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Signals Regulating Dormancy in Vegetative Buds

Wun S. Chao* • Michael E. Foley • David P. Horvath • James V. Anderson

Biosciences Research Laboratory, Plant Science Research, 1605 Albrecht Blvd., Fargo, ND 58105-5674, USA

Corresponding author: * **wun.chao@ars.usda.gov**

ABSTRACT

Dormancy in plants involves a temporary suspension of meristem growth, thus insuring bud survival and maintenance of proper shoot system architecture. Dormancy regulation is a complex process involving interactions of various signals through specific and/or overlapping signal transduction pathways. In this review, environmental, physiological, and developmental signals affecting dormancy are discussed. Environmental signals such as temperature and light play crucial roles in regulating development and release of bud dormancy. Physiological signals including phytochrome, phytohormones, and sugar are associated with changes in dormancy status that occur when plants perceive environmental signals. Developmental signals such as flowering and senescence also have an effect on bud dormancy. Currently, many genes and/or gene products are known to be responsive directly or indirectly to these signals. The potential roles for these genes in dormancy progression are discussed.

Keywords: flowering, hormones, phytochrome, senescence, signaling, sugar, temperature
Abbreviations: **ABA**, abscisic acid; **ABI1-3**, ABSCISIC ACID INSENSITIVE 1-3; **CK**, cytokinin; ***DAD1***, *DECREASED APICAL DOMINANCE1*; **IAA**, indole-3-acetic acid; **IPT**, ADENOSINE *PHOSPHATE-ISOPENTENYLTRANSFERASE*; **GA**, gibberellic acid; **MDS**, MAX-dependent signal; ***MAX1-4***, *MORE AXILLARY GROWTH1-4*; **PHYA**, phytochrome A; ***PIN1-4***, *PINOID1-4*; ***RMS1-5***, *RAMOSUS1-5*; **SD**, short day; **SMS**, shoot multiplication signal

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INTRODUCTION

Dormancy helps to protect plants from unfavorable conditions and ensures appropriate architecture under favorable conditions. Dormancy has been described as the temporary suspension of visible growth of any plant structure containing a meristem (Lang *et al*. 1987). In vegetative buds, dormancy is further divided into three categories based on how growth is arrested. Ecodormancy takes place when growth is arrested by external environmental factors. Paradormancy (also known as correlative inhibition) occurs when growth is arrested by physiological factors external to the affected structure. Endodormancy (also known as innate dormancy) takes place when growth is arrested by internal physiological factors. Dormancy in vegetative buds has been studied in annual species like arabidopsis (*Arabidopsis thaliana* L.) and pea (*Pisum satvum* L.) and perennials including tubers of potato (*Solanum tuberosum* L.) and yam (*Dioscorea rotundata*); woody plants such as apple (*Pyrus malus* L.), grape (*Vitis vinifera* cv. 'Perlette'), birch (*Betula pendula*), and poplar/aspen (*Populus* spp.); and weeds such as leafy spurge (*Euphorbia esula* L.).

Signals originating from environmental, physiological, and developmental factors are involved in facilitating the well-defined phases of dormancy. Environmental signals such as temperature and light play crucial roles in regulating induction and release of bud dormancy. Physiological signals including phytochrome, sugar, and phytohormones are associated with direct phenotypic changes that occur when plants perceive environmental signals. Developmental pathways regulating flowering and senescence are receiving considerable attention in dormancy research due to crosstalk between signals affecting these pathways. In this context, under favorable growing conditions, plants perceive

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Invited Review

specific physiological signals from other organs/tissues to inhibit uncontrolled bud growth. Specific environmental signals can bring about endodormancy in anticipation of unfavorable conditions, which is important to maintain growth arrest during the transition between seasons (fall to winter or wet to dry). Paradoxically, extended unfavorable environmental conditions cause a transition from endodormancy to ecodormancy, which is important for bud survival during prolonged unfavorable conditions.

This review provides updated information on how these signals regulate dormancy induction and release. However, the information is undoubtedly linked to model plant systems used to perform the research. For example, in the case of paradormancy where much of the research was performed using pea and arabidopsis, similar signals affect bud outgrowth differently (Beveridge 2006; Dun *et al*. 2006). Since pea and arabidopsis are annuals, the information is only relevant to paradormancy. In contrast, woody perennials such as trees and shrubs can be used to study para-, endo- and ecodormancy in primary and axillary buds. Finally, the herbaceous perennial leafy spurge has been used extensively to study well-defined phases of dormancy in underground adventitious buds (referred to in the literature as crown and root buds).

