bárcena, A., Zamkic, J., Jezoprat, M., Fabian, M., and Udrea, P. (2012). Dormancy development during cold hardening of in vitro cultured 

Medicago sativa: plants in relation to their frost resistance and cryotolerance. Trees Struct. Funct. 26, 1181–1192. doi: 10.1007/s12225-011- 1192v1 

Borchi, N., Bouché, N., Schild, S., Stahl, W., Bouchet, D., and Fromm, H. (2012). A novel family of calcineurin-binding transcription activators in multialbulin organisms. J. Biol. Chem. 287, 14851–14861. doi: 10.1074/jbc.M112072200 

Carvalho, M. A., Pinto, M. T., Jendick, E., Zhou, C., Dambly, C., Shi, B. H., et al. (2011). A comparison of the low temperature transcriptional and 

CBF regulons of three plant species that differ in freezing tolerance. Solanum commersonii, Solanum tuberosum, and Anthoxanthum odoratum. J. Exp. Bot. 62, 3807–3818. doi: 10.1093/jxb/err295 

Cattafesta, L. J., Molina, J., and Salina, J. (2011). Integration of low 

temperature and light signaling during cold acclimation response in Anthoxanthum odoratum. Plant Physiol. 159, 160–168. doi: 10.1104/pp.110.160569 

Campbell, R. K., and Sugano, A. I. (1979). Genealogy of bud-burst pheno
dology in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079 

Campion, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011 

Campion, J. A., Baltz, D., Cook, N. G., Allerd

man, L., and Eppig, J. A. (2011). High temperatures and time to budbreak in low chill apricot ‘Palsteyn’. Towards a better understanding of chill and heat requirements for 

fruit set. HortScience 45, 869–875. doi: 10.21273/HORTSCI.45.7.869 

Carvalho, M. A., Pinto, M. T., Jendick, E., Zhou, C., Dambly, C., Shi, B. H., et al. (2011). A comparison of the low temperature transcriptional and 

CBF regulons of three plant species that differ in freezing tolerance. Solanum commersonii, Solanum tuberosum, and Anthoxanthum odoratum. J. Exp. Bot. 62, 3807–3818. doi: 10.1093/jxb/err295 

Cattafesta, L. J., Molina, J., and Salina, J. (2011). Integration of low 

temperature and light signaling during cold acclimation response in Anthoxanthum odoratum. Plant Physiol. 159, 160–168. doi: 10.1104/pp.110.160569 

Campbell, R. K., and Sugano, A. I. (1979). Genealogy of bud-burst pheno
dology in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079 

Campyon, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011 

Campion, J. A., Baltz, D., Cook, N. G., Allerd

man, L., and Eppig, J. A. (2011). High temperatures and time to budbreak in low chill apricot ‘Palsteyn’. Towards a better understanding of chill and heat requirements for 

fruit set. HortScience 45, 869–875. doi: 10.21273/HORTSCI.45.7.869 

Carvalho, M. A., Pinto, M. T., Jendick, E., Zhou, C., Dambly, C., Shi, B. H., et al. (2011). A comparison of the low temperature transcriptional and 

CBF regulons of three plant species that differ in freezing tolerance. Solanum commersonii, Solanum tuberosum, and Anthoxanthum odoratum. J. Exp. Bot. 62, 3807–3818. doi: 10.1093/jxb/err295 

Cattafesta, L. J., Molina, J., and Salina, J. (2011). Integration of low 

temperature and light signaling during cold acclimation response in Anthoxanthum odoratum. Plant Physiol. 159, 160–168. doi: 10.1104/pp.110.160569 

Campyon, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011 

Campion, J. A., Baltz, D., Cook, N. G., Allerd
manship in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079 

Campyon, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011

Preston and SandvePlant adaptations to winter

Phenology in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079

Campyon, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011

Campyon, J. A., Baltz, D., Cook, N. G., Allerd
manship in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079

