

## Do Strigolactones Regulate Bud Winter Dormancy and Characteristic Secondary Metabolism in Tea?

Lin Feng<sup>1</sup>, Ziming Gong<sup>1,\*</sup>, Guofeng Liu<sup>2</sup> and Yanli Liu<sup>1</sup>

<sup>1</sup>Institute of Fruit and Tea, Hubei Academy of Agricultural Science/Hubei Tea Engineering and Technology Research Centre, Wuhan, 430064, China

<sup>2</sup>College of Life Sciences, Xinyang Normal University, Xinyang, 464000, China

\*Corresponding Author: Ziming Gong. Email: ziminggong@163.com

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**Abstract:** Tea (*Camellia sinensis* [L.] O. Kuntze.) is an important cash crop, which mainly uses tender shoots and young leaves for manufacturing. Due to the marketing characteristic that earlier made tea has higher price, the time of the breaking of winter dormancy buds in spring is extremely important in tea industry. Strigolactones are a group of carotenoids-derived metabolites which regulates bud outgrowth, shoot branching, tiller angle and environmental stress responses. The role of strigolactones in tea plant was briefly summarized in the current review, with an emphasis of the association of strigolactones on bud dormancy and shoot branching. The involvement of strigolactones on the biosynthesis of the tea characteristic metabolites flavonoids, caffeine and theanine were also discussed. Moreover, recent advances on the biosynthesis of strigolactones and its regulation by microRNAs and environmental stresses were also presented. This review provides a basis for future investigations underlying the mechanisms of strigolactones on bud winter dormancy and tea secondary metabolism.

**Keywords:** *Camellia sinensis*; strigolactones; winter dormancy; secondary metabolites

### 1 Introduction

Tea (*Camellia sinensis* [L.] O. Kuntze.) is used for producing a non-alcoholic beverage consumed worldwide with unique flavor and health benefits [1]. The quality of processed tea is basically determined by the secondary metabolites constituents in tea leaves, include flavonoids and alkaloids (the main contributors determining tea flavour and astringency), amino acids (the main contributors towards the umami taste of tea infusions) [2–4]. As an evergreen perennial crop, tea plants initiate shoot elongation and undergo winter dormancy in late autumn in each annual growth cycle to resist against environmental stresses, especially low temperatures, for survival during the winter. When environmental conditions are suitable in the early spring, the buds break dormancy and begin a new growth cycle. Tea yield largely depends on newly sprouted shoot tips with two unfolded leaves, which are generally harvested for green tea processing. Bud outgrowth activity has long been a target of breeding selection, because it



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significantly affects crop yields by affecting both tiller number and inflorescence complexity [5]. Bud dormancy release time is pivotal in influencing spring tea price and yield [6]. However, winter dormancy molecular mechanisms are not well elucidated so far.

The relationship between winter dormancy and plant hormones has been intensively uncovered. The changes in the level of active gibberellins (GAs) is associated with induction of growth cessation primarily regulated by circadian clock [7]. Numerous genes related to hormone metabolism or signaling are differentially expressed in transcriptome studies of dormant bud in *Euphorbia esula* [8]. In addition to the well-known isoprenoid phytohormones such as cytokinins (CK), abscisic acid (ABA), brassinosteroids (BR) and gibberellic acid (GA), strigolactones, a group of carotenoids-derived metabolites, suppress shoot branching [9], bud development in addition to several additional biological functions [10,11]. Moreover, association of ABA in strigolactone pathway could facilitate to control buds paradormancy [12]. Additionally, auxin regulated strigolactone depletion is a significant aspect for branching after shoot apices removal [13,14]. These findings offer more understanding about the mechanism of tea winter dormancy. This mini-review focuses on the possible involvement of strigolactones in tea winter dormancy and the biosynthesis of some secondary metabolites.

## 2 Strigolactones and Winter Dormancy

Strigolactones are derived from  $\beta$ -carotene; their biosynthetic pathway has gradually been elucidated (Fig. 1): First,  $\beta$ -carotene isomerase catalyzes the 9-*cis*/all-*trans* isomerization of  $\beta$ -carotene, followed by the stereospecific C9'-C10' cleavage of 9-*cis*- $\beta$ -carotene mediated by carotenoid cleavage dioxygenase 7 [CCD7, MORE AXILLARY GROWTH 3 (MAX3) in *Arabidopsis*], then, the transformation of intermediate 9-*cis*- $\beta$ -apo-10'-carotenal into carlactone is mediated by CCD8 (MAX4 in *Arabidopsis*) [15–18]. In addition, several other proteins such as  $\alpha/\beta$ -hydrolase (AtD14 in *Arabidopsis*, D14/D88/HTD2 in rice) and F-box protein (MAX2 in *Arabidopsis*, D3 in rice) are involved in strigolactones signal transduction [13,17,18].