ENVIRONMENTAL SIGNALS

Temperature and light

Evidence suggests that dormancy induction and release in temperate climates is primarily regulated by cold temperatures and day length. However, the extent that these signals regulate dormancy induction, and the crosstalk between the signaling pathways regulated by these environmental cues appears to be largely species, and sometimes variety dependent. Short day (SD) conditions at normal growing temperatures commonly results in full endodormancy in many northern deciduous perennials including poplar (Howe *et al*. 1995; Jeknić and Chen 1999), birch (Li *et al*. 2004), red osier dogwood (*Cornus stolonifera* Michx) (Smithberg and Weiser 1968), wild grape (*Vitus riparia*) (Wake and Fennell 2000), and orpine (*Sedum telephium*) (Heide 2001), among others. Both cold and SD are required for dormancy induction in domesticated grape (*Vitus* ssp.) (Wake and Fennell 2000), Scotch heather (*Calluna vulgaris* L.) (Kwolek and Woolhouse 1982) and leafy spurge (Anderson *et al*. 2005). Occasionally, temperature alone can also induce dormancy in some species such as willow (*Salix paraplesia*), where it was also demonstrated that ecotypic differences resulted in differential responses to low temperatures (Li *et al*. 2005).

Short day responses require the involvement of phytochrome A (*PHYA*). Experiments done in black cottonwood (*Populus trichocarpa* Torr. & Gray) provided evidence that short pulses of red light during the dark cycle completely inhibited bud dormancy, whereas inhibition of dormancy by red light was reversed by pulses of far-red light in a genotypic dependent manner (Howe *et al*. 1996). Additionally, unlike wild-type, *PHYA* over-expressing aspens (*Populus tremula* × *Populus tremuloides* Michx.) act as though they are in constitutive long day, and do not cease growth, cold harden, nor develop dormant buds under SD conditions (Welling *et al*. 2002). However, *PHYA* over-expressing aspens could cold-harden in response to low temperatures just like wild-type. These results suggest that SD induces cold-hardening via a pathway different from that of low temperature. However, induction of cold-responsive gene expression by low temperatures was greatly enhanced under short day conditions in wild-type plants (Puhakainen *et al*. 2004). This phenomenon might partially be explained by a recent study on cold-regulated promoters in arabidopsis indicating a strong correlation among cold-regulated genes and PHYA binding sites (Benedict *et al*. 2006). These interactions may also explain some of the observed differential responses to low temperature and day length influencing endodormancy in various perennial species (**Fig. 1**).

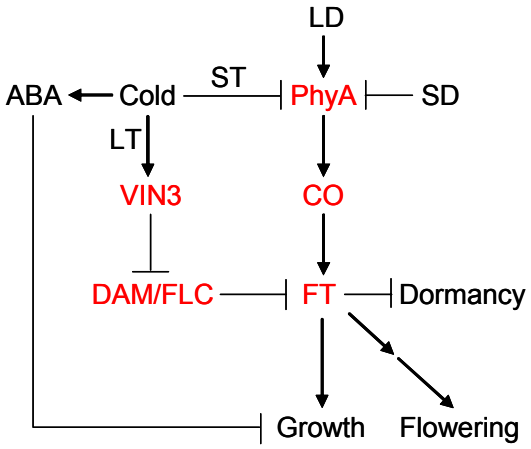

Fig. 1 Interaction of signals impacting dormancy, flowering, and growth. Effects of environmental factors such as long term (LT)- and short term (ST)-cold and long day (LD)- and short day (SD)-length on the expression of proteins such as Phytochrome A (PhyA), VERNALIZATION INSENSITIVE3 (VIN3), CONSTANS (CO), FLOWERING LOCUS T (FT), DORMANCY AFFECTING MADSBOX (DAM), FLOWERING LOCUS C (FLC), and on plant hormone abscisic acid (ABA) are shown. These proteins and hormones in turn impact Growth, Flowering and Dormancy. Arrows indicate stimulation of the signal, gene action, or developmental process, and bars indicate inhibition. Cold (ST) and SD both inhibit PhyA action. Inhibition of PhyA in turn down regulates CO then FT thus inhibiting flowering and growth and stimulating dormancy. Likewise, cold (LT) induces VIN3 and blocks expression of DAM/FLC and thus stimulates FT, flowering, growth, and breaks dormancy.

PHYA (and thus SD) also appears to act through or interact with both ethylene and abscisic acid (ABA) signaling pathways. Several papers have noted that loss of ethylene or ABA responsiveness can inhibit some of the physiological responses associated with dormancy induction. When placed in SD conditions, Ruonala *et al*. (2006) noted that ethylene-insensitive birch ceased growth but did not form primary buds. These buds also did not show the characteristic increase in ABA levels or induction of β-xylosidase commonly associated with SD-induced dormancy. Likewise, Rohde *et al*. (2002) determined that ABA-insensitive poplar produced more leaves and less bud scales than ABA-hypersensitive poplar.

