Brassinosteroids: A Class of Plant Hormone

Shamsul Hayat • Aqil Ahmad
Editors

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Springer

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Dedicated To The
Aligarh Muslim University
Aligarh

Contents

Foreword

Brassinosteroids (BRs) are endogenous plant growth-promoting hormones found throughout the plant kingdom that influence cellular expansion and proliferation and the phenotype of mutants affected in BR biosynthesis or signaling clearly show that these plant steroids are essential regulators of a variety of physiological processes including organ elongation, vascular differentiation, male fertility, timing of senescence, and leaf development. BRs are structurally similar to animal steroid hormones, and like their animal counterparts, BRs regulate the expression of hundreds of genes, impact the activity of numerous metabolic pathways, and help control overall developmental programs leading to morphogenesis. Several books covering various aspects of BR biology and chemistry appeared in 1991, 1999 and 2003. However, in the past seven years a great deal of progress has been made in understanding specific components of BR signal transduction and in clarifying mechanisms by which BR perception ultimately results in changes in the expression of specific genes associated with different developmental programs. The number of physiological processes known to involve BR action has also expanded and significant experiments quantifying the utility of BR application in practical agricultural have been documented. Therefore, it is very timely that the editors of the current volume have collected and integrated a series of informative chapters on BR molecular biology, physiology, metabolism and practical applications.

BR signaling has been intensively studied over the past ten years, becoming one of the best-characterized plant hormone pathways. The role of membrane-bound receptor kinases and their cytoplasmic targets in perceiving and propagating the BR signal have been elucidated and novel BR-dependent transcription factors that regulate hundreds of different genes have been characterized. Two chapters in the current volume expound on these advances in BR signaling and a third chapter is devoted to the use of global proteomic and genomic technologies that have further advanced our understanding of BR mechanisms. Besides signal transduction, regulation of endogenous BR levels in the plant is critical to BR function and two chapters in the current edition thoroughly address these issues. The known and proposed physiological processes involving BR action are then documented in detail in a total of six chapters, covering general physiology, interactions with light and the role of BRs in abiotic and biotic stress responses. In view of the multitude of demonstrated effects BR application has on crop plants, it is highly appropriate that the remaining six chapters of this book are devoted to a variety of topics involving practical BR applications including horticulture, phytoremediation, herbicide protection and medicine.

The extensive coverage of a range of BR topics presented in this volume, written by active researchers in the field, will provide a useful resource for plant hormone biologists and graduate students in plant physiology, biochemistry, horticulture and agronomy. The editors should be commended for adding another useful edition to the ever-growing body of BR literature.

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Preface

The entire range of the developmental processes in plants is regulated by a shift in the hormonal concentration, tissue sensitivity and their interaction with the factors operating around the plants. Out of the recognized hormones, attention has largely been focused on five (Auxins, Gibberellins, Cytokinin, Abscisic acid and Ethylene). However, in this book, the information about the most recent group of phytohormone (Brassinosteroids) has been incorporated by us. It is a class of over 40 polyhydroxylated sterol derivatives, ubiquitously distributed throughout the plant kingdom. A large portion of these steroids is restricted to the reproductive organs (pollens and immature seeds). Moreover, their strong growth-inducing capacity, recognized as early as prior to their identification in 1979, tempted the scientists to visualize the practical importance of this group of phytohormones.

