Kiwifruit *SVP2*, a dormancy regulator

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Summary

Kiwifruit (*Actinidia* spp.) are woody perennial vines where bud dormancy and outgrowth affect flower development. MADS-box genes similar to *Arabidopsis* *SHORT VEGETATIVE PHASE* (*SVP*) have been implicated in the regulation of flowering in annual species and in bud dormancy in perennial species. Four kiwifruit *SVP*-like genes have been identified. Their roles in dormancy and flowering have been analysed in *Arabidopsis*, tobacco and a high-chill and a low-chill kiwifruit species, *Actinidia chinensis* var. *deliciosa* and *A. eriantha*. Our detailed study of kiwifruit *SVP2* that elevated expression of *SVP2* suppressed bud outgrowth in the high-chill kiwifruit *A. chinensis* var. *deliciosa*. Sufficient winter chilling and the dormancy-breaking agent hydrogen cyanamide (Hi-Cane®) could overcome the *SVP2* effect. Transcriptomic analyses of kiwifruit *SVP2* transgenic lines suggested that *SVP2* mimics the well-documented effect of abscisic acid (ABA) in plant dehydration response.

Keywords

kiwifruit dormancy, *SVP*, DAM, ABA, dehydration pathways

Significance of this study

What is already known on this subject?

- *SVP*-like genes have demonstrated roles in regulation of flowering time in annuals and suggested roles in regulation of dormancy in perennials.

What are the new findings?

- This review describes a conservation in mechanism of action between *SVP* genes of taxonomically distant *Arabidopsis* and a woody perennial kiwifruit; highlights the role of kiwifruit *SVP* in suppression of meristem activity to prevent precocious budbreak before the fulfilment of winter chilling requirement; presents a mode of action of *SVP2* associated with dormancy release in kiwifruit.

What is the expected impact on horticulture?

- Such knowledge can help to develop new kiwifruit varieties through conventional breeding or through genetic engineering, targeting budbreak and flowering dates which ensure optimal growth and adequate production in different growing regions and environments.

Introduction

Flowering in temperate woody perennials is associated with bud dormancy, when growth is repressed to ensure survival during unfavourable winter conditions. Bud dormancy is a period of temporary suspension of growth activity in response to environmental conditions, such as seasonality or extreme heat, drought, or cold. Endodormancy is the deepest state of dormancy, where inhibition of growth originates within the bud meristem and a certain amount of chilling is required before growth can resume. This is so in kiwifruit (*Actinidia* spp.), where the lack of sufficient chilling results in delayed budbreak, subsequently reduces flowering and impacts on fruit yield (McPherson et al., 2001; Sibley et al., 2005; Walton et al., 2009).

The molecular mechanisms that regulate dormancy in woody perennials are largely unknown. MADS box genes with similarity to *Arabidopsis* *SVP* have, however, been implicated in regulation of flowering time in annuals, and in bud dormancy in perennial species. In kiwifruit, four *SVP*-like genes have been identified and characterised in *Arabidopsis* (Wu et al., 2012). *SVP2* and *SVP3* are closely related, but with dissimilar seasonal expression profiles. Overexpression of *SVP2* and *SVP3* exhibited different competencies on preventing winter bud outgrowth (Wu et al., 2014, 2017b). This review will briefly describe the conserved and divergent roles of *SVP*-like genes in annual and woody perennials, in particular when associated with dormancy in *Actinidia* spp.

SVP in *Arabidopsis*

In *Arabidopsis*, two MADS-box genes, *SVP* and *AGAMOUS*-like 24 (*AGL24*), are closely related, but have opposite effects in the control of flowering time (Gregis et al., 2006). *SVP* is expressed in vegetative seedlings, and is barely detectable in the main inflorescence apical meristem (Hartmann et al., 2000). *SVP* represses the floral transition. The *svp* mutants cause early flowering (Hartmann et al., 2000), whereas ectopic expression of *SVP* results in late flowering, and causes floral reversion (Brill and Watson, 2004; Masiero et al., 2004). *AGL24* is expressed during vegetative and floral development (Yu et al., 2002). *AGL24* promotes the floral transition. The *agl24* mutants cause late flowering, whereas overexpression of *AGL24* accelerates flowering (Michaels et al., 2003; Yu et al., 2004).