Although day length may not play a significant role during paradormancy, there is some evidence that light-regulated responses can negatively impact bud out-growth following loss of auxin transport. In leafy spurge, buds can be released from paradormancy if both polar auxin transport and photosynthesis are inhibited (Horvath 1998 and 1999). The signal produced by photosynthesizing leaves is suspected to be sugar, possibly acting synergistically with ABA signaling. This hypothesis was strengthened by the studies of Chao *et al*. (2006) demonstrating that sugar, ABA, and gibberellic acid (GA) likely interact to regulate paradormancy of leafy spurge underground adventitious buds.

Cold temperatures are known to enhance initiation of endodormancy. However, extended periods of cold result in release of endodormancy (Horvath *et al*. 2003; Rohde and Bhalerao 2007). Under temperate field conditions, bud growth does not occur immediately following endodormancy release because ecodormancy is maintained by low temperatures. Mechanisms involved in ecodormancy maintenance are unknown, although a role for ABA is suspected (Horvath *et al*. 2003) (**Fig. 1**). Endodormancy release and vernalization processes needed for flowering both require extended periods of low temperature, a commonality first noted by Chouard (1960). Horvath *et al*. (2003) extended this analogy to suggest a role for chromatin remodeling as a possible mechanism to "remember" that dormancy induction occurred, even if the plants are moved to growth-inducing conditions. However, Rohde and Bhalerao (2007)

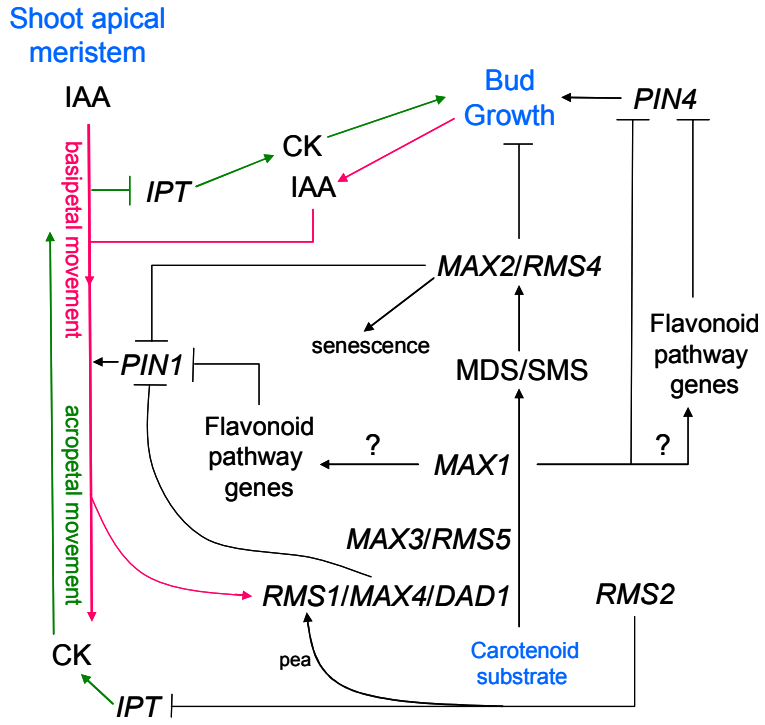

Fig. 2 A model for regulation of axillary bud dormancy and outgrowth. IAA derived from the shoot apex moves basipetally in the stem preventing bud outgrowth, while cytokinin (CK) derived from roots and tissues proximal to buds, promote outgrowth. Auxin (IAA) negatively regulates CK biosynthesis by controlling the expression of *ADENOSINE PHOSPHATE-ISOPENTENYLTRANSFERASE* (*IPT*). Basipetal auxin efflux also enhances expression of *RAMOSUS1* (*RMS1*) and perhaps *MORE AXILLARY GROWTH4* (*MAX4*) preventing bud outgrowth. Auxin efflux carrier PIN-FORMED (PIN) proteins facilitate basipetal IAA movement in the stem and other tissues. *PIN* gene expression is regulated by MAX either directly or indirectly (see?) via flavonoids. A mobile feedback signal in pea derived from *RAMOSUS2* (*RMS2*) expression might also feedback regulate *RMS1*and *IPT*. Lines with arrows indicate promotion or up-regulation; lines with bars represent inhibition or down regulation. Red illustrates polar auxin transport/efflux, green cytokinin action, and black shoot multiplication signal (SMS)/ MAX-dependent signal (MDS) pathway of the shoot and root.

noted that the relative lengths of time needed for vernalization and endodormancy release are often different, and thus the mechanisms may not be identical.