In biosynthesis, which is included carotenoid cleavage dioxygenases7 (CCD7, MAX3, RMS5, or DAD3) [15] and CCD8 (MAX4, RMS1, D10 or DAD1) [17], and one cytochrome P450 monooxygenase (MAX1) [15]. For strigolactones signal transduction, which is involving MAX2/RMS4/D3 [13], an F-box leucinerich protein and DWARF14 (D14)/D88/HTD2, a member of the  $\alpha/\beta$ -fold hydrolase superfamily [18].

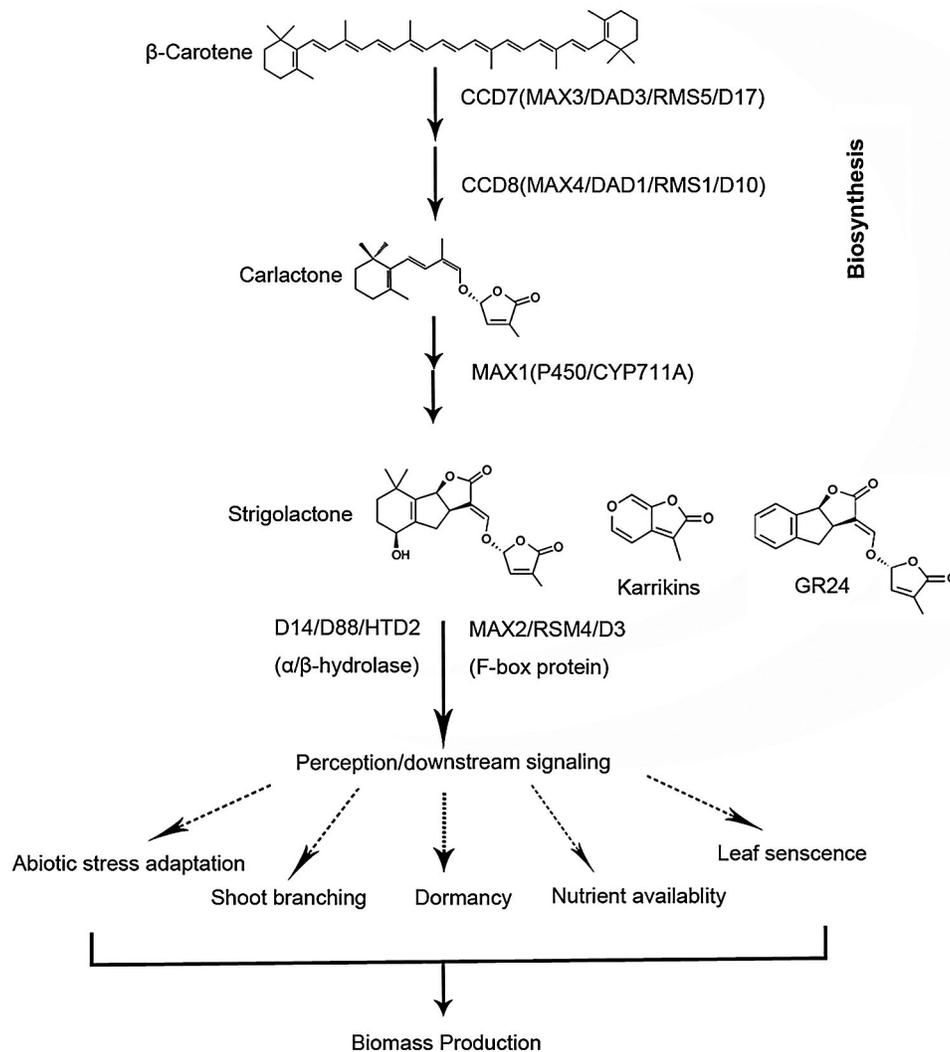
Genes associated with strigolactones pathway, such as MAX genes in *Arabidopsis* and their orthologs in *Pisum sativum* is tightly correlated with bud dormancy [16–19]. MAX2 plays a significant role in conferring dormancy and boosting shoot growth [16,20]. Indeed, *max2* mutant exhibit reduced expression of dormancy-associated gene 1/auxin-repressed protein (DRM1/ARP). MAX2 transcript levels were found being elevated in endodormant crown buds in *leafy spurge* [8], further strengthening that strigolactones function in ecodormancy induction. In the tillering dwarf *Oryza sativa* mutants *d3*, *d10*, *d14*, *d17* and *d27*, axillary meristems develop normally but with weakened ability of the dormancy in tiller buds [21]. Strigolactones bind to  $\alpha/\beta$ -hydrolase fold-containing proteins, which activates MAX2, ultimately leading to lateral bud inhibition and dormancy [22]. In rice, TB1 (Teosinte branched 1)/FC1 (Fine Culm1) and D14 interact with dormancy release marker MADS57 to regulate shoot branching [23]. In addition, MADS57 is a target of miR444a, suggesting that MADS57 plays a role in the strigolactone signaling pathway. To further investigate the regulation of tea winter dormancy, studies are required to detect interactions between tea analogs of MAX2 in the strigolactones pathway and other strigolactones signals or miRNAs.

