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Review

Practical applications of brassinosteroids in horticulture—Some field perspectives

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ABSTRACT

Brassinosteroids (BS) are a class of polyhydroxylated steroidal plant hormones. They are of ubiquitous occurrence in plant kingdom and are implicated in a wide range of physiological, biochemical and molecular responses in plants, such as seed germination, cell division and elongation, vascular differentiation, photomorphogenesis, photosynthesis, enzyme activation and senescence. They have also been found to protect plants from various abiotic and biotic stress factors, such as salt, temperature, water, heavy metals and pathogens. BS also enhance the yield of several cereal, legume, and oil seed crops. Moreover, they also increase the fruit production and quality of the fruits, in different plants of horticultural importance. The number of such reports is comparatively lesser, yet an attempt has been made to review such studies and is presented here, comprehensively.

1. Introduction

Brassinosteroids (BS) constitute a new group plant hormones that has been given different designations such as “New Class of plant hormones” (Clouse and Sasse, 1998; Khripach et al., 1999), polyhydroxylated steroidal plant hormone (Fariduddin et al., 2014) and a new and unique class of plant growth regulators (Sirhindi, 2013). They were for the first time discovered in the pollen grains of *Brassica napus*, after which they are given the name “Brassinosteroids”, which were initially named as “Brassins”. They were of ubiquitous occurrence in plant kingdom and have also been reported in different plant parts. However their quantity varies in different plant parts. Young growing tissues contain a higher content of BS than mature tissues. Pollen and immature seeds are the richest sources of BS with a range of 1–100 $\mu g\ kg^{-1}$ (fresh tissue), whereas shoots and leaves usually possess lower amounts of 0.01–0.1 $\mu g\ kg^{-1}$ (fresh tissue).

The role assigned to them, in the beginning, was the reproductive development (Clouse and Sasse, 1998). However, later research proved that they play pivotal and decisive roles in a wide spectrum of growth and developmental responses. The processes influenced by BS include cell division and cell elongation in stems and roots, photo-morphogenesis, reproductive development, leaf senescence, and also in stress responses (Ali et al., 2007; Sirhindi, 2013; Fariduddin et al., 2014). Clouse and Sasse (1998) and Sasse (2003) proposed that BS are essential for normal growth and development. The essentiality of BS in plant growth and development has been proved in different studies wherein “brassinazole” an inhibitor of BS biosynthesis has been used. The other processes influenced by BS include shoot and root growth, fertility and seed germination, cell elongation, vascular differentiation, xylem formation in epicotyls, and also in the regulation of expression of several genes involved in xylem development (Clouse and Sasse, 1998; Taiz and Zeiger, 2004). They also affect cotyledon growth, root elongation, leaf formation and growth, and plant biomass. Exogenous application of BS also improves the activities of different enzymes such as carbonic anhydrase, nitrate reductase (Ali et al., 2006; Alam et al., 2007), rubisco (Yu et al., 2004) and those involved in Calvin cycle (Fedina et al., 2008). In addition to this, BS have a great potential to confer resistance to plants against various biotic and abiotic stresses, such as salinity (Ali et al., 2007), water stress (Vardhini and Rao, 2002), temperature extremes (Sirhindi, 2013), and heavy metals (Hayat et al., 2007; Ali et al., 2008a,b; Yusuf et al., 2012). Besides these key roles, BS have also been found to affect whole physiology of the plant, starting from seed germination to harvest or seed maturation. Application of BS has been found to enhance the seed germination in chickpea (Ali et al., 2005), Indian mutard (Sirhindi, 2013) and tobbacco (Leubner-Metzger, 2001). Furthermore, the exogenous application of BS has been found to enhance the yield of a number of crop plants such as *Brassica juncea*, *Arachis hypogeal, Vigna radiata* (Vardhini and Rao, 2002), *Lycopersicon esculentum* (Ali et al., 2006) and *Cicer arietinum* (Ali et al., 2007), both under stress and stress free conditions. However, few treatments have been performed in the field, under real growing condition. Most of the studies have been conducted with plants grown under controlled environmental conditions in the laboratory. Many BS and BS-analogues that showed high biological activity in bioassays or controlled-

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environment experiments failed to stimulate plants grown under field conditions (Hola et al., 2010). This can be explained by various reasons such as the timing of BS application (Nunez et al., 2003), duration of exposure and the BS treatment, frequency of BS treatment and the dose, type and mode of BS can also substantially affect the growth/yield promoting activity of these compounds (Hola et al., 2010). However, more accurate studies on dosage, mode and time of application, fit brassinosteroid suitability for the plant or cultivar, and association with other phytohormones are needed.

The preliminary results regarding the increases of crop yield and antistress effects on several plants are effective at very low doses. Besides this, they are easily metabolized, as seen for tomato and serradella (Adam and Schneider, 1999; Schneider, 2002) and are recommended as ecologically safe plant growth promoters (Kang and Guo, 2011) with promising properties for practical use in agriculture and horticulture. In an attempt to reduce the cost of BR synthesis and increase BR stability when applied, many types of BS spirostane analogues have been produced (Zullo and Adam, 2002), including spirostanean alogues of BS, such as BB6 and MH5, DI-31 (BB16) and DI-100. These BS analogues are characterized by the presence of a spiroketalic ring instead of the typical BR side chain, and these chemicals possess BS-like activity (Bajguz and Tretyn, 2003).