Campyon, J. A., and Eppig, D. B. R. (2011). Dormancy in temperate fruit trees in a global warming context. Sci. Hort. (Amsterdam) 130, 577–572. doi: 10.1016/j.scienta.2011.07.011 

Campion, J. A., Baltz, D., Cook, N. G., Allerd
manship in Douglas-fir: response to 

flashing temperature and chilling. Bot. Gaz. 140, 223–231. doi: 10.1086/337079
Preston and Sandve Plant adaptations to winter

Coustham, V., Li, P., Strange, A., Lis-Clayton, W. D., and Renvoize, S. A. (2001). Temperature to minimum freezing temperatures: a winter sensitivity of leaves and xylem balance in response to low temperature. New Phytol. 153, 9000–9005. doi: 10.1043/0028-6467(93)90242-3

Li, H., Goto, S., and Hagiwara, S. (2007). Differing vernalization requirements in provenances of Pinus sylvestris. Can. J. For. Res. 37, 191–208. doi: 10.1139/x06-207

Chen, I., Aitken, S. N., and Yin, C. C. (2012). Roles for ABA and environmental control of dormancy. Annu. Rev. Plant Biol. 63, 109–133. doi: 10.1146/annurev-arplant-042811-105358

van den Ende, E. J., and Smith, S. A. (2005). Grass architecture: its relations to dormancy. Plant Physiol. 137, 961–966. doi: 10.1104/pp.104.055914

van der Niet, A., van der Windt, A. E., and van der Schoot, V. C. (2011). AtNUP160, is critical for RNA export through the nucleoporin, Nup107, and required for plant tolerance to cold stress. Mol. Cell. Biol. 31, 263–275. doi: 10.1128/MCB.01048-11

Erez, A., and Couvillon, G. A. (1987). Expression of a plastid and nuclear genome, overlapping molecular networks impacting endodormancy maintenance in leafy spurge crown buds. J. Plant Res. 100, 213–218. doi: 10.1007/BF00041924

Green, A. J., Trewavas, A., and Cameron, A. C. (2007). Different regulation of freezing tolerance via distinct regulatory pathways in wheat. Plant Physiol. 144, 2185–2197. doi: 10.1104/pp.107.108388

Domínguez, T., Hernández, M. I., Ponnampalam, J. C., Jiménez, P., Martínez-Rima, J. M., Sato, C., et al. (2010). Increasing omega-3 fatty acid expression in tomato results in altered aroma profile and enhanced resistance to cold stress. Plant Physiol. 153, 455–463. doi: 10.1104/pp.110.154815

Dong, C. H., Hu, X., Yang, W., Zhang, X., Kim, Y. S., Lee, B. H., et al. (2006). A putative Arabidopsis mackinonii, ANP205, is critical for RNA export and required for plant tolerance to cold stress. Mol. Gen. Genet. 276, 953–964. doi: 10.1007/s00438-005-0381-8

Doughty, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. Proc. Natl. Acad. Sci. U.S.A. 105, 15489–15494. doi: 10.1073/pnas.0806210105

Doust, A. N. (2007). Grass architecture: genetic and environmental control of branching. Curr. Opin. Plant Biol. 10, 1–5. doi: 10.1016/j.pbi.2006.11.013

Dow, S., Small, W. S., Han, L., Worrall, D., Smallwood, M., and Rodeb, D. (2010). Regulation and characterization of oat winter acclimation reveal a novel role of CRY2. Nat. Genet. 42, 435–440. doi: 10.1038/ng.597

Erez, A., and Couvillon, G. A. (1987). Characterization of the influence of light and temperature on endodormancy in Mimulus guttatus. J. Am. Soc. Hortic. Sci. 112, 677–680.
acclination in Arabidopsis thaliana. Plant Physiol. 87, 745–750. doi: 10.1104/pp.5.7.745

Gould, S. J., and Vrba, E. S. (1982). Adaptations in a mating term in the science of form. Paleobiology. 8, 4–15.

