

総説

Developmental Control of Horticultural Plants Using Strigolactone to Improve Marketability

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Abstract

Height control, branching, adventitious root formation, shelf life are very important traits that determine the quality and marketability of horticultural plants so that various type of plant growth regulators and synthetic analogs are widely used. In particular, branching and plant height control are the key traits for cut flower and pot plant production in floricultural industry. Strigolactone is a new phytohormone known to control branching and leaf senescence in many plants. However, commercial application related to strigolactone biosynthesis and signaling has not been developed despite its structure and physiological role has been identified. In this review, we suggest potentiality of commercial application related to strigolactone in order not only to control growth and development but also to improve marketability of horticultural plants.

Keywords: Branching, Cuttings, Ethylene, Height control, Ripening, Shelf life

Introduction

Phytohormones, also called plant growth regulators are small chemical substances but profoundly influence the growth and development of plants. There are five classical plant hormones such as abscisic acid (ABA), auxin, cytokinin, gibberellin, and ethylene. In addition, brassinosteroids, polyamines, salicylic acid, peptides involved in cell-to-cell signaling, and strigolactones are also considered plant hormones. Various types of synthetic phytohormones have been widely used in order to control plant growth

and development in horticultural industry. Synthetic auxins are not only used for stimulation of pigmentation, enlargement, ripening of fruits such as tomato, eggplant, melon but also used for prevention of fruit falling of apple and pear (Ada et al., 2013; de Jong et al., 2009; Watanabe et al., 2008). Indole-3-butyric acid (IBA) and 1-naphthaleneacetic acid (NAA), synthetic auxins, are used in order to stimulate adventitious root formation of apple stock for grafting and various ornamental plants (Fig. 1A and B) (Divin et al., 2011; Karakurt et al., 2009). 2, 4-dinitrophenylhydrazine (2,

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4-D) is widely used for herbicide (Fig. 1C) (Egana et al., 2011; Schulz and Segobye, 2016). Gibberellins are used for induction of seedless fruits, stimulation or delay of ripening, enlargement of cucumber fruit, flowering stimulation of azalea and cyclamen, stimulation of germination and the growth of flowering plants (Chen and Chang, 1972; de Jong et al., 2009; Martínez et al., 1994; Vendrell 1969; Yamaguchi and Kamiya, 2001). In addition, benzyl adenine (6-benzyl aminopurine, BA), thidiazuron (TDZ), forchlorfenuron (1-(2-Chloro-4-pyridyl)-3-phenylurea), belong to cytokinin family and these are used as a stimulant for the pigmentation and enlargement of fruits, fruiting, and so on (Fig. 1D, E and F). Ethephon, converted to ethylene in plant, accelerates fruit ripening and pigmentation of apple, persimmon, and peach and stimulates flowering of pineapple and mango (Fig. 1G).

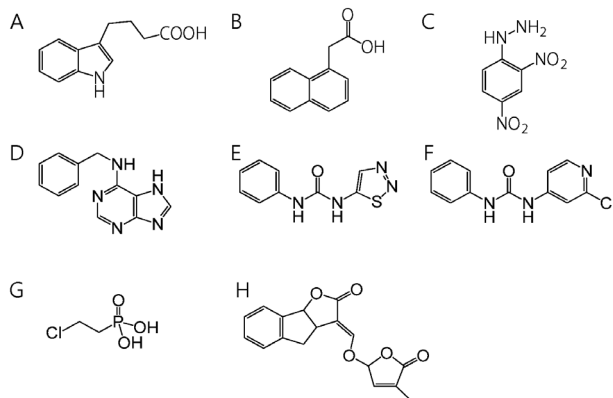


Fig.1 Plant hormones in plants.

A: Indole-3-butyric acid (IBA), B: 1-naphthaleneacetic acid (NAA), C: 2,4-dinitrophenylhydrazine (2,4-D), D: benzyl adenine (6-benzyl aminopurine, BA), E: thidiazuron (TDZ), F: forchlorfenuron (1-(2-Chloro-4-pyridyl)-3-phenylurea), G: Ethephon, H: Strigolactone.

