The chemical characteristic and distribution of brassinosteroids in plants

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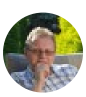

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Review

The chemical characteristic and distribution of brassinosteroids in plants

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Abstract

Brassinosteroids represent a class of plant hormones with high-growth promoting activity. They are found at low levels in pollen, anthers, seeds, leaves, stems, roots, flowers, grain, and young vegetative tissues throughout the plant kingdom. Brassinosteroids are a family of about 60 phytosteroids. The article gives a comprehensive survey on the hitherto known brassinosteroids isolated from plants. The chemical characteristic of brassinosteroids is also presented.

Keywords: Brassinosteroids; Distribution; Structure

Contents

1. Introduction

Brassinosteroids (BRs) represent a new sixth class of plant hormones with wide occurrence in the plant kingdom in addition to auxins, gibberellins, cytokinins, abscisic acid and ethylene. They have unique biological effects on plant growth and development (for reviews see Sasse, 1997, 1999). However, their physiological functions in plants are not fully understood to date. BRs are also growth-promoting plant hormones with structures similar to animal steroidal hormones—ecdysteroids. The biosynthetic and metabolic pathways with enzymatic studies and the molecular mode of action of BRs have been investigated (for reviews see Clouse and Feldmann, 1999; Bishop and Yokota, 2001; Friedrichsen and Chory, 2001; Müssig and Altmann, 2001; Schneider, 2002). Recently, the first BR-biosynthesis inhibitor, brassinazole, was reported (Asami and Yoshida, 1999). In addition to their role in plant development, BRs have the ability to protect plants from various environmental stresses, including drought, extreme temperatures, heavy metals, herbicidal injury and salinity (Sasse, 1999).

This review describes the structural characteristics of BRs and their distribution in the plant kingdom.

2. Chemical structure of brassinosteroids

The history of BRs started when Mitchell et al. (1970) screened pollen from nearly sixty species and half of them caused growth of bean seedlings. The substances from various pollen sources were named ‘‘brassins’’ (for reviews see Yokota, 1999b). In 1979 a steroidal lactone,

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termed brassinolide (BL), was isolated from pollen of rape (*Brassica napus*) (Grove et al., 1979). Its structure was determinated by spectroscopic analysis (EI-MS, FAB-MS, NMR) and X-ray diffraction to be (22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one. The second BR, termed castasterone (CS), has been isolated in 1982 by Yokota et al. (1982a) from the insect galls of chestnut (*Castanea crenata*). The structure of CS was established as (22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one. Since the discovery of BL, the natural occurrence of more than 50 