## 3 Strigolactones and Secondary Metabolite Biosynthesis

### 3.1 Strigolactones and Flavonoid Biosynthesis

Many genes associated with the biosynthesis of flavonoid metabolites are differentially expressed during different phases of dormancy [8]. Chalcone synthase, flavone isomerase, theobromine synthase, caffeine synthase and glutamate (or theanine) synthase, were found being expressed in a dormant tea bud. These

genes and their encoded enzymes can protect plants from UV damage and are upregulated during dormancy in raspberry and leafy spurge [24]. Flavonoid signaling pathway was found involved in maintaining of underground adventitious bud paradormancy and paradormancy release in leafy spurge. This signaling pathway together with the action of auxin, ABA, GA, CK, JA, ethylene and BR levels/signals, control the dormancy and the initiation of shoot growth [14,25].



**Figure 1:** Major steps of strigolactones biosynthesis and signal transduction in plants.

Some studies strengthened a framework among auxin, flavonoids and strigolactones. For example, crosstalk modulates strigolactones and auxin levels [26], and flavonoid modulates auxin flow in stems and buds (regulated by MAX1) helps regulating bud repression in *Arabidopsis* [27]. Flavonoids in tea help determining its flavor and astringency [2]. In *Arabidopsis*, MAX1 directly or indirectly regulates the 11 flavonoid genes and transcription factor An2 [27]. One hypothesis is that in the absence of MAX1, the flavonoid level is reduced, result in some auxin transporters derepression and subsequently increase auxin transport in the bud, thereby controlling tea winter dormancy.

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### 3.2 *Strigolactones and Theanine Biosynthesis*

Defective glutamine synthetase (GS1;2) and NADH-dependent glutamate synthase 1 (NADH-GOGAT1) lead to reduced bud outgrowth in rice but some studies have demonstrated that defective *GS1;2* results in reduction of tiller number in the *GS1;2* mutant [28–30], likely due to increased concentration of strigolactones. *CsGS* in tea, encoding glutamine synthetase (which is involved in theanine biosynthesis) is downregulated (42% reduced expression) during winter dormancy [31]. Further investigations are needed to determine how *CsGS* influences theanine biosynthesis and interacts with strigolactones, consequently affecting tea winter dormancy.

### 3.3 *Strigolactones and Caffeine Biosynthesis*

Expression of the gene encoding caffeine synthase and caffeine content decrease during tea dormancy as allantoin contents increase, indicating that caffeine degradation is activated or caffeine biosynthesis is inhibited due to tea winter dormancy [32,33]. Indeed, differential expression of theobromine synthase and caffeine synthase genes occurs during different phases of tea dormancy [34]. In addition, these genes alter bud dormancy status by controlling auxin transport, which is mediated by *MAX1* [24]. It is also known that cytokinins can be transported through PUP1 (purine permease) transport system as adenine and caffeine [35]. Further studies are needed to elucidate how the transport system functions during bud dormancy and whether it interacts with strigolactones to regulate caffeine metabolism in tea.