Strigolactone is a brand new phytohormone and plays an important role in inhibition of branching in many plants the synthetic analog, e.g. GR24, was developed and has been widely used in hormonal regulation research in plants (Fig 1 H). Strigolactone is involved in the symbiosis with fungi by acting recognition signals in the soil and controls shoot branching in many plants (Akiyama et al., 2005; Gomez-

Roldan et al., 2008; Umehara et al., 2008; Alder et al., 2012). In 1966, it was firstly reported and its structure was identified (Cook et al., 1966; Cook et al., 1972; Siame et al., 1993). Strigolactones are derived from carotenoid pathway, terpenoid lactones (Matusova et al., 2005; Alder et al., 2012). Various types of strigolactones have been identified in many plant species. However, all strigolactones have four rings as their common structure (Fig. 2). Three rings (ring A, B, and C) form tricyclic lactone and another is butenoic group (ring D). Of four basic rings in strigolactone, conformation of two rings (A and B) varies depending on side groups whereas other two rings, C and D, are not only highly conserved in most strigolactones but also considered playing an important role in biological activity (Xie et al., 2010).

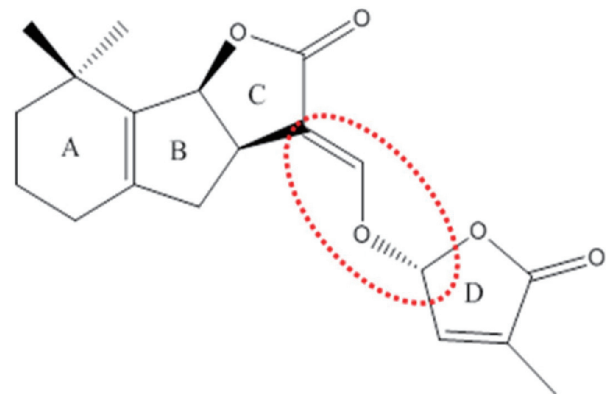


Fig.2 Basic structure of strigolactones.

Red dot circle shows enol-ether bridge between tricyclic lactone (ring A, B, and C) and butenoic group (ring D) (modified from Kohlen et al., 2013).

Height control, branching, adventitious root formation and shelf life are very important features which determine the quality and marketability of horticultural plants so that various type of plant growth regulators, synthetic analogs, inhibitors have been widely applied. This review will focus on the physiological role of strigolactones and the potential applicability in order not only to control growth and development but also to improve marketability of horticultural plants.

Biosynthesis of Strigolactone in plant

A decade ago, it was suggested that strigolactones might be synthesized from carotenoid pathway (Matusova et al., 2005). Various genes involved in strigolactones biosynthesis and signaling have been identified and characterized in *Arabidopsis* (*AtD27*, *MAX3*, *MAX4*, *MAX2*, *AtD14*, *BRC1*), pea (*Psd27*, *RMS5*, *RMS1*, *RMS4*, *PsBRC1*), rice (*D27*, *D17/HTD1*, *D10*, *D3*, *D14*, *FC1*), and petunia (*DAD3*, *DAD1*, *PhMAX2A-B*, *DAD2*). Precursor of strigolactones, carlactone is produced by three steps. All-*trans*- β -carotene is isomerized to 9-*cis*- β -carotene catalyzed by D27 (Alder et al., 2012). 9-*cis*- β -carotene is cleaved by CCD7 so that it produces β -apo-10'-carotenal which is then cleaved by CCD8 to produce carlactone. D-ring, one of the basic structures of strigolactones, is formed in this step (Fig. 3).