Chapter 1 of this book (which embodies a total of 17 chapters), gives a comprehensive survey of the occurrence and chemical structure of brassinosteroids. Chapter 2 deals with currently available data on brassinosteroid signaling pathway and the latest findings on brassinosteroid signaling regulatory mechanisms in plants. The recent progress in brassinosteroid research in relation to the regulation of brassinosteroid metabolism is discussed in Chapter 3. Chapter 4 summarized the recent advances in brassinosteroids signaling research in rice. The Chapter 5 views the physiological action of brassinosteroids which depends on their concentration in a plant, the medium, the method of exogenous treatment, light of different spectral composition and the mechanism of regulation of the photomorphogenesis. Chapter 6 summarizes the current knowledge of the impact of brassinosteroids on the chloroplasts, and on various components of photosynthetic apparatus. Chapter 7 discusses the physiological modifications that occur in cells, tissue or whole plants when exposed to brassinosteroids and their practical use in agriculture, describing the analogues and the dosages used in field and laboratory experiments. An insight into the genomic and non-genomic events involved in the brassinosteroid promoted plant cell growth is covered in chapter 8. Practical application of BRs to horticultural crops for enhancing crop production and their protection is discussed in Chapter 9. Chapter 10 specifically discusses potential roles for heat shock proteins, antioxidant metabolites and enzymes in brassinosteroid-induced thermal tolerance. In addition, as stress mechanisms are not exclusive of plants, therefore this chapter also discusses the possible way of involving BRs in protection during normal growth stimulation. The Chapter 11 reports data on the protective effect of brassinosteroids on plants, treated with herbicides that inhibit photosynthetic electron transport at the PSII level. It also discusses the biochemical and physiological causes of their protective effects. Role of brassinosteroids under biotic stress is discussed in Chapter 12. Chapter 13 describes how to use a variation in the controls in solving the problems of the interpretation, where it may be another factor contributing to the non reproducibility and/or ambiguity in the results, obtained in relation to brassinosteroids. The Chapter 14 summarizes the latest developments in the field of immunoassay of brassinosteroids. The use of transcriptomics and proteomics techniques to study the regulation of brassinosteroids in plants is introduced in Chapter 15. Role of brassinosteroids for phytoremediation application is discussed in Chapter 16. Finally in Chapter 17 prospects of brassinosteroids in clinical application has been described.

This book is not an encyclopedia of reviews but includes a selected collection of newly written, integrated, illustrated reviews describing our knowledge of brassinosteroids. The aim of this book is to tell all about brassinosteroids, by the present time. The various chapters incorporate both theoretical and practical aspects and may serve as baseline information for future researches through which significant developments are possible. It is intended that this book will be useful to the students, teachers and researchers, both in universities and research institutes, especially in relation to biological and agricultural sciences.

With great pleasure, we extend our sincere thanks to all the contributors for their timely response, their excellent and up-to-date contributions and consistent support and cooperation. The authors are thankful to Aligarh Muslim University, Aligarh (U.P.) India that gave us the employment and the seat to work. We are also thankful to Dr. Zaki A. Siddiqui and Dr. Qazi Fariduddin, Department of Botany, Aligarh Muslim University, Aligarh for their encouragement. Thanks are also due to Mr. Mohd Irfan, Research student in the Department of Botany for typesetting and proof reading of the manuscript. We are extremely thankful to Springer, The Netherlands for expeditious acceptance of our proposal and completion of the review process. Subsequent cooperation and understanding of their staff is also gratefully acknowledged. We express our sincere thanks to the members of our family for all the support they provided and the neglect and loss they suffered during the preparation of this book.

Finally, we are thankful to the Almighty God who provided and guided all the channels to work in cohesion and coordination right from the conception of the idea to the development of the final version of this treatise 'Brassinosteroids: A Class of Plant Hormone' until the successful completion of the job.

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About Shamsul Hayat

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Chapter 1

BRASSINOSTEROIDS – OCCURENCE AND CHEMICAL STRUCTURES IN PLANTS

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Abstract: Brassinosteroids (BRs) are a class of plant polyhydroxysteroids that have been recognized as a new kind of phytohormones that play an essential role in plant development. BRs occur at low concentrations throughout the plant kingdom. They have been detected in all plant organs (pollen, anthers, seeds, leaves, stems, roots, flowers, and grains) and also in the insect and crown galls. BRs are structurally related to animal and insect steroid hormones. Natural 69 BRs identified so far, have a common 5α-cholestan skeleton, and their structural variations come from the kind and orientation of oxygenated functions in rings A and B. As regards the B-ring oxidation, BRs are divided into 7-oxalactone, 6-ketone (6-oxo) and 6-deoxo (non-oxidized). These steroids can be classified as C_{27}, C_{28} or C_{29} BRs depending on the alkyl-substitution on the C-24 in the side chain. In addition to free BRs, sugar and fatty acid conjugates have been also identified in plants.