DEVELOPMENTAL SIGNALS

Flowering

Studies have confirmed the link between mechanisms regulating flowering and dormancy in several tree species (reviewed in depth by Rohde and Bhalerao 2007) (**Fig. 1**). Böhlenius *et al*. (2006) demonstrated that the constitutive expression of the floral regulator *FLOWERING LOCUS T* (*FT*) was sufficient to prevent dormancy induction in poplar. In arabidopsis, *FT* is positively regulated by day length through the action of PHYA and CONSTANS (CO) and is negatively regulated by *FLOWERING LOCUS C* (*FLC*) (He and Amasino 2005; Helliwell *et al*. 2006). In addition, a putative *FLC* orthologue identified in poplar (Chen and Coleman 2006) is down-regulated following endodormancy release. There is also evidence in several perennial species that alternative splicing may play a role in the action of this gene (and other *FLC*-like genes) in response to specific environmental conditions involved in endodormancy release (Chen and Coleman 2006; Horvath unpublished; Bielenberg pers. comm.). Another finding that strongly implicates *FLC*-like genes in dormancy regulation is that the *EVERGROWING* mutation in peach, which prevents trees from entering endodormancy in response to SD, is due to deletion of a locus containing a tandem repeat of *FLC*-like genes (Bielenberg *et al*. 2004; Li *et al*. 2006). Several MADS-box transcription factors of the SHORT VEGETATIVE PHASE (SVP) family are preferentially up-regulated upon dormancy induction in leafy spurge (Horvath unpublished observations) and down regulated upon dormancy release in raspberry (*Rubus idaeus* L.) (Mazzitelli *et al*. 2007). SVP MADS-box transcription factors are known to be regulated by vernalization and have an impact on flowering time in arabidopsis (Michaels et al. 2003).

Senescence

In temperate regions of the world, well-defined phases of dormancy are required to ensure survival during periods of stress that would otherwise result in death. For example, many plants transition from active summer growth into a period of seasonal dormancy induced by various environmental signals (Horvath *et al*. 2003; Anderson *et al*. 2005; Volaire and Norton 2006). This transition can involve senescence and induction of endo- or ecodormancy in meristematic tissues such as primary, axillary, and adventitious buds required for resumption of growth (Fedoroff 2002; Horvath *et al*. 2003; Anderson *et al*. 2005; Volaire and Norton 2006). The environmental signals required for the onset of senescence generally involve light, drought, and/or temperature extremes, suggesting that changes in phytohormones and phytochrome play important signaling roles (Gribic and Bleecker 1995; Beveridge 2000; Anderson *et al*. 2001; Woo *et al*. 2001; Fedoroff 2002; Stirnberg *et al*. 2002; Horvath *et al*. 2003; Gibson 2005; Snowden *et al*. 2005). Furthermore, these environmental and physiological signals likely affect the C:N ratio, which has also been implicated in signaling the onset of senescence (Gibson 2005).

Biochemical and molecular evidence implicates the ubiquitin pathway in plant senescence, which is thought to involve bulk protein degradation to facilitate nutrient recycling (Belknap and Garbarino 1996). MORE AXILLARY GROWTH (MAX)2/ORESARA (ORE)9 is involved in ubiquitin-mediated proteolysis and is a common link in the response to phytohormone-induced leaf senescence and bud outgrowth (Woo *et al*. 2001; Stirnberg *et al*. 2002) (**Fig. 2**). Ubiquitin-mediated proteolysis of Aux/IAA proteins (short lived transcriptional repressors) has been reported to regulate auxin response (Gray 2004). Indeed, a member of the *Seven In Absentia* (*SINA*) family of ubiquitin ligases, implicated in auxin signaling, is upregulated during cambial endodormancy in poplar (Schrader *et al*. 2004). In addition, changes in auxin signaling and transport affecting cambial endodormancy were also linked to the down-regulated expression of *pin-formed1* (*PIN1*) and *PIN2* efflux carriers (Schrader *et al*. 2004). Since these genes affect basipetal polar auxin transport (**Fig. 2**), these data suggest that auxin transport may play a signaling role in inducing endodormancy. Likewise, a *dormancy-associated auxin-repressed* (*DAAR*) gene in underground adventitious buds of leafy spurge was progressively upregulated during fall senescence of shoots, suggesting that a decrease in polar auxin transport could play a role in signaling the transition from para- to endodormancy (Anderson *et al*. 2005).

