

To Bring Flowers or Do a Runner: Gibberellins Make the Decision

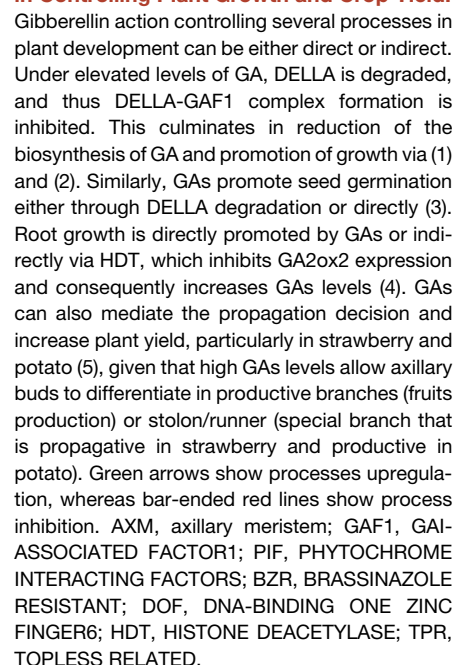
Gibberellins (GAs) are involved in several growth and developmental processes ranging from stem elongation, leaf expansion, transition to flowering, pollen maturation, fruit set, and seed germination (Figure 1). GAs are associated with these phenomena via their direct effects on cell division and expansion as well as via integration of internal and external stimuli (Yoshida et al., 2014; Davière and Achard, 2016). Although GAs are commonly synthesized at their site of action, they can also be transported among cells, tissues, and organs. The biosynthesis of bioactive GAs involves the action of six enzymes, with the ultimate and penultimate steps catalyzed by the cytosolic enzymes GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox). In addition to their rates of biosynthesis, the final level of bioactive GAs is also regulated by inactivation, which is catalyzed by the GA 2-oxidase (GA2ox) enzyme. All three of these enzymes are encoded by multigene families, the members of which are regulated by a number of intrinsic and extrinsic factors but dominated by feedback and feedforward regulation. The importance of another, hitherto unheralded player is now recognized by a recent elegant study concerning the runner-flowering decision in strawberry (*Fragaria spp.*; Tenreira et al., 2017).

A peculiarity of diploid strawberry (*Fragaria vesca*) is that the axillary meristem (AXM) can generate either an aerial stolon (runner) to produce daughter plants via clonal propagation or an inflorescence that yields fruits. The molecular mechanisms underlying this differentiation decision remained poorly understood to date. By using a combination of classical mapping and mapping-by-sequencing approaches coupled with biochemical and pharmacological techniques, Tenreira and colleagues demonstrated that a natural 9 bp deletion within the coding region of the *FveGA20ox4* gene, which encodes a key enzyme in GA₁ synthesis, led to the switch in the fate of axillary buds in strawberry. This mutation, which is found in the stolon-deficient runnerless (*r*) mutant of woodland strawberry, and results in the production of an activity-deficient protein, either maintains the AXM in a dormant status or alternatively increase the number of inflorescences due to the production of secondary shoots. Regulation of the inflorescence/runner fate is of high economic importance in strawberry since vegetative reproduction occurs at the expense of fruit yield (Barrett, 2015). Thus, the *FveGA20ox4* gene represents a new tool for the improvement of productivity in this species by controlling the trade-off between sexual reproduction and vegetative propagation.

By conducting an *N*-ethyl-*N*-nitrosourea (ENU) mutagenesis screen in the runnerless Yellow Wonder (YW) plants, Caruana et al. (2017) recently identified the *suppressor of runnerless* (*srl*) mutant, which develop runners. The *srl-1* mutants are capable of developing stolons with a considerable number of daughter

plants, differently from its parental line YW that does not produce any stolons. To identify the genetic basis of this interestingly phenotype, the authors used a mapping-by-sequencing strategy allowing the definition of a single nucleotide polymorphism that resulted in the generation of the *srl-1* mutant phenotype. This single-base exchange promoted the generation of a stop codon, 10 amino acids residues prior to the native stop codon. This change in the reading frame occurs at the C-terminal portion of one of the five annotated DELLA genes, *FveRGA1* (Kang et al., 2013). Although strawberry plants have five DELLA genes, only *FveRGA1* is functional due to the presence of the full DELLA motif, which allows their interaction with GAs. The *srl-1* mutation affected the region required for the normal DELLA activity in repressing GA signaling. Thus, this mutation resulted in a constitutive GA response and, consequently, the constant development of runners. Unlike *FveGA20ox4*, which is preferentially expressed in AXM tissues (Tenreira et al., 2017), *FveRGA1* is ubiquitously expressed in flowers, fruits, and vegetative tissues (Caruana et al., 2017). It thus seems reasonable to assume that another regulatory approach to the inflorescence/runner destination can be mediated by GA signaling. This allows us to speculate that not only the GA levels in the AXM but also the presence of functional DELLA protein is seemingly responsible for determining the inflorescence/runner fate in strawberry. Given the diverse effects mediated by GA levels and signaling, it seems that this highly ubiquitous hormone is responsible for integrating environmental and endogenous signals during flowering transition at the same time that it affects distinct organs and tissues.

GAs regulate their own biosynthesis via a DELLA-dependent process (Figure 1). Within this process, increases in GA levels lead to ubiquitination of DELLA proteins and their subsequent degradation via the 26S proteasome, while in the absence of DELLA, the expression of GA responsive genes occurs. In addition, repression of the biosynthetic enzymes GA20ox and GA3ox and expression of GA2ox, which degrades bioactive GAs, occur. GA20ox and GA3ox are negatively regulated by increased GA levels. By contrast, opposite effects are expected when GA contents are reduced. DELLA does not interact with DNA by direct binding to target promoters. For this purpose, transcriptional factors mediating the regulatory activity of GAs via DELLA are required such as the GAI-ASSOCIATED FACTOR1 (GAF1) (Fukazawa et al., 2014). GAF1 binds to DELLA and the promoter regions of different genes functioning either as activator or repressor in a manner fully dependent on the



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