Gray, G. B., Chauvin, L. P., Sarihan, F., and Hutter, N. P. A. (1997). Cold acclimation and freezing tolerance: a complex interaction of light and temperature. Plant Physiol. 114, 467–474.

Groump, A. G., Sasi, S., Oliver, S. N., Tabel, M. J., Dennis, E. S., Humming, M. N., et al. (2010). ODDO2 is a MADS-box floral repressor that is down-regulated by vernalization in temperate cereals. Plant Physiol. 153, 1082–1075. doi: 10.1104/pp.109.152488

Groump, A. G., Sasi, S., Oliver, S. N., Wallace, S. A., Miller, A. A., and Terasaka, B. (2011). Transcription analyses of the vernalization response in barley (Hordeum vulgare) seedlings. PLoS ONE 6, e17900. doi: 10.1371/journal.pone.0017900

Grillini, M., and Ishii, M. W. F. (2004). Antioxidant proteins in overwintering plants: a task of two activities. Trends Plant Sci. 9, 399–405. doi: 10.1016/j.tplants.2004.05.007

Guo, L., Jiazhong, R., and Weiler, C. (2013). Plant cold acclimation: the role of abscisic acid. J. Plant Physiol. 169, 495–502. doi: 10.1016/j.jplph.2012.07.001

Ha, J. B., and Suh, B. (2016). Vernalization-mediated epigenetic silencing by a long noncoding ncRNA. Science 353, 76–79. doi: 10.1126/science.aac7940

Hetherington, S. J., Lee, Z., and Smilde, R. M. (1999). Photoinhibition at low temperature in chilling-sensitive and resistant plants. Plant Physiol. 90, 1619–1625. doi: 10.1104/pp.90.4.1609

Hosono, H., Hanafey, M. K., Tingey, S. V., and Amasino, R. M. (2009). Cold-induced transcriptional repression of the barley (Hordeum vulgare L.) FLOWERING LOCUS T duplication coordinates reproductive and vegetative growth in perennial poplar. Proc. Natl. Acad. Sci. U.S.A. 106, 10796–10771. doi: 10.1073/pnas.0904893

Humphries, A. M., and Lindner, H. P. (2013). Evidence for recent evolution of cold tolerance in grasses suggests current distribution is not limited by low temperature. New Phytol. 198, 1243–1273. doi: 10.1111/nph.12244

Hisano, H., Kusunoki, G., Hurry, V., Kredl, M., Fuk, S., and Griffith, M. (1993). Phenothrin/phototransduction and low temperature acclimation in cold tolerant plants. Photosynth. Res. 37, 19–39. doi: 10.1007/BF00218486

Itoh, W., and Zuo, D., and Dean, C. (2012). Flowering time control: another window to the connection between abiotic stress and photomorphogenesis. Trends Genet. 28, 445–452. doi: 10.1016/j.tig.2012.08.002

Imamura, T. (2010). Arabidopsis circadian clock and photoperiodism: the key to flower induction and flowering time. Curr. Opin. Plant Biol. 13, 43–48. doi: 10.1016/j.pbi.2009.09.007

Iino, L. C., Petersen, W. F., and Lobmann, K. (2006). Cold frost-tolerant plants as a possible cause of mass extinctions at the Eocene/Oligocene boundary. Nat Rev. 35, 877–890. doi: 10.1038/nrd30044

Jiang, S., Marchal, V., Penuelas, K. C., Wenzel, S., Sophie, W., and Wang, X. W., et al. (2008). Arabidopsis COPII shapes the temporal pattern of CO2 accumulation conferring a photosynthetic flowering response. EMBO J. 27, 1277–1288. doi: 10.1038/emboj.2008.68

Jankun, A., April, A., Zamecnik, J., Cattarel, L., and Owend, J. (2011). Transcriptional responses of winter barley to cold indicate nucleosome repositioning and potential regulatory genes involved in seasonal dormancy transitions in late flowering (bluegrass subtaxon L). BMC Genom. 9538. doi: 10.1186/1471-2164-12-120