PHYSIOLOGICAL SIGNALS

Sugar

Sugars are known to act as signaling molecules that can regulate gene expression during changes in plant development (Koch 1996; Jang 1997; Sheen *et al*. 1999; Ho 2001; Gibson 2005). Pathways responsive to sugar are also known to exhibit cross-talk with numerous other signaling pathways, including those responsive to phytohormones and light (Gibson 2005). Sugar signaling is important for maintaining paradormacy, likely affecting cell cycle progression at the G1/S phase (Anderson *et al*. 2001; Horvath *et al*. 2002; Arora *et al*. 2003; Horvath *et al*. 2003), and is also thought to be involved during the transition of vegetative buds from paradormancy to endodormancy (Arora *et al*. 2003; Anderson *et al*. 2005; Chao *et al*. 2006).

The effects of sugar signaling in regulating well-defined phases of vegetative bud dormancy has been extensively studied using the model perennial weed, leafy spurge. Sugars from leaves of leafy spurge have been linked to suppression of underground adventitious bud growth during paradormancy (Horvath 1999), and further research has shown that glucose or sucrose can inhibit root bud growth in a mechanism reversed by GA (Horvath *et al*. 2002; Chao *et al*. 2006). Shoot removal prior to senescence causes a rapid degradation of starch and a decline in sucrose, concurrent with the transition from paradormancy to active shoot growth (Horvath *et al*. 2002; Chao *et al*. 2006). In contrast, during fall senescence, conversion of starch to sucrose occurs in leafy spurge underground adventitious buds, which is also paralleled by a transition from paradormancy to endodormancy (Anderson *et al*. 2005). Additionally, in poplar, genes involved in starch degradation were upregulated in the cambial meristems during endodormancy (Schrader *et al*. 2004). Based on these and other findings, it is proposed that sugars play an important role in regulating vegetative bud dormancy through cross-talk with phytohormones (Anderson *et al*. 2001; Horvath *et al*. 2003; Anderson *et al*. 2005). Specifically, sugars are antagonistic to GA perception and likely play a role in signaling pathways required for inducing endo- and ecodormancy via enhanced ABA perception.

Abscisic acid

The plant hormone ABA is a C_{15} sesquiterpenoid derived from cleavage of carotenoids in plastids followed by subsequent conversion steps in the plastid and cytosol (Nambara and Marion-Poll 2005). It is involved in stress responses, abscission, seed dormancy and germination, and vegetative growth, including arrested development or dormancy of vegetative buds (El-Antably *et al*. 1967; Cline and Choonseok 2006). Research with axillary buds of potato tubers provides evidence that ABA is required for initiation and maintenance of endodormancy (Suttle and Hultstrand 1994). Expression analysis of genes involved in the biosynthesis (*9-cis-epoxycarotenoid dioxygenase*; *StNCED*) and catabolism (*cytochrome P450*; *StCYP707A*) of ABA in tubers suggest maintenance of ABA is a balance between biosynthesis and catabolism, with catabolism being favored as dormancy ends (Destefano-Beltrán *et al*. 2006). Other investigations have revealed that ethylene may lead to increased ABA and prolonged endodormancy (Suttle 1998; Korableva *et al*. 2002). Likewise, ethylene insensitive mutants of poplar did not accumulate ABA in response to SD as does wild-type (Rounala *et al*. 2006). Based on these observations, it is likely that ethylene is required for ABA accumulation. ABA is also involved in dormancy induction in other plants with underground vegetative buds. For example, increased ABA levels are correlated with induction of summer dormancy by long days in bulbous bluegrass (*Poa bulbosa*) (Ofir and Kigel 1998).

Temperate zone woody plants like birch and poplar have annual cycles that tightly regulate bud growth and endodormancy in relation to environmental signals. Induction of apical and lateral bud endodormancy in birch under short day conditions correlates with increased levels of ABA (Rinne *et al*. 1994), and the increased levels preceded endodormancy development (Li *et al*. 2003a). Growth responses of birch to ABA are ecotype and stage of growth dependent, with northern ecotypes being more responsive to exogenously applied ABA than southern ecotypes (Li *et al*. 2003b). In contrast with endodormancy development, release of bud endodormancy by chilling was not correlated with ABA levels in buds (Rinne *et al*. 1997). These results indicate that ABA plays a role in induction but not release of bud endodormancy.

ABA concentrations in primary buds of poplar increased many fold after 24 to 27 days in short day conditions (Rohde *et al*. 2002). Expression of poplar *ABSCISIC ACID-INSENSITIVE3* (*PtABI3*) in primary buds coincides with increased ABA in autumn. It is thought that PtABI3 acts with ABA by regulating the growth and differentiation of embryonic leaves inside the bud in preparation for endodormancy. Expression of *ABSCISIC ACID-INSENSITIVE1* (*PtABI1*) in buds coincides with that of *PtABI3* at the time of growth arrest (Rohde *et al*. 2002). *PtABI1* maps to an interval in the poplar genome containing a bud flush quantitative trait loci (QTL) (Frewen *et al*. 2000), but it is not know if it represents the underlying gene for this QTL. ABI3 mediates the regulation of ABA-responsive genes in seeds and the shoot apex of arabidopsis, while ABI1 is a negative regulator of ABA signal transduction in seeds. Thus, similarities may exist between some aspects of seed and bud dormancy as they relate to ABA.