SVP and *AGL24* are essential to prevent premature differentiation of floral meristems and to determine the appropriate timing of floral organ development (Gregis et al., 2003; Yu et al., 2004; Liu et al., 2009). Genetic interaction models have shown that the *SVP* protein directly binds to the promoters of the key flowering genes *SOC1*, *FLOWERING LOCUS T* (*FT*) and its paralogue *TWIN SISTER OF FT* (*TSF*) to repress flowering (Lee et al., 2007; Jang et al., 2009), while *AGL24* promotes *SOC1* expression during floral transition (Michaels et al., 2003; Liu et al., 2008). *SVP* and *AGL24* are also capable of interacting with other proteins in response to developmental and environmental cues during floral transition (Lee et al., 2007; Li et al., 2008; Fujiwara et al., 2008; Jang et al., 2009;

Gregis et al., 2013; Lee et al., 2014; Andrés et al., 2014). Presence and absence of SVP in the shoot apical meristem modulates gibberellin biosynthesis, and subsequently integrates gene expression in response to inductive photoperiods (Andrés et al., 2014). The interaction between AGL24 and SOC1 mediated the effect of gibberellins on flowering under short-day conditions (Liu et al., 2008). A floral repressor complex comprising SVP and FLOWERING LOCUS C (FLC) strongly delays or prevents flowering in response to vernalisation under non-inductive environments (Li et al., 2008; Mateos et al., 2015). Furthermore, *SVP* has been identified as a key hub gene in a transcriptional network during drought stress, linking changes in primary metabolism and the initiation of stress responses (Bechtold et al., 2016).

***SVP* genes in perennial plants**

SVP-like genes in woody perennials have been proposed in regulation of growth cessation and bud dormancy during winter. *SVP*-like *DORMANCY ASSOCIATED MADS-box* (*DAM*) genes were first implicated as having a role in dormancy in a mutant peach (*Prunus persica*) named *evergrowing* (*evg*) (Wang et al., 2002). The mutant peach trees fail to set terminal buds in autumn under the dormancy-inducing short-day conditions and have a reduced chilling requirement in lateral buds to break dormancy. This mutation is caused by a deletion of six tandemly repeated *DAM* (*DAM1-6*) genes

at the peach *EVERGROWING* locus (*EVG*) (Bielenberg et al., 2008). Expression of peach *DAM1*, 2, 4 is correlated with growth cessation and bud set. *DAM3* does not show a distinct expression pattern throughout the annual cycle, while *DAM5* and *DAM6* are upregulated by SD conditions and downregulated by low temperature (Li et al., 2009). Highly similar *DAM* genes are also upregulated expression and proposed association with regulation of endodormancy in other *Rosaceae* species: *Malus* spp., *Rubus idaeus*, *Prunus* spp., and *Pyrus pyrifolia* (Mazzitelli et al., 2007; Yamane et al., 2008; Ubi et al., 2010; Leida et al., 2012; Liu et al., 2012; Takemura et al., 2013; Mimida et al., 2015; Niu et al., 2016; Wu et al., 2017a). Ectopic expression of the *Prunus mume* *DAM* gene in transgenic poplar and apple *DAMb* and *SVPa* in apple 'Royal Gala' delayed budbreak, implicating *SVP*-like genes in the regulation of dormancy (Sasaki et al., 2011; Wu et al., 2017a). *SVP*-like genes from plants outside the *Rosaceae*-specific *DAM* subclade, such as grape, leafy spurge, citrus, and sapphire dragon tree eucalyptus, have also been suggested to be involved in regulation of dormancy (Prakash and Kumar, 2002; Brill and Watson, 2004; Diaz-Riquelme et al., 2009; Li et al., 2010; Horvath et al., 2010; Liu et al., 2012; Sun et al., 2016). However, most of these proposals were based simply on observing elevated expression during endodormancy: evidence of causality is lacking.