Key words: chemical structures, conjugates, occurrence

1. INTRODUCTION

Brassinosteroids (BRs) are a class of plant polyhydroxysteroids that have been recognized as a new kind of phytohormones that play an essential role in plant development. Brassinosteroids are structurally related to animal and insect steroid hormones. Intensive research conducted on BRs reveals that they elicit a broad spectrum of physiological and morphological responses in plants, including stem elongation, leaf bending and epinasty, induction of ethylene biosynthesis and proton pump activation, synthesis of nucleic acid

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and proteins, regulation of carbohydrate assimilation and allocation, and activation of photosynthesis. Furthermore, BRs can protect plants from various biotic and abiotic stresses, such as those caused by salt, high temperatures, and heavy metals (Sasse, 2003; Bajguz and Hayat, 2009).

2. OCCURENCE OF BRASSINOSTEROIDS

Brassinosteroids are plant growth promoting molecules found at low concentrations throughout the plant kingdom and are widely distributed in lower and higher plants (Tables 1–6). They have been detected in all plant organs such as pollens, anthers, seeds, leaves, stems, roots, flowers, and grains. BRs are also present in the insect and crown galls, for example the galls of *Castanea crenata*, *Distylium racemosum* or *Catharanthus roseus*. These plants have higher levels of BRs than the normal tissues. Also, young growing tissues contain higher levels of BRs than mature tissues. Pollen and immature seeds are the richest sources of BRs 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. In the pollen of *Cupressus arizonica* the concentration of 6-deoxotyphasterol (6-deoxoTY) can be about 6400-fold greater than brassinolide (BL). Furthermore, the highest concentration of BR, 6.4 mg 6-deoxoTY per kilogram pollen, has been detected in *Cupressus arizonica*. BRs occur endogenously at quite low levels. Compared to the pollen and immature seeds, the other plant parts contain BRs in the microgram or nanogram levels of BRs per kilogram 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) (Tables 1–4), 6 gymnosperms (Table 5), 1 pteridophyte (*Equisetum arvense*), 1 bryophyte (*Marchantia polymorpha*) and 3 algae (*Chlorella vulgaris*, *Cystoseira myrica* and *Hydrodictyon reticulatum*) (Table 6) (Fujioka, 1999; Bajguz and Tretyn, 2003).

Table 1. The occurrence of brassinosteroids in the monocotyledons

Family/Species	**Plant parts**	**Brassinosteroid**	**Isolated quantity (μg/kg fresh wt.)**	**References**
Arecaceae				
Phoenix dactylifera L.	Pollen	24-epiCS		Zaki *et al*. (1993)
Gramineae				
Lolium perenne L.	Pollen	25-MeCS	0.001	Taylor *et al*. (1993)
Oryza sativa L.	Shoots	CS	0.014	Abe *et al*. (1984b)
		DS	0.008	Abe (1991)
		BL		

	Bran	6-deoxoCS 28-homoTE 28-homoTY		Abe *et al*. (1995a)
	Seeds	CS TE 6-deoxoCS		Park *et al*. (1994b)
Phalaris canariensis L.	Seeds	CS TE	5 0.7	Shimada *et al*. (1996)
Secale cereale L.	Seeds	CS TY TE 6-deoxoCS 28-norCS SE		Schmidt *et al*. (1995b)
	Seedlings	SE 2,3-diepiSE secasterol		Antonchick *et al*. (2003, 2005)
Triticum aestivum L.	Grain	CS TY TE 6-deoxoCS 3-DT		Yokota *et al*. (1994)
Gramineae				
Zea mays L. dent corn	Pollen	CS TY TE	120 6.6 4.1	Suzuki *et al*. (1986)
sweet corn	Pollen	CS 28-norCS DS	27.2 18.3 16.9	Gamoh *et al*. (1990)
	Primary roots	BL CS 6-deoxoCS 6-deoxoCT 6-deoxoTE 6-deoxoTY 28-norCS		Kim *et al*. (2000a, 2005, 2006)
Liliaceae				
Erythronium japonicum Decne	Pollen anthers	TY	5	Yasuta *et al*. (1995)
Lilium elegans Thunb.	Pollen	BL CS TY TE	1–5 10–50 10–50 1–5	Suzuki *et al*. (1994b) Yasuta *et al*. (1995)
Lilium longiflorum Thunb.	Pollen	BL CS TY		Abe (1991)
	Anthers	3-DT TE-3-La TE-3-My TE-Glu	 720	Abe *et al*. (1994) Asakawa *et al*. (1994, 1996) Soeno *et al*. (2000)
Tulipa gesneriana L.	Pollen	TY		Abe (1991)
Typhaceae				
Typha latifolia Mey	Pollen	TY TE	68	Schneider *et al*. (1983) Abe (1991)