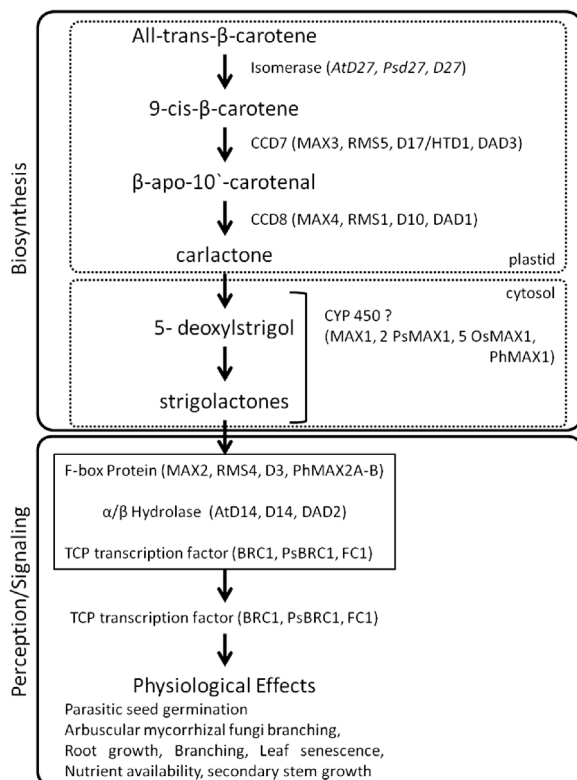


Fig.3 Strigolactone biosynthesis and genes involved in plants (modified from Czarnecki et al., 2013 and de Saint Germain et al., 2013).

MAX2 isolated from *Arabidopsis* and *D14* (*DWARF14*) from rice, which belong to F-box protein and α/β -hydrolase respectively, are considered strigolactone receptor (Arite

et al., 2009; Beveridge and Kyoizuka, 2010). *D14* is known to involve in the downstream of strigolactone biosynthesis as a signaling hormone or convert strigolactone to be active by cleaving D-ring. *D14* protein group, *DAD2*, *AtD14* and *OsD14*, share the same common structure of a hydrophobic active site that contains Ser-His-Asp. Three amino acids are conserved in all *D14* protein groups. Nocturnal condition or senescence signal induces expression of strigolactone synthesis genes, *MAX3* and *MAX4*, in the leaves of *Arabidopsis* resulting in accelerated leaf senescence by enhancing strigolactone signal pathway (Ueda and Kusaba, 2015). In addition, *MAX3* and *MAX4* are induced in the leaves under drought and salt stresses (Ha et al., 2014) by suggesting the strong possibility of strigolactone synthesis in plant leaves.

Height control and Branching

Cut flowers account for the largest market share in floricultural industry followed by pot plants. In order to produce high quality cut flowers, long and strong flower stalk and one big flower are required. In addition nutrient should be concentrated only a single stalk. On the other hand, pot plants require short plant height with large number of branches with many flowers. Considering such requirements for cut flower and pot plant production, branching control can be the main key factor for cut flowers and pot plants quality, one branch versus many branches. Pinching has been widely used to control the plant height and induce branching for pot plants. When the apical meristem was removed by pinching, plants lose apical dominance governed by auxin synthesized from apical meristem. Therefore, axillary buds start to develop resulting in formation of new branches. In addition, various dwarf reagents such as; ancymidol, daminozide, paclobutrazol, chlormequat chloride, ethephon, and uniconazole-P are used for controlling plant height by inhibiting stem elongation. Ancymidol, paclobutrazol, and uniconazole-P

are applied by a drench, whereas daminozide is applied by a foliar spray. Chlormequat chloride can be applied by both methods.

Several mutants were found with increased shoot branching phenotype, *more axillary growth (max)* in *Arabidopsis* (Stirnberg et al., 2002; Sorefan et al., 2003; Booker et al., 2004), *ramous (rms)* in pea (Beveridge et al., 1994, 1996; Beveridge et al., 2000), and *dwarf (d)* and *htd* genes in rice (Ishikawa et al., 2005; Zou et al., 2006; Arite et al., 2007; Jiang et al., 2013). *e9* mutant (*d53*) of rice, a dominant mutant, has a phenotype of dwarf and high-tillering even though amount of 2'-epi-5-deoxystigol is much higher in the wild type suggesting this mutant is involved in strigolactone signaling (Jiang et al., 2013). In this mutant, D53 proteins are accumulated so that it blocks strigolactone signaling resulting in dwarf and high tillering phenotype. *High-tillering dwarf (htd)* in rice (*Oryza sativa*) produces a lot of axillary buds leading increased number of tillers and also *htd* showed dwarf phenotype due to reduction of internode and panicle (Zou et al., 2005). A recessive gene, *htd1*, controls high-tillering and dwarf phenotype in rice. There is a nucleotide substitution in *OsCCD7* leading an amino acid substitution from proline to leucine resulting in *htd1* gene in mutant. *OsCCD7* is an orthologous gene of *MAX3/CCD7* in *Arabidopsis*. For *max3* mutant, a recessive gene of *MAX3* exhibits shorter petiole and reduced length of leaf blade (Booker et al., 2004). Therefore, these mutants imply some genes involving in the biosynthesis of strigolactone may be related to form tight and small rosette which causes various physiological disorder of flowering perennials. For chrysanthemums in particular, rosette is the one of the physiological dormant phenomenon and appears when chrysanthemums are exposed to high temperature followed by the low temperature during the autumn. Under these environmental conditions, internode of chrysanthemums is not elongated and rosette, as a result, is formed resulting in delayed growth of chrysanthemum and

