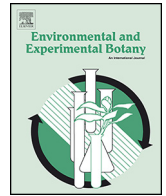




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## Photosynthetic responses to temperature-mediated dormancy induction in contrasting ecotypes of red-osier dogwood (*Cornus sericea* L.)

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### ABSTRACT

Dormancy development in plants is synchronized with the cessation of environmental conditions that favour plant growth. The timing of this response is important in trees for growth and survival. Woody plants, such as dogwood (*Cornus sericea* L.) have evolved different ecotypes that are closely adapted to local climatic conditions, which are differentiated by irradiance, photoperiod and/or temperature. While short photoperiods are well known to play a key role in dormancy induction in northern ecotypes, low temperatures alone can by-pass the photoperiodic requirement. It is well established that the combination of low temperature and even low to moderate light intensities predispose plants to photoinhibition of photosynthesis. However, plants possess numerous photoprotective mechanisms to minimize photoinhibition including increased rates of photosynthesis as well as non-photochemical dissipation of excess excitation energy, a process involving xanthophyll cycle carotenoids. We used two ecotypes of dogwood, the northern ecotype of Northwest Territories (NWT 62° N latitude) and the southern Utah, U.S.A. (42° N latitude) ecotype, which exhibit differential responses to photoperiodic- and temperature-induced dormancy. These ecotypes were exposed to various combinations of photoperiod and low temperature treatments and monitored for photosynthetic and photoprotective processes as the plants entered dormancy. Our results demonstrate differential long- and short-term responses to photoinhibition at low temperatures between the two ecotypes. The northern ecotype was more tolerant to photoinhibition of photosynthesis than the southern ecotype potentially through a zeaxanthin-independent mechanism of photoprotection. Furthermore, anthocyanin accumulation may be involved in the LD-Cold treatment through putative sugar sensing mechanisms to trigger dormancy.

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**Abbreviations:** A, antheraxanthin; Chl, chlorophyll; Cold, 23/5 °C (day/night); EPS, epoxidation state; ETR, relative linear electron transport rates through PSII;  $F_v/F_m$ ,  $F_v'/F_m'$ , maximal and effective quantum yields of PSII photochemistry, respectively; FW, fresh weight; LD, long day (22/2 h); NPQ, non-photochemical quenching; PPFD, photosynthetic photon flux density; PSII, photosystem II;  $q_0$ , antenna quenching; SD, short day (8/16 h); V, violaxanthin; Warm, 23/23 °C (day/night); Z, zeaxanthin;  $1 - q_p$ , relative reduction state of PSII;  $\Phi_{PSII}$ , effective quantum yield of PSII electron transport.

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### 1. Introduction

Dormancy refers to a period of arrested plant growth and represents an adaptive strategy where plants can survive in climates which are unsuitable for growth, such as a winter season (Hänninen and Tanino, 2011). Dormancy is closely associated with environmental conditions and can be triggered after a normal growing season by decreasing temperatures and/or shortened day length. For example, the initiation of dormancy in woody species such as hybrid poplar, begins with a phase of growth cessation, which in northern latitudes, is synchronized, along with cold acclimation and the acquisition of freezing tolerance, to seasonal changes like photoperiod shortening and the onset of low autumn temperatures (Kalcits et al., 2009a,b). Because the timing of cold acclimation is associated with growth cessation, the

timing of dormancy events is important in short-season, northern temperate regions where late dormancy attainment would prevent attainment of full low-temperature tolerance (Smithberg and Weiser, 1968; Stevenson, 1994; Caprio and Quamme, 1999; Lindén, 2001).

During the cold acclimation process soluble sugars, particularly sucrose, accumulate (Levitt, 1980; Pollock and Lloyd, 1987). In overwintering herbaceous plants, freezing tolerance has been strongly correlated to the photosynthetic capacity of these plants and soluble carbohydrate accumulation (Öquist et al., 1993; Stitt and Hury, 2002). While precise roles for soluble sugars remains to a large extent unknown, they are thought to perform multiple functions as compatible osmolytes, cryoprotectants, scavengers of reactive oxygen species and signalling molecules (Theocharis et al., 2012). Sugar signalling has been implicated with the control of growth and development as well as stress responses (Rolland et al., 2006; Theocharis et al., 2012). Day length is important in sucrose accumulation as it is a contributing factor that determines the opportunity for overall carbon acquisition.

Changes in seasonal photoperiod provide an important environmental signal that affects the timing of winter dormancy in perennial, deciduous and temperate tree species. In these species, long days (LDs) sustain shoot elongation, whereas short days (SDs) induce growth cessation, formation of terminal buds, cold acclimation and bud dormancy (Weiser, 1970). It is well established that dormancy is induced by short photoperiods involving a phytochrome sensing mechanism (Garner and Allard, 1923; Wareing, 1956; Weiser, 1970). However, recent studies indicate that temperature may be more important relative to the effect of photoperiod in dormancy induction for northern ecotypes (Junttila, 1980; Howe et al., 2000; Heide, 2003; Tanino et al., 2010). Red-osier dogwood (*Cornus sericea* L.), a temperate woody perennial shrub, is distributed throughout North America (Smithberg and Weiser, 1968; Eyde, 1988). As such, it has adapted to a variety of environments and is a model plant for abiotic stress and dormancy research (Weiser, 1970; Fuchigami et al., 1982; Hummel et al., 1982; Renault, 2005).