Table 2. The occurrence of brassinosteroids in the dicotyledons – the Apetalae

Family/Species	**Plant parts**	**Brassinosteroid**	**Isolated quantity (µg/kg fresh wt.)**	**References**
Betulaceae				
Alnus glutinosa (L.) Gaertn.	Pollen	BL CS		Plattner *et al*. (1986)
Cannabaceae				
Cannabis sativa L.	Seeds	CS TE	600 1800	Takatsuto *et al*. (1996b)
Caryophyllaceae				
Gypsophilla perfoliata L.	Seeds	24-epiBL		Schmidt *et al*. (1996)
Lychnis viscaria L.	Seeds	24-epiCS 24-epiSE		Friebe *et al*. (1999)
Chenophyllaceae				
Beta vulgaris L.	Seeds	CS 24-epiCS		Schmidt *et al.* (1994)
Fagaceae				
Castanea crenata Sieb. et Zucc.	Galls	CS BL 6-deoxoCS	1 4–12 9–26	Yokota *et al*. (1982a) Ikeda *et al*. (1983)
	Shoots leaves	CS 6-deoxoCS	2–6 15–30	Arima *et al*. (1984)
Polygonaceae				
Fagopyrum esculentum Moench	Pollen	BL CS	5 7.1	Takatsuto *et al*. (1990b)
Rheum rhabarbarum L.	Panicles	BL CS 24-epiCS		Schmidt *et al*. (1995a)

Table 3. The occurrence of brassinosteroids in the dicotyledons – the Chloripetalae

Family/Species	**Plant parts**	**Brassinosteroid**	**Isolated quantity (µg/kg fresh wt.)**	**References**
Apiaceae				
Apium graveolens L.	Seeds	2-deoxyBL		Schmidt *et al*. (1995c)
Daucus carota Ssp. *sativus* L.	Seeds	BL CS 24-epiCS		Schmidt *et al*. (1998)

Brassicaceae				
Arabidopsis thaliana (L.) Heynh.	Shoots ecotype Columbia (wild-type)	CS	0.75	Fujioka *et al*. (1996, 1997, 2000a) Nomura *et al*. (2001) Katsumata *et al*. (2008)
		6-deoxoCS	0.71	
		TY	0.11	
		6-deoxoTY	0.95	
		BL	0.04	
		TE	0.025	
		6-deoxoCT	1.96	
		6-deoxoTE	0.1	
		6-deoxo-3DT	0.13	
		3-epi-6-deoxo -28-norCT		
		28-norCS		
		28-norTY		
		7-oxTY		
		7-oxTE		
	Seeds ecotype Columbia (wild-type)	BL	0.5–1.9	Fujioka *et al*. (1998)
		24-epiBL	0.22	
		CS	0.4–5	
		6-deoxoCS	1.5–3	
		TY	1.3	
		6-deoxoTY	0.5–5.4	
		6-deoxoTE	0.5–1	
	Seeds (ecotype 24)	24-epiBL	0.22	Schmidt *et al*. (1997)
		CS	0.36	
Brassicaceae				
Arabidopsis thaliana (L.) Heynh.	Root callus	BL		Konstantinova *et al*. (2001)
		3-epiBL		
Brassica campestris var. *pekinensis* L.	Seeds	BL	940	Abe *et al*. (1982, 1983) Ikekawa *et al*. (1984)
		28-norBL	1300	
		CS	1600	
		28-norCS	780	
		28-homoCS	130	
Brassica napus L.	Pollen	BL	100	Grove *et al*. (1979)
Raphanus sativus L.	Seeds	BL	0.3	Schmidt *et al*. (1991, 1993b)
		CS	0.8	
		TE		
		28-homoTE		
Fabaceae				
Cassia tora L.	Seeds	BL	0.018	Park *et al*. (1994a)
		CS	0.16	
		TY	0.007	
		TE	0.04	
		28-norCS	0.008	
Robinia pseudo-acacia L.	Pollen	CS		Abe *et al*. (1995b)
		TY		
		6-deoxoCS		

(*continued*)

(*continued Table 3.*)