chrysanthemum cannot flower even if optimum temperature and day-length are given.

Branching is the one of the important phenotype required to produce pot plants in floricultural practice. Once plants lose the function of strigolactone resulting in increasing number of branches, it affects plant height as a result. Therefore, branching and low plant height can be controlled without pinching and application of dwarf reagents. Furthermore, it will be possible to induce desirable phenotypes, if we can control the strigolactones at a certain level in plants or its signaling pathway. In addition, this may contribute not only to protect the environment by reducing the amount of dwarf reagents but also to reduce the labor costs.

Adventitious root formation for cuttings

Cutting is the most common techniques widely used for proliferation of clones whose genetic background is identical. It is not only the easy way to maintain good genotypic characteristics but also guarantees the same quality for farmers. In order to stimulate adventitious root formation from cutting, NAA is usually treated and adventitious roots are formed from the basal part.

It has been known that strigolactones inhibit adventitious root formation in *Arabidopsis* and pea (Rasmussen et al., 2012b). It was also reported that the formation of adventitious root was promoted, when biosynthesis of strigolactone was inhibited (Rasmussen et al., 2012a). Number of adventitious roots was significantly increased for both mutants with defective in biosynthesis of strigolactones and in response. For three mutants defective in biosynthesis, *max1*, *max3*, and *max4*, number of adventitious root increased by 3 times at maximum than wild type. *max1*, unresponsive mutant to strigolactone signal, showed 5 times of increase in number of adventitious root in *Arabidopsis* (Rasmussen et al., 2012b). GR24, synthetic strigolactone, inhibited adventitious root formation of *max1*, *max3*, and *max4* whereas *max2* formed adventitious root even

though GR24 is treated. Therefore, these results suggest strigolactone signaling rather than biosynthesis pathway is involved in the adventitious root formation of cuttings.

In addition, Rasmussen et al. (2012a) suggested inhibition of strigolactone would improve adventitious root formation of horticultural plants. Fluridone, known as a carotenoid inhibitor and herbicides widely used, was treated to five commercial plants, *Tradescantia fluminensis* (Wandering Jew), *Trachelospermum jasminoides* (Chinese jasmine), *Jasminum polyanthum* (Pink jasmine), *Plumbago auriculata* (Cape leadwort), and *Pongamia pinnata* (Indian Beech Tree) (Rasmussen et al., 2012a). Application of fluridone improved rooting and number of adventitious roots of *P. auriculata* and *J. polyanthum* cuttings and optimum concentration was 100 nM. However, application did not affect rooting of *T. fluminensis* and *T. jasminoides*. For the Genus *Tradescantia*, stem cuttings is the technique widely used and adventitious roots are formed very well even though synthetic auxin for inducing rooting is not treated on the basal part. Combined application of fluridone with commercial rooting hormone did not improve the rooting percentage compared to rooting hormone treatment, moreover, number of adventitious roots in *P. auriculata* and *J. polyanthum* decreased.