Hypotheses to explain the action of auxin on bud paradormancy have invoked ABA as a secondary inhibitor which acts by moving into the bud (Shimizu-Sato and Mori 2001). The auxin response of lateral buds of wild-type and *abi1-1* mutants in arabidopsis were similar, providing evidence that ABA is not acting as a secondary messenger in auxin-mediated inhibition of bud outgrowth (Chatfield *et al*. 2000). Apparently, ABA has an independent role in regulating bud growth and development.

Gibberellic acid

Gibberellic acid alone or in conjunction with other hormones controls numerous aspects of plant growth and development (Fleet and Sun 2005). GA-response pathways involve the feedback regulation of GA biosynthesis. DELLA proteins are thought to play important roles for normal GA response through negative regulation of GA signaling (Fleet and Sun 2005; Gomi and Matsuoka 2003). A downstream component of the GA response is the GA-inducible MYB transcription factor (GAMYB), an activator of α-amylase expression (Fleet and Sun 2005). Our knowledge on GA's role in regulating the induction and release of bud dormancy is rudimentary, despite extensive research on plant responses to GA (Razem *et al*. 2006). In general, GA is involved in two major regulatory roles during dormancy: 1) SD-induced growth cessation in trees and 2) vegetative bud growth following dormancy release.

SD-induced growth cessation in trees

Trees cease growth and set buds in autumn in response to SD in temperate regions. Many lines of research indicate that SD inhibits the biosynthesis of GA before growth cessation occurs. Olsen *et al*. (1995a) found that the amount of active GA_1 and GA_{20} decreased dramatically in young leaves and stem tissue of bay willow (*Salix pentandra*) seedlings after 2 days of SD exposure. They also found that after 5 days of SD exposure, there was a 50% decrease in the levels of GA_1 in the shoot tip (5-20 mm below apex), which preceded cessation of shoot elongation (Olsen *et al*. 1995b). Application of GA_1 induced shoot elongation under SD, mimicking long day-induced bud growth (Junttila and Jensen 1988). In addition, long day-induced bud break and

growth initiation in bay willow is associated with a rapid transient increase in GA_1 levels in shoot tip (Olsen *et al*. 1997a).

Over-expression of oat *PHYA* in hybrid aspen (*Populus tremula* × *tremuloides*) changed its photoperiodic response such that GA was no longer responsive to SD exposure, suggesting that GAs function downstream of phytochrome in the signaling pathway (Olsen *et al*. 1997b). Although bud set and cold hardiness can be obtained under long day-length conditions in aspen when exposed to low temperature and paclobutrazol, a GA biosynthesis inhibitor, such treatment was unable to induce dormancy (Mølmann *et al*. 2005). These data were taken to suggest separate signaling pathways for bud set/cold acclimation and development of dormancy in trees.

Vegetative bud growth following dormancy release

The exogenous application of GAs released potato tuber endodormancy (Brian *et al*. 1955; Rappaport *et al*. 1958). However, endogenous GAs may not regulate the onset of tuber dormancy directly (Suttle 2004), since the endogenous contents of GA_1, GA_{19}, and GA_{20} were similar in tubers exiting dormancy and in those under deep dormancy. Dramatic increases in GA were only observed after sprout growth initiation. Moreover, the pattern of dormancy progression in potato tubers of a wild-type and dwarf mutant was near-identical at all stages of dormancy, despite the absence of detectable GA_1 levels in the mutant. Additionally, pretreatment of underground adventitious buds of intact leafy spurge plants with paclobutrazol inhibited bud outgrowth even after shoot removal; exogenous application of GA promoted bud growth. This result implied that GA was synthesized in the buds after decapitation, and accumulation of higher GA levels induced bud growth. Combined, this research suggests that GA plays a role in elongation, but not dormancy release.

Auxin

Auxin plays an important role in almost every aspect of plant development (Leyser 2002). Auxin's role in endodormancy has been described in different plant species. Levels of the auxin indole-3-acetic acid (IAA) decline gradually under SD in parallel with increasing endodormancy in bay willow and silver birch (Olsen *et al*. 1997a; Li *et al*. 2003a). The endogenous levels of IAA are low in endodormant potato tubers and increase in shoot buds prior to the onset of growth (Hemberg 1949; Sorce *et al*. 2000). Additionally, paradormant axillary and underground adventitious buds are inhibited by auxin after growth induction by decapitation (Horvath *et al*. 1999; Cline 2000; Chao *et al*. 2006; Wan *et al*. 2006).