Family/Species	Plant parts	Brassinosteroid	Isolated quantity (µg/kg fresh wt.)	References
Fabaceae				
Dolichos lablab L.	Seeds	DL	160	Baba *et al*. (1983)
		DS	50	Yokota *et al*. (1982b,
		28-homoDS	20	1983b, 1984)
		28-homoDL	12	
		BL		
		CS		
		6-deoxoCS		
		6-deoxoDS		
Vicia faba L.	Seeds	BL	190	Park *et al*. (1987)
		24-epiBL	5	Ikekawa *et al*. (1988)
		CS		
		28-norCS		
	Pollen	BL	181	Gamoh *et al*. (1989)
		CS	134	
		28-norCS	628	
		DS	537	
	Shoots	6-deoxoCT	1.27	Fukuta *et al*. (2004)
		6-deoxoTE	0.17	
		6-deoxoTY	0.40	
		6-deoxoCS	3.57	
		TY	0.02	
		CS	0.37	
Psophocarpus tetragonolobus (Stickm.) DC.	Seeds	BL		Takatsuto (1994)
		CS		
		6-deoxoCS		
		6-deoxoDS		
Fabaceae				
Ornithopus sativus Brot.	Seeds	CS	5	Schmidt *et al*. (1993a)
		24-epiCS	25	
	Shoots	CS		Spengler *et al*. (1995)
		6-deoxoCS		
		24-epiCS		
		6-deoxo-24-epiCS		
		6-deoxo-28-norCS		
Theaceae				
Thea sinensis L.	Leaves	28-norCS	0.002	Abe *et al*. (1983,
		28-homoCS	<0.001	1984a)
		BL	0.006	Morishita *et al*. (1983)
		CS	0.1	Ikekawa *et al*. (1984)
		TY	0.06	
		TE	0.02	

Camellia sinensis (L.) Kuntze	Leaves	6-deoxoCS 24-epiBL 3-DT TY 3-deoxoTY 28-homoDL	Gupta *et al*. (2004)
	Immature seeds	6-deoxo-28-norCT 6-deoxo-28-norTE 3-dehydro-6-deoxo-28-norTE 6-deoxo-28-norTY 6-deoxo-28-norCS	Bhardwaj *et al*. (2007)
Fabaceae			
Phaseolus vulgaris L.	Seeds	BL CS 2-epiCS 3-epiCS 2,3-diepiCS 3,24-diepiCS TY TE 6-deoxoCS 3-epi-6-deoxoCS 1β-OH-CS 3-epi-1α-OH-CS DL DS 6-deoxoDS 6-deoxo-28-homoDS 25-MeDS 2-epi-25-MeDS 2,3-diepi-25-MeDS 2-deoxy-25-MeDS 2-epi-2-deoxy-25-MeDS 3-epi-2-deoxy-25-MeDS 6-deoxo-25-MeDS 25-MeDS-Glu 2-epi-25-MeDS-Glu	Yokota *et al*. (1983c, 1987c) Kim *et al*. (1987, 1988, 2000b); Kim (1991) Park *et al*. (2000)
Fabaceae			
Pisum sativum L.	Seeds	BL CS TY 6-deoxoCS 2-deoxyBL	Yokota *et al*. (1996)

(*continued*)

(*continued Table 3.*)

Family/Species	Plant parts	Brassinosteroid	Isolated quantity (µg/kg fresh wt.)	References
	Shoots	BL CS 6-deoxoCS TY 6-deoxoCT 6-deoxoTE 6-deoxo-3DT 6-deoxoTY	0.2–0.8 0.4–2.4 5.2 1 3.75 0.047 0.074 0.8	Nomura *et al*. (1997, 1999, 2001)
Myrtaceae				
Eucalyptus calophylla R. Br.	Pollen	BL		Takatsuto (1994)
Eucalyptus marginata Sn.	Pollen	DS		Takatsuto (1994)
Rosaceae				
Eriobotrya japonica (Thunb.) Lindl.	Flower buds	CS		Takatsuto (1994)
Rutaceae				
Citrus unshiu Marcov.	Pollen	BL CS TY TE		Abe (1991)
Citrus sinensis Osbeck	Pollen	BL CS	36.2 29.4	Motegi *et al*. (1994)
Aegle marmelos (L.) Correa	Leaves	24-epiBL		Sondhi *et al*. (2008)