T. fluminensis is monocot and herbaceous plant and *T. jasminoides* woody and has very long stems. Climbing is the common characteristic of Both plants. In particular, *T. jasminoides* is likely to restore apical dominance when apical meristem is removed because the very next node produces axillary bud and then new main stem elongates. *J. polyanthum* and *P. auriculata* are shrubs and have climbing characteristics. However, there is lack of information about effect of combination or fluridone only treatment on rootings of herbaceous horticultural plants such as chrysanthemums, carnations, poinsettias, bulbs, cacti, woody plants, etc. These plants are used as pot plants and cut

flowers and accounts for large amount of annual yield. Therefore, it is necessary to identify how strigolactone signaling affects adventitious root formation in various horticultural plants in order to develop practical techniques to stimulate rooting.

Ripening and Senescence process of fruits and vegetables

Quality control of postharvest fruits, vegetables, and flowers are very important due to their short shelf-life (Paliyath et al., 2008). During the ripening processes of fruits or senescence process of leafy vegetables or flowers, various physiological and biochemical changes occur from a cellular level to tissue level, by changing biochemical characteristics such as color, flavor, texture, and taste. Ethylene biosynthesis and signaling is one of the key factors for fruit ripening and senescence of leafy vegetables and cut flowers. Methionine, for the first step in ethylene biosynthesis, is converted to S-Adenosyl methionine (SAM) by Methionine adenosyl transferase and then, as a sequential step, SAM is converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase. ACC oxidase oxidizes ACC to produce ethylene (Wang et al., 2002). Leaves of *Arabidopsis* mutants lack of strigolactone biosynthesis showed delayed senescence phenotype under the dark condition (Ueda and Kusaba, 2015), whereas *MAX3* and *MAX4*, genes involved in biosynthesis of strigolactones in *Arabidopsis*, were strongly expressed by ethylene treatment under the same condition. In addition, it is suggested strigolactones is synthesized in the leaf under abiotic stresses such as drought and salt stresses (Ha et al., 2014), although it has been widely known that strigolactone or its precursor are synthesized in the root and transported through xylem (Kohlen et al., 2011). Therefore, strigolactone can be possibly synthesized in other organs, such as flowers, fruits, because many flowers and fruits synthesize carotenoid as a component of pigments in the way that strigolactone is

involved in fruit ripening or flower senescence via complex hormonal responses (Zhu et al., 2010; Su et al., 2015).

Leaves of strigolactone insensitive mutant (*Atd14*) and signaling defective mutants (*max2*) kept green even though GR 24 was treated. This result implies induction of senescence in leaves is stimulated by strigolactone signaling rather than by strigolactone content. Also, strigolactone stimulates leaf senescence by enhancing signaling pathway mediated by ethylene. Therefore strigolactone may affect the leaf senescence in combination with ethylene so that crosstalk of hormonal signaling should not be ignored in postharvest physiology. Hormonal signaling crosstalk between ethylene and strigolactone would induce enhanced senescence of leafy vegetables and cut leaves under the dark condition where they are stored during transportation. On the other hand, hormonal relationship between ethylene and strigolactone has not been identified in fruits and flowers yet. In tomato, for example, various type of strigolactones, such as Orobanchol, 7-oxoorobanchol, solanacol, didehydroorobanchol, has been isolated but their physiological role in tomato is not clear (Kohlen et al., 2013).

Conclusion

Strigolactones have been identified in 1960s but their physiological role in plants have been receiving attention recently (Cook et al., 1966; Umehara et al., 2008). Various physiological effects such as; crosstalk with auxin, hyphal growth of mycorrhizal fungi, response to soil nitrogen and phosphate, branching inhibition of axillary buds in plants, accelerated senescence in plant leaves, have been reported in many plants including *Arabidopsis*, rice, petunia and so on, and strigolactones are considered a new plant hormones. Analogs of plant hormones are widely used in horticultural industry in order to induce adventitious root formation in cuttings, differentiation, redifferentiation,

and dedifferentiation in tissue culture and inhibitors of hormones are applied to improve shelf life of cut flowers, fruits, etc. On the other hand, few reports can be found that make an attempt in order to control growth and development of horticultural plants. Therefore, if the role of strigolactone is known better, it will be possible to develop application technique using strigolactones, analogs, or inhibitors in order to improve marketability of horticultural plants not only by controlling branching of axillary buds but also by inhibiting ethylene biosynthesis.

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