The dormancy cycle has largely evolved as an adaptation to survive environmental stressors. In northern temperate regions, short day warm temperature conditions are well recognized as a key environmental cue to induce dormancy in woody plants (Kramer, 1936; Weiser, 1970). However in high northern latitudes where day lengths reach 24 h, environmental cues of a critical short photoperiod may not be reached in time to cease growth and develop cold hardiness. Low temperature has been shown to be an effective trigger for dormancy induction, even under 24 h photoperiods, in northern woody tree species such as birch (Junttila, 1980) and poplar (Howe et al., 2000; Kalcsits et al., 2009a; Tanino et al., 2010). We have shown that dormancy induction in southern ecotypes of dogwood is dependent on short photoperiods, whereas in northern ecotypes dormancy is induced by either short photoperiods or low temperature (Stevenson, 1994; Svendsen et al., 2007; Tanino et al., 2010). Thus, low temperatures can by-pass the short photoperiod requirement, but only in the northern ecotypes. However, compared with photoperiod-induced dormancy, relatively little work has been conducted on the phenomenon of low-temperature induction of dormancy.

Photosynthesis, the energy conversion from sunlight into biochemical energy, is the basis of plant growth. The exposure of plants to excess light, sometimes referred to as photoinhibition, can result in deleterious effects on photosynthetic reactions (Huner et al., 1993; Long et al., 1994; Vass, 2012). As such, plants utilize varying photoprotective strategies to optimize energy use and avoid damage. There are many factors which determine the effectiveness of these strategies including growth irradiance and exposure to stress conditions. Species-specific differences are also observed. During the induction of dormancy (growth cessation) many long-term

metabolic changes occur, which are associated with the cold acclimation process and the acquisition of freezing tolerance (Weiser, 1970; Christersson, 1978; Bigras et al., 2001). The photoperiod and low-temperature cues to trigger this process also serve to down regulate metabolism and result in potential imbalances between light capture and energy utilization. In order to prevent photooxidative damage to the photosynthetic apparatus, these events must be balanced through a process known as photostasis (Huner et al., 1998; Öquist and Huner, 2003; Ensminger et al., 2006; Hüner and Grodzinski, 2011). This has recently been shown to be an especially important process in overwintering evergreen conifers (Busch et al., 2007, 2008).

Photostasis can be achieved by many means, one of which involves an increase in the dissipation of excess light energy as heat and is observed as the non-photochemical quenching of chlorophyll fluorescence (NPQ). The formation of NPQ is considered a universal photoprotective mechanism and involves a restructuring of the light-harvesting antenna, the PSII subunit PsbS, as well as interconversions of carotenoids (violaxanthin (V), zeaxanthin (Z)) in the xanthophyll cycle (Demmig-Adams and Adams, 1992; Müller et al., 2001; Li et al., 2009). This may be further subdivided into dynamic quenching ( $q_E$ ) and sustained quenching ( $q_I$ ). Dynamic quenching (zeaxanthin-dependent) is rapidly inducible and occurs in response to the formation of the pH gradient while  $q_I$  (zeaxanthin-independent) may serve to dissipate excess energy as heat independent of a pH gradient (Horton and Ruban, 2005; Ensminger et al., 2006). In evergreen conifers, sustained quenching is induced in connection with a loss of functional PSII (Ensminger et al., 2009) and associated with the termination of growth and induction of cold hardiness (Öquist and Huner, 2003). In addition, these species are able to shift between the dynamic and the sustained antenna quenching ( $q_0$ ) strategies for dissipating excess energy (Öquist and Huner, 2003). A zeaxanthin-independent mechanism for quenching has also been described in the reaction centre of PSII (Ivanov et al., 2008), as have alternative xanthophyll cycles (García-Plazaola et al., 2012).

Previously, we have reported that a northern dogwood ecotype (Alaska) demonstrated an increased tolerance to low temperature photoinhibition in comparison to a southern ecotype (Utah) after growth under dormancy-inducing conditions (Tanino et al., 2010). This was most pronounced under a long day and low temperature (LD-Cold) treatment. Interestingly, this treatment is able to by-pass the photoperiod requirement for dormancy induction, but only in the northern ecotype. In both ecotypes, the tolerance to photoinhibition under all dormancy-inducing growth conditions was associated with an active xanthophyll cycle and by increased xanthophyll pool size (V + antheraxanthin (A) + Z) (Gray and Tanino, unpublished data). However, the changes in these parameters were more pronounced in the Alaska ecotype, suggesting NPQ as a possible photoprotective mechanism. Since the photoinhibitory tolerance between ecotypes was greatest under LD-Cold, this led to our hypothesis that enhanced NPQ under this growth treatment may allow for higher photosynthetic efficiency with reduced photoinhibition and this, in turn, may in some manner permit triggering of dormancy induction in absence of a photoperiod requirement.

In this study, the effects of growth under dormancy-inducing conditions on photosynthetic responses were examined in northern (NWT) and southern (Utah) ecotypes of dogwood. The goal of our study was to obtain a more detailed understanding of the photosynthetic changes occurring as a result of growth under these various combinations of photoperiod and temperature which signal dormancy induction. We hypothesized that the low temperature-mediated dormancy induction in northern latitude ecotypes is triggered by signals related to its ability to manage excess light (photoinhibition) under the combination

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