Auxin signaling in paradormancy has been well studied. Different terms such as "release of apical dominance", "bud initiation", "regrowth", "branching", "axillary bud outgrowth", etc. have been used to describe growth induction of lateral buds following release of paradormancy (Cline 1997). Thimann and Skoog (1933) proposed that auxin is synthesized in the primary shoot apex, moves basipetally through the stem, and inhibits the growth of axillary buds. Further research indicated that other phytohormones are also involved in regulating bud outgrowth (Cline 1997; Shimizu-Sato and Mori 2001; Dun *et al*. 2006). Recently, molecular and genetic approaches have identified many genes involved in regulating branching (Stirnberg *et al*. 1999; Booker *et al*. 2005; Foo *et al*. 2005; Snowden *et al*. 2005). Multiple overlapping hypotheses have been proposed for the regulatory role of auxin. Auxin acts through secondary messengers, the capacity of auxin transport affects branching, and buds must be competent to respond to these signals (Shimizu-Sato and Mori 2001; McSteen and Leyser 2005; Beveridge 2006; Dun *et al*. 2006).

Basipetal movement of auxin in the stem influences the acropetal movement of secondary messengers (McSteen and Leyser 2005; Dun *et al*. 2006) (**Fig. 2**). One of these second messengers is cytokinin. Cytokinin is synthesized in the roots and stem and transported into the buds, and is well known to promote bud outgrowth. Auxin inhibits cytokinin synthesis and reduces the amount of cytokinin in the transpiration stream (Eklof *et al*. 1997; Nordstrom *et al*. 2004). Another second messenger is the shoot multiplication signal (SMS)/MAX-dependent signal (MDS) (Bennett *et al*. 2006; Beveridge 2006). SMS is produced in plastids of shoots and roots and inhibits bud outgrowth. Molecular evidence indicated that SMS is a carotenoid derivative (Sorefan *et al*. 2003; Schwartz *et al*. 2004). The synthesis of SMS requires carotenoid cleavage dioxygenases DECREASED APICAL DOMINANCE 1 (DAD1) (petunia)/MORE AXILLARY GROWTH (MAX)4 (arabidopsis)/RAMOSUS (RMS)1 (pea) and MAX3/RMS5 (Napoli 1996; Bouvier *et al*. 2005; McSteen and Leyser 2005; Beveridge 2006; Dun *et al*. 2006). In the SMS pathway, *MAX1* encodes a class III cytochrome P450 and acts downstream of *MAX3/4* (Booker *et al*. 2005). Decreased auxin transport causes depletion of *RMS1* transcript in pea stems (Foo *et al*. 2005), and exogenous auxin reverses this response (Sorefan *et al*. 2003). However, expression of *MAX4* is not regulated by auxin transport in arabidopsis (Bainbridge *et al*. 2005). The SMS pathway in pea is also controlled by a long-distance feedback signal through RMS2 which positively regulates the expression of *RMS1* transcripts (Morris *et al*. 2001; Foo *et al*. 2005; Beveridge 2006) and negatively regulates the abundance of cytokinin content in the xylem sap (Morris *et al*. 2001; Dodd *et al*. 2004; Beveridge 2006). *RMS4* of pea is homologous to *MAX2* of Arabidopsis (Johnson *et al*. 2006). The leucine-rich repeat F-box MAX2/RMS4 appears to be involved in the perception of SMS (Johnson *et al*. 2006).

The auxin transport hypothesis emphasizes that bud outgrowth requires auxin export from lateral buds into the basipetal auxin transport stream (McSteen and Leyser 2005; Dun *et al*. 2006) (**Fig. 2**). This hypothesis suggests that if auxin transport is at capacity in the primary stem, auxin efflux from axillary buds is inhibited. Excision or blockage of auxin transport from the apical buds allows flow of auxin from axillary buds into the primary stem, activating bud outgrowth. Auxin transport capacity is higher in the primary stem of *rms* and *max* mutants compared to wild-type plants, and these mutants have increased branching (Beveridge *et al*. 2000; Bennett *et al*. 2006). Bennett *et al*. (2006) describes that increased auxin transport capacity in stem allows simultaneous flow of auxin from the primary apex and axillary buds into the stem. Auxin transport requires PIN protein efflux carriers (Morris and Johnson 1990). PIN1 protein is known to stimulate efflux of auxin and the SMS pathway down-regulates *PIN* expression in the stem and inhibits branching (Bennett *et al*. 2006; Petrášek *et al*. 2006). Additionally, two hypotheses have been proposed for PIN-dependent auxin transport (Bennett *et al*. 2006; Lazar and Goodman 2006). Although both postulate that flavonoids are known regulators of PIN-dependent auxin transport, one specifies a *MAX1*-dependent maintenance of high flavonoid levels (Lazar and Goodman 2006), while the other specifies *MAX*-dependent expression of PIN that is independent of the flavonoid pathway (Bennett *et al*. 2006) (**Fig. 2**).