Khan, R. M., and Amasino, R. M. (2007). A Norway spruce FLOWERODDSOC2 is a MADS-box floral versatile proteins for complex mechanisms of cold acclimation in temperate cereals. Plant Physiol. 144, 248–257. doi: 10.1104/pp.107.095802

Krol, M., Falk, S., and Griffith, M. K. C., Wenkel, S., Soppe, W., and Chen, T. H. H. (2003). From Arabidopsis to Populus: genotype to phenotype: unraveling the complexities of cold adaptation in grasses. Trends Plant Sci. 8, 536. doi: 10.1016/s1360-1385(03)00374-3

Kawamura, M., Nishita, E., Ohara, H., Okahara, K., and Matsu, H. (2002). Changes in the intensity of bud dormancy and internal composition of current shoot in Fagus. Jpn. Soc. Hortic. Sci. 71, 177–182. doi: 10.2558/jshs.71.177

Kawamura, H. C., and Guenot, I. (2010). The influence of vernalization time and day length on flower induction in radish (Raphanus sativus L.) under controlled and field conditions. J. Jpn. Agric. Res. 40, 401–406. doi: 10.3956/jjr.0901-14

Khakhlovskaya, M., Hichens, R., Petersen, J., Wu, H., and Li, Y. (2006). Enhanced cold tolerance in transgenic tobacco expressing a dimerin s=5 fatty acid desaturase gene under the control of a cold-inducible promoter. Planta 225, 1090–1100. doi: 10.1007/s00425-004-0314-5

Kim, D. H., Drolet, M. R., Sung, S., and Amasino, R. M. (2009). Vernalization: winter and the timing of flowering in plants. Annu. Rev. Cell Dev. Biol. 25, 277–299. doi: 10.1146/annurev.cellbio.24.092207.105759

King, R. W., and Heide, O. M. (2005). Seasonal flowering and evolution: the heritage from Charles Darwin. Funct. Plant Biol. 32, 1027–1036. doi: 10.1071/FB040170

Kusunoki, G., Hurry, V., Kredl, M., Fuk, S., and Griffith, M. (1992). The influence of vernalization time to think about location. Curr. Opin. Plant Biol. 13, 43–48. doi: 10.1016/j.pbi.2009.09.007

King, R. W., and Heide, O. M. (2005). Seasonal flowering and evolution: the heritage from Charles Darwin. Funct. Plant Biol. 32, 1027–1036. doi: 10.1071/FB040170
Kubota, S., Momose, H., Yoneda, K., Krug, H. (1991). Investigations of Karlsson, G. H. (1988). Photoinhibition of light acclimation. J. Exp. Bot. 42, 1295–1302.

Kubota, S., Momose, H., Yoneda, K., Krug, H. (1991). Investigations of light acclimation. J. Exp. Bot. 42, 1295–1302.

Kramer, P. J., and Kozlowski, T. T. (1980). Investigations of light acclimation. J. Exp. Bot. 42, 1295–1302.

Kobayashi, F., Takumi, S., and Larcher, W. (2005). Climatic constraints for production and forcing. J. Exp. Bot. 42, 1295–1302.

Kobayashi, F., Takumi, S., and Larcher, W. (2005). Climatic constraints for production and forcing. J. Exp. Bot. 42, 1295–1302.

Kobayashi, F., Takumi, S., and Larcher, W. (2005). Climatic constraints for production and forcing. J. Exp. Bot. 42, 1295–1302.