## 4 Regulators of Strigolactone Functions

### 4.1 *Regulated by miRNAs*

Overexpression of miR156 increases branching in *Brassica napus* [36] and *Arabidopsis* [36,37] and similar branching phenotype has been observed in loss-of-function *max3* and *max4* mutants [38], suggesting a link between strigolactones metabolism and miR156 expression. Some of strigolactones pathway genes such as MAX1, MAX3, MAX4 in *Arabidopsis* and D3, D10, D27 in rice holds target fragments recognized by miR156a–g [39]. *Osa-miR156* overexpressing in rice results in a reduced *D27* transcript level but elevated *D3* and *D14* transcript levels, suggesting a feedback mechanism in strigolactones pathway [40]. Altogether, these studies unveiling a new regulatory pathway of strigolactones function by *osa-miR156* to control dormancy [39].

In active and dormant tea buds, numerous tea miRNAs which are differentially expressed have been detected [41]. An HXXXD-type acyl-transferase-like protein-coding gene, targeted by cs-miR414, is involved in maintaining BR homeostasis [42]. Strigolactones (possibly regulated by cs-miRNA 164), auxin (by cs-miRNA 397), CK (by cs-miRNA 1846), ABA (by cs-miRNA408) and GA (by cs-miRNA 1886) are also downstream products of regulatory gene network of cs-miRNAs [41]. Some target transcripts have been identified being differentially expressed in a dormant bud-specific suppression subtractive hybridization (SSH) library [34,43].

### 4.2 *Regulated by Environmental Stress*

Unfavorable external factors, such as nutrients, water and low temperature, would induce the growth to dormancy and will quickly resume growth in the absence of these unfavorable factors [44]. In accordance with the central roles of strigolactones in stress responses, strigolactones biosynthetic genes *MAX1*, *MAX3* and *MAX4* are influenced by drought, salt and ABA in *Arabidopsis* leaves, further supporting the notion

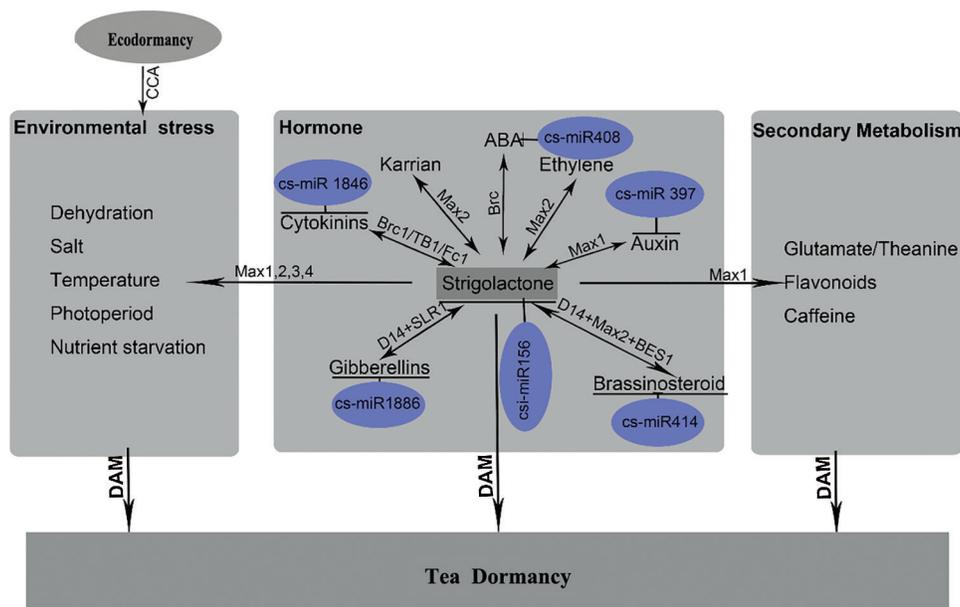
that stress-mediated strigolactones homeostasis is essential for boosting plant resistance against environmental stresses [45]. Application of strigolactone analogue GR24 improves drought tolerance in *Arabidopsis*, demonstrating positive regulatory role of strigolactones for improving plant tolerance to drought in both an ABA-dependent and ABA-independent manner [46]. So, we speculated that strigolactones may play dominant roles in adaptation to abiotic stress in tea.