Table 4. The occurrence of brassinosteroids in the dicotyledons – the Sympetalae

Family/Species	Plant parts	Brassinosteroid	Isolated quantity (µg/kg fresh wt.)	References
Apocynaceae				
Catharanthus roseus G. Don.	Cultured cells	BL CS 6-deoxoTY 6-deoxoTE 6-deoxoCS CT 6-deoxoCT 3-epi-6-deoxoCT 3-epi-6-deoxo-28-norCT 3-DT TY TE	0.4–8.7 0.6–4.5 0.76 0.047 5.9–18.9 2–4 30	Choi *et al*. (1993, 1996, 1997) Fujioka *et al*. (1995, 2000b) Park *et al*. (1989) Suzuki *et al*. (1993, 1994a, 1994c, 1995) Yokota *et al*. (1990)

Asteraceae				
Zinnia elegans L.	Cultured cells	CS TY 6-deoxoCS 6-deoxoTY 6-deoxoTE 6-deoxoCT	0.2 0.8 0.3 0.3 8.7	Yamamoto *et al*. (2001, 2007)
Helianthus annuus L.	Pollen	BL CS 28-norCS	106 21 65	Takatsuto *et al*. (1989)
Solidago altissima L.	Shoots	BL		Takatsuto (1994)
Boraginaceae				
Echium plantagineum L.	Pollen	BL		Takatsuto (1994)
Convolvulaceae				
Pharbitis purpurea Voigt	Seeds	CS 28-norCS	1.1 0.2	Suzuki *et al*. (1985)
Cucurbitaceae				
Cucurbita moschata Duch.	Seeds	BL CS		Jang *et al*. (2000)
	Pollen	BL CS		Pachthong *et al*. (2006)
Lamiaceae				
Perilla frutescens (L.) Britt.	Seeds	CS		Park *et al*. (1994b)
Solanaceae				
Nicotiana tabacum L.	Cultured cells	CS		Park *et al*. (1994b)
Lycopersicon esculentum Mill.	Shoots	CS 6-deoxoCS 28-norCS	0.2 1.7 0.03	Yokota *et al*. (1997d)
	Root	6-deoxo-28-norCT 6-deoxo-28-norTY 6-deoxo-28-norCS	0.22 0.13 0.09	Yokota *et al*. (2001)
-dwarf mutant	Shoots	6-deoxoCT 6-deoxoTE 6-deoxo-3DT 6-deoxoTY 6-deoxoCS 6α-OH-CS CS BL TY 3-DT TE CT	1.1 0.04 0.03 0.5 5.2 0.2 < 0.001 < 0.001 < 0.001 < 0.001 < 0.001	Bishop *et al*. (1999)

Table 5. The occurrence of brassinosteroids in gymnosperms

Family/Species	Plant parts	Brassinosteroid	Isolated quantity (µg/kg fresh wt.)	References
Cupressaceae				
Cupressus arizonica Greene	Pollen	6-deoxoTY *6-deoxo-3DT* 6-deoxoCS CS TY TE 28-homoCS 3-DT BL	6400 2300 1200 1000 460 5 4 2 <1	Griffiths *et al*. (1995)
Ginkgoaceae				
Ginkgo biloba L.	Seeds	TE	15	Takatsuto *et al*. (1996a)
Pinaceae				
Piceae sitchensis Trantv. ex Mey	Shoots	CS TY	5 7	Yokota *et al*. (1985)
Pinus silvestris L.	Cambial region	BL CS		Kim *et al*. (1990)
Pinus thunbergii Parl.	Pollen	TY	89.5	Yokota *et al*. (1983a)
Taxodiaceae				
Cryptomeria japonica D. Don.	Pollen anthers	TY DL 3-DT 28-homoBL 28-homoDL 23-dehydroBL (cryptolide) 2-epi-23-dehydroBL 3-epi-23-dehydroBL 2,3-diepi-23-dehydroBL		Yokota *et al*. (1998) Watanabe *et al*. (2000)

Table 6. The occurrence of brassinosteroids in lower plants

Family/Species	Plant parts	Brassinosteroid	Isolated quantity (µg/kg fresh wt.)	References
Hydrodictyaceae (green alga)				
Hydrodictyon reticulatum (L.) Lager.	Whole plant	24-epiCS 28-homoCS	0.3 4.0	Yokota *et al*. (1987b)