Kobayashi, F., Takumi, S., and Larcher, W. (2005). Climatic constraints for production and forcing. J. Exp. Bot. 42, 1295–1302.
Natural variation of flowering time and vernalization responsiveness in Brassicaceae areal plants. Front Ecol Rev 3, 36–46. doi: 10.1017/S1356164395000060

Sakurai, H., Furukawa, H., Fukuda, K., and Ohashi, H. (2005). The transcription factor FLC confers flowering time in Arabidopsis. Plant Physiol. 138, 820–827. doi: 10.1104/pp.105.062543

Shinozaki, K. (2000). Molecular mechanisms of transcriptional regulation in the low temperature transcriptional program in Arabidopsis. Mol. Genet. Genomics 263, 549–554. doi: 10.1007/s00438-000-0533-z

Shinozaki, K., and Yamaguchi-Sato, S. (2007). The transcription factor FLC confers flowering time in Arabidopsis. Proc. Natl. Acad. Sci. U.S.A. 95, 14570–14575. doi: 10.1073/pnas.95.24.14570

Shinozaki, K., and Yamaguchi-Sato, S. (2008). How do environmental stresses affect flowering time in Arabidopsis thaliana? Curr. Opin. Plant Biol. 11, 71–79. doi: 10.1016/j.pplb.2007.09.009

Simm, S. N., and Lavender, D. P. (1994). Seasonal patterns of environmental regulation of free hardness in seeds of seedlings of Thuya plicata, Chamaecyparis nootkatensis, and Pinus contorta. Can. J. Bot. 72, 509–516. doi: 10.1139/b94-040

Streit, N. A., and Schulz, M. (2005). Regulation of the maize frigida gene by the maize frigida gene. Plant Physiol. 138, 641–648. doi: 10.1104/pp.104.056026

Streuter, B., Adamec, J., Sunmi, M., and Donoghue, M. J. (2011). Understanding angiosperm diversification using large and small phylogenies. Annu. Rev. Ecol. Evol. Syst. 42, 343–368. doi: 10.1146/annurev-ecolsys-012010-112621

Tavener, R., Badger, M., Hemming, M. N., Poulsen, W. J., Dennis, E. S., and Sheldon, C. (2005b). Short negative flower-size-like MADS-box genes inhibit floral meristem identity in barley. Plant Physiol. 137, 225–235. doi: 10.1104/pp.104.059865

Teravenko, B., Hemming, M. N., Poulsen, W. J., and Dennis, E. S. (2006). HvVRN2B responds to daylength, whereas HvVRN1 is regulated by vernalization and developmental status. Plant Physiol. 141, 1397–1405. doi: 10.1104/pp.105.075846

Thomas, M., Joseph, R. A., and Steponkus, P. L. (1995). Cold acclim- atization of Arabidopsis thaliana (effect on plasma membrane lipid compos- ition and freeze-induced lesions). Plant Physiol. 109, 25–30.

Urrutia, M. E., Duman, J. G., and Knight, C. A. (1992). Plant ther- mal hysteresis proteins. Biochem. Biophys. Acta 1121, 199–206. doi: 10.1016/0167-4838(92)91355-H

USCRBP. (2009). Global Climate Change Impacts in the United States. New York: Cambridge University Press.

Vaknin, Y., and Van den Ende, W. (2008). Plant fructans in stress envi- ronments: emerging concepts and future prospects. J. Exp. Bot. 59, 2905–2916. doi: 10.1093/jxb/erm164

Van Buulke, H. A., and Thomas, M. F. (2006). Arabidopsis translation factors regulate cold acclimation. Plant Physiol. 142, 72–80. doi: 10.1104/pp.105.072643

Vogel, A. (1964). Dormancy in higher plants. Annu. Rev. Plant Physiol. 15, 185–224. doi: 10.1146/annurev.pp.15.060164.001155

Vogel, J. T., Zarka, D. G., Buskirk, H. A., Foster, S. G., and Thomashow, M. F. (2005). Role of the CBF2 and ZAT12 transcription factors in conferring the low temperature tran- scriptional programme of Arabidopsis. Plant J. 41, 105–115. doi: 10.1111/j.1365-313X.2004.02088.x