Nutrient starvation-induced phenotypes can be affected by the strigolactones biosynthetic pathway. Moreover, the extreme branching phenotype associated with nitrogen application levels of the strigolactone biosynthetic mutant *max4* indicate that the influence of nitrogen limitation on branching is mediated (at least in part) by strigolactones. Phosphorous deficiency, which is regulated by strigolactones, affects tillering in rice [47]. GR24 application can increase wild-type pea nodule number and restore the reduced nodule number to wild-type in the strigolactone-deficient *rms1* mutant. The modified strigolactones derivatives application to enhance crops nodule growth would be a cost-effective way to contribute to nitrogen-fixing and plant development [48]. It is interesting to find out whether strigolactones are involved in the high ammonium utilization capacity in tea.

Strigolactones levels or signaling can be affected by light intensity [49]. strigolactones act downstream of the phyB-dependent responses to different red-to-far red light (R: FR) ratios [50]. *Arabidopsis* phyB mutants are defective in detecting R: FR ratios, and in high R: FR light, these mutants exhibit reduced branching, whereas *max2* mutants are highly branched [51]. Similar, In *sorghum*, both null mutation of phyB and low R: FR ratios induced by shading and defoliation affect branching and upregulate the expression of *Sbtb1* (*Teosinte branched 1*), *SbMAX2* and *SbDRM1* [52], suggesting that phyB helps determine whether buds become dormant or active via strigolactones. strigolactones might play a role in determining growth status via a series of *MAX2* or *BRC* (branched) of its biosynthesis or signaling to preserve normal growth.

Strigolactones are positive regulators by controlling the expression of different stress or ABA-responsive genes related to plant growth and environment stress responses in stress and diverse ABA signaling pathways. Moreover, defective strigolactones signaling transmission also results in depressed CK degradation oxidase (CKX) genes expression. Altogether, these results reveal that coordinated network among strigolactones, ABA and CK regulates plants adaptation to different abiotic stress [45]. strigolactones in conjunction with other phytohormones could favor nutrients and water assimilate by promoting root development [49]. Therefore, the use of strigolactones derivatives could favor the adaptation of the plant architecture to such as drought and phosphates abiotic stress [48].

Thus, we propose a model explaining the interactions between strigolactones and terpenoid hormones (auxin, cytokinin, ABA, GA, BRs), secondary metabolism and abiotic stress in tea (Fig. 2). This model will pave the way for uncovering the mechanism underlying secondary metabolism, growth and winter dormancy regulation in tea. However, further investigations should be performed to obtain direct evidence for the role of strigolactones biosynthesis and signaling in tea, especially in the regulation of tea winter dormancy.



**Figure 2:** A predicted functional network underlying winter dormancy in tea. The phytohormones strigolactones and their integration with secondary metabolism and environmental stress regulatory pathways may control the dormancy process in tea

## 5 Conclusions and Future Perspective

Strigolactones are crucial for efficient nutrient allocation in plants, especially under Pi and N deficiency. Strigolactones also play essential roles in responding to drought and salt environment. Moreover, strigolactones can also stimulate seed germination and inhibit shoot branching. The observation that strigolactone mutants exhibit weakened bud dormancy activity suggests that strigolactones play a dominant role of dormancy in plants; Strigolactones, along with ABA, GA, BR, CK, ethylene and auxin, may act directly on buds to coordinately regulate bud outgrowth and dormancy. In tea, genes encoding caffeine synthase and flavonoid synthase differentially express in various dormancy phases. These enzymes change bud development through regulating auxin flow, which is mediated by MAX1, a protein involved in strigolactones biosynthesis or attributed to the same transport system as strigolactones. Therefore, strigolactones may mediate secondary metabolism in tea during the winter dormancy period.

The regulation of dormancy and, more importantly, the control of growth activation at bud burst are highly important for maintaining productivity and building biomass in perennial plants [53,54]. We have merely begun to understand some aspects of the roles of strigolactones as a phytohormone, and its interactions with secondary metabolism and abiotic stress tolerance in tea are yet to be elucidated. Doing so will build a more complete picture of the role of strigolactones in the growth of perennial plants. Further elucidating how strigolactones regulates the processes of dormancy, cold acclimation, and freezing tolerance will help us develop crop plants that are better adapted to new and changing climates, thus increasing tea yields and quality.

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**Conflicts of Interest:** The authors declare that they have no conflicts of interest to report regarding the present study.

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