FIGURE 1. The mode of action of *SVP2* in regulation of dormancy in kiwifruit. A. Insufficient winter chilling resulted in delayed budbreak. Absciscic acid (ABA) and dehydration responsive genes promote bud dormancy and repress dormancy release. When the chilling requirement is not satisfactorily met, *SVP* modulates expression of dehydration responsive genes to maintain bud at dormant states. B. Sufficient winter chilling promotes budbreak. Once chilling requirement is met, *SVP* effects are removed, which allows budbreak. Lines with arrows represent activation, while lines with bar heads represent repression. The red crosses denote inactivation.

***SVP* genes in kiwifruit (*Actinidia* spp.)**

Kiwifruit and kiwiberry (*Actinidia* spp.) are economically important fruit crops. All *Actinidia* species are deciduous perennial plants with a vigorous climbing or straggling growth habit (Ferguson, 2013). The process of flower development is spread over two growing seasons (Walton et al., 1997, 2001). Four *SVP*-like genes have been identified and characterized (Wu et al., 2012). The seasonal expression analyses revealed increased transcript levels of three of *SVP*-like genes (*SVP1*, 2 and 4) over the winter dormancy period, while *SVP3* was not coordinated with seasonal change. Overexpression of *SVP3* in kiwifruit *A. chinensis* var. *deliciosa* and *A. eriantha* did not delay budbreak in the spring, but affected floral development and anthocyanin biosynthesis pathways (Wu et al., 2014). *SVP2* (which is closely related to *SVP3*) was expressed in all vegetative tissues, predominantly in the buds. Seasonal expression analysis showed that *SVP2* expression was elevated over the winter and declined prior to budbreak. The expression of *SVP2* declined more rapidly on the vines treated with dormancy-breaking agent, hydrogen cyanamide (Hi-Cane®) treated vines than non-treated vines (Wu et al., 2012). *SVP2* exhibited a growth inhibition role in transgenic tobacco on seed germination, root formation and plant height (Wu et al., 2017b). Ectopic expression of *SVP2* in kiwifruit had a detrimental effect on regeneration and growth during the tissue culture stage. The most striking phenotypic effect of *SVP2* was delayed budbreak in spring in the high-chill kiwifruit species, *A. chinensis* var. *deliciosa*. In contrast, *SVP2* overexpression had a minimal effect on dormancy in the low-chill species, *A. eriantha*. Furthermore, sufficient winter chilling could overcome the *SVP2* effect on dormancy. Transcriptomic analysis of *SVP2* in *A. chinensis* var. *deliciosa* transgenic lines identified that most *SVP2* downstream targets were associated with ABA and dehydration response pathways (Wu et al., 2017b). Genome-wide identification of direct targets of *SVP2* in kiwifruit *A. chinensis* using chromatin immunoprecipitation followed by high-throughput sequencing (ChIP-seq) technology confirmed target genes in ABA- and dehydration-mediated growth repression. Kiwifruit *SVP2* target genes also are largely overlapping with *Arabidopsis* *SVP* targets (Wu et al., 2017c).

To summarise what is currently known about kiwifruit *SVP2*, a proposed mode of action of *SVP2* in regulation of dormancy in the high-chill kiwifruit species is shown in Figure 1. ABA enhances the dormancy establishment and suppresses dormancy release, which also regulates genes associated with dehydration pathways. *SVP2* also regulates genes in the dehydration pathway. With insufficient winter chilling, *SVP2*, combined with dehydration pathway genes, acts to repress bud dormancy release. When chilling requirement is fulfilled, *SVP2* effects are removed, resulting in budbreak.

Perspective

The work reviewed here has demonstrated the role of *SVP2* in preventing precocious budbreak by suppressing meristem activity during winter dormancy (Wu et al., 2017b). Kiwifruit *SVP2* also played a growth inhibition role during plant development. It is highly likely that *SVP2* protein associate with other proteins to regulate gene expression. Indeed, *SVP2* may have multiple downstream targets that assist in dormancy maintenance and release. Future work should focus on identifying the genes regulated by *SVP2* and the proteins that interact with and modify the function of *SVP2*: this will elucidate the genes, pathways and biochemical aspects underlying the growth inhibitory role of *SVP2*.

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