Wang, R., Faronova, S., Vincent, C., Jordan, A., Schels, H., and Tuch, F. (2006a). PEP1 regulates peroxidase activity in Arabidopsis aliphatic. Nat. Genet. 38, 423–429. doi: 10.1038/nature03798

Wang, H., Moore, M. J., Solis, P. S., Bell, C. D., Brockington, S. F., Alexan- drova, R. (2008b). Rolda radiation and the rapid rise of angiosperm- dominated forests. Proc. Natl. Acad. Sci. U.S.A. 105, 3835–3838. doi: 10.1073/pnas.0801737105

Wells, C. O., and Donoghue, M. J. (2005). Phylogenetic tree assem- bly for angiosperm phylogeny. Mol. Ecol. 14, 3787–3805.
Plant adaptations to winter

Werner, J. D., Borevitz, J. O., Worrall, D., Elias, L., Ashford, D., Smillie, C. M., and Runkle, E. S. (2012). Determining the flowering requirements of two Agapetes cultivars. Plant Cell 35, 1261–1264.

Wilson, B. C., Sibley, J. L., and Alford, J. R. (2002). Chilling duration affects foliar budbreak of linden cultivars. HortScience 37, 660–662.

Xiong, Y., Ahn, J. H. (2007). Control of flowering time and cold response by a MADS-domain protein in Arabidopsis. Plant Cell Physiol. 48, 1819–1825. doi: 10.1093/pcp/pcm128

Xiong, Y., Fei, S.-Z. (2006). Functional and phylogenetic analysis of a DREB/CBF-like gene in perennial ryegrass (Lolium perenne L.). Planta 224, 878–888. doi: 10.1007/s00425-006-0273-5

Yamamoto, T., Ito, S., Noda, T., Kambhir, A., Nakamura, N., and Minato, T. (2006). Involvement of Arabidopsis clock-associated proteinresponsive regulators in diurnal oscillations of gene expression in the presence of environmental time cues. Plant Cell Physiol. 48, 1819–1825. doi: 10.1093/pcp/pcm128

Yan, L., Li, C., Fei, C.-Z., Arora, R., and Hamaguchi, D. (2010). Ice recrystallization inhibition proteins of perennial ryegrass enhance freezing tolerance. Plant Cell Physiol. 51, 175–184. doi: 10.1093/pcp/pcq205

Zhang, J., Li, Z. M., Mei, L., Yan, L., Loukoianov, A., Blechl, A., Kim, S., Xia, Z., Li, C., and Hu, C. G. (2009). PtFLC homolog from trifoliate orange (Poncirus trifoliata) is regulated by alternative splicing and experiences seasonal fluctuations in expression level. Planta 229, 687–693. doi: 10.1007/s00425-008-0869-x

Zhou, Z., Wang, M.-J., Zhao, X.-T., Hu, J.-J., and Lu, M.-Z. (2009). Changes in freezing tolerance in hybrid poplar caused by up- and down-regulation of PtFAD2 gene expression. Tree Genet. Genomes 9, 959–968. doi: 10.1007/s11295-009-9349-x

Zuther, E., Shulz, E., Childs, L. H., Thomas, E., and Billups, K. (2001). Inheritance of non-obligate vernalization inhibition proteins of perennial ryegrass with NILs segregating for vernalization requirement for flowering time and cold response by a MADS-domain protein in Arabidopsis. Plant Cell Physiol. 42, 1344–1354. doi: 10.1093/pcp/42.9.1344

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 04 February 2013; accepted: 13 May 2013; published online: 05 June 2013.

Citation: Preston JC and Sandve SR (2013) Adaptations to seasonality and the winter freeze. Front. Plant Sci. | 4:267. doi: 10.3389/fpls.2013.00267

The article was submitted to Frontiers in Plant Evolution and Development, a specialty of Frontiers in Plant Science. Copyright © 2013 Preston and Sandve. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in other forums, provided the original authors and source are credited and any copyright notices are retained and any third-party graphics etc. are not subject to any copyright notices concerning any third-party graphics etc.