Ethylene

The ethylene signaling pathway has been well characterized. Ethylene participates in the regulation of multiple physiological and developmental processes in plants including fruit ripening, seed germination, flowering, abscission, senescence, and stress (Bleecker and Kende 2000). This signaling pathway is known to interact with phytohormones and other signals such as glucose and light (Chen *et al*. 2005; Stepanova and Alonso 2005). Many key components of the ethylene signal transduction pathway were identified based

on genetic screens of mutant arabidopsis seedlings (Chen *et al*. 2005). Despite enormous advances in our information on ethylene perception and signaling, the role of ethylene in the development of bud dormancy is not well understood. Nevertheless, ethylene involvement in the development of endodormancy in vegetative buds appears to be important. For example, Suttle (1998) suggested that endogenous ethylene is important for the development of adequate endodormancy in microtubers and the involvement of ethylene is restricted to the initial phase of endodormancy induction. In birch, the ethylene signal facilitates SD-induced terminal bud formation, as well as normal endodormancy development (Ruonala *et al*. 2006). In addition, ethylene-insensitive trees exhibited bush-like appearance due to reduced apical dominance, suggesting the ethylene signal interacts with ABA and auxin signaling pathways (Ruonala *et al*. 2006).

Cytokinins

Cytokinins are a class of plant hormones noted for promotion of cell division and organ formation that are invoked as key regulatory signals promoting axillary bud outgrowth when the apical meristem is removed. Direct application of cytokinin to buds of intact plants often induces breaking of paradormancy, and cytokinin levels rise in buds prior to outgrowth (Suttle and Banowetz 2000; Leyser 2003). Root-tip derived cytokinins may be transported to the shoot in intact plants to exert their physiological effect (Bangerth 1994). However, cytokinin synthesized in close proximity to buds in stem tissue plays a key role (Shimizu-Sato and Mori 2001; Tanaka *et al*. 2006), because a rise in cytokinin levels occurs in axillary buds of excised shoots prior to or at the same time as bud outgrowth (Sachs and Thimann 1967).

Various hypotheses exist to explain how cytokinins interact with auxin to regulate bud outgrowth (Bennett *et al*. 2006; Dun *et al*. 2006). In pea nodal segments, expression of *adenosine phosphate-isopentenltransferase* (*IPT*), a key gene in cytokinin biosynthesis, is induced by removal of the primary bud. Auxin applied exogenously to buds or transported basipetally from the shoot apex represses *PsIPT* expression in nodal stem tissue (Tanaka *et al*. 2006). Cytokinin levels increase in nodal stems prior to increasing in axillary buds, suggesting that cytokinins are transported into dormant buds from the adjacent node. Thus, these results suggest that cytokinin biosynthesis is negatively regulated by auxin (Nordstrom *et al*. 2004). Analysis of the branching control system in *rms* and *max* mutants of pea and arabidopsis, respectively, indicates a SMS pathway feedback control system that regulates the supply of cytokinin (Morris *et al*. 2001; Foo *et al*. 2005; Beveridge 2006).

CONCLUSION AND FUTURE PROSPECTS

Sessile organisms like plants are required to constantly monitor changes in the environment and respond with phytohormone changes. Although the structure and function of several hormone receptors are known (Gazzarrini and McCourt 2003; Bishopp *et al*. 2006), their roles in regulating dormancy have yet to be elucidated. Conservation in gene sequences should allow some of these receptors to be cloned from plants commonly used as models for studying bud dormancy (Cline 2000; Arora *et al*. 2003; Suttle 2004; Chao *et al*. 2005; Beveridge 2006; Volaire and Norton 2006). Studies on the regulation of seed and bud dormancy also indicate that growth arrest is partially due to blockage of cell division (Devitt and Stafstrom 1995; Campbell *et al*. 1996; de Castro and Hilhorst 2000; Shimizu-Sato and Mori 2001; Horvath *et al*. 2003). Hormones such as ABA, auxin, brassinosteroids, cytokinins, GA, and jasmonic acid and sugar, which regulate dormancy induction and release also regulate cell cycle progression (Anderson *et al*. 2001; Horvath *et al*. 2003; del Pozo *et al*. 2005). Further investigation on hormone receptors regulating dormancy release and cell division may shed new light on the connections between these signaling networks.

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