The regulation of plant growth and development and the subsequent yield is a highly complex phenomenon, which is governed by a spectrum of factors, both exogenous and endogenous. Among the endogenous ones, plant hormones are very critical, which are extensively exploited in order to improve crop performance/yield (Montoya et al., 2005). Although, it is well established that BS have a beneficial effect on the growth and productivity of many agricultural and horticultural crops. However, these are very costly and cannot be afforded by the farmers of developing countries. To make them cost effective, some commercial analogues of many BS have been synthesised and are used in many countries.

2. Occurrence

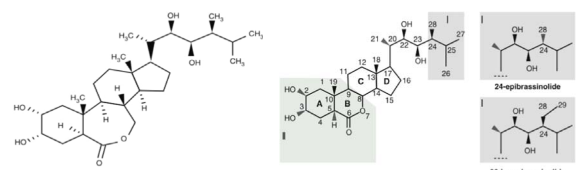
The brassinosteroids; brassinolide (BL) and castasterone (CS) ubiquitously occur in the plant kingdom. The presence of brassinosteroids (BS) has been demonstrated in almost every part of plants, such as pollen, flower buds, fruits, seeds, vascular cambium, leaves, shoots and roots. These steroidal compounds occur in free form and conjugated to sugars and fatty acids. To this date, about 69 BS have been isolated from plants (Bajguz and Tretyn, 2003). BS are also present in the insect and crown galls, for example the galls of *Castanea crenata, Distylium racemosumor* and *Catharanthus roseus*. These plants have higher levels of BS than the normal tissues. Also, young growing tissues contain higher levels of BS than mature tissues. Pollen and immature seeds are the richest sources of BS with a range of 1–100 μg kg^{-1} fresh weight, while shoots and leaves usually have a lower amounts of 0.01–0.1 μg kg^{-1} fresh weight. Since the discovery of BL in 1979, 69 BRs have been isolated from 64 plant species including 53 angiosperms (12 monocotyledons and 41 dicotyledons), 6 gymnosperms, 1 pteridophyte (*Equisetum arvense*), 1 bryophyte (*Marchantia polymorpha*) and 3 algae (*Chlorella vulgaris, Cystoseira myrica and Hydrodictyon reticulatum*) (Table 1; Bajguz and Tretyn, 2003).

Table 1
Occurrence of brassinosteroids in different plant species/families.

Plant Group	Number/name of plants
Angiosperms (Monocots)	12
Angiosperms (Dicots)	41
Gymnosperms	06
Pteridophytes	01
Bryophytes	01
Algae	03
Total	64

3. Structure

Plant sterols, which can be converted to BL via teasterone, typhasterol and castasterone, are synthesised by an isoprenoid biosynthetic pathway including acetyl CoA, mevalonate, isopentenyl pyrophosphate, geranyl pyrophosphate and farnesyl pyrophosphate (Symons et al., 2008). Brassinosteroids are polyhydroxy steroid lactone with the structure of brassinolide (BS) and the structure of steroids having the same carbon skeleton of animal steroids as cholestane, ergostane, and stigmastane. However, the chemists and plant physiologists used an approach in which the most active and first identified representative of this class of compounds, i.e., brassinolide (BL), is taken as the basis structure of the system. A great diversity in the basic structure at cyclic and side chain is found which is responsible for important metabolic transformations to form two other highly active analogues of BS namely 24-Epibrassinolide (EBL) and 28-Homobrassinolide (HBL) (Figure A and B). Furthermore, BS are nontoxic (Esposito et al., 2011) and environmentally-friendly hormones (Kang and Guo, 2011).



A. Brassinolide (BL) **B.** 24-Epibrassinolide (EBL) and 28-Homobrassinolide (HBL)

4. Application of BS in horticulture

Horticultural plants include herbaceous plants (annual and perennial), fresh fruits and vegetables. They exhibit a wide variation and diversity in their cultivated varieties with differences in flower or fruit colour, shape and value. Horticulture and associated green industries are rapidly developing professional fields with increasing importance to society. However, it is well known that the production of horticultural plants is also typified by intense management, high management cost, environmental control, significant technology use and high risk. Different ways have been explored to enhance the productivity of the horticultural plants, which include the fertilizers, high yielding cultivars/hybrids, pesticides, insecticides etc. However, their frequent and repetitive use is proving counter productive. Moreover, some of them are hazardous to the environment and the ecosystem. Among the eco-friendly means, the application of the plant growth regulators in general and BS in particular are proving highly beneficial for plant productivity. In order to meet the development of horticulture industry, the focus of this review is to detail the role of BS, a kind of nontoxic and environmentally friendly hormone, on horticultural crops. Moreover, the progress in chemical synthesis technology and practical application of BS in horticultural crops for enhancing yield, quality and stress tolerance have a promising prospects in near future.

4.1. Effects on tomato

There are a large number of studies wherein tomato plants have been given BS treatment at different stages and through different modes such as pre-sowing seed soaking, root dipping and foliar spray. Application of BL and related compounds as pre-sowing seed treatment for 4 h in 1 ppm solution enhanced the yield of tomato plants under green house conditions (Takematsu and Izumi, 1985). The application of 22,23,24-triepibrassinolide and 28-homobrassinolide increased tomato fruit setting by 43–111%, while with 28-homobrassinolide this increase was 118–129% (Mori et al., 1986). Similarly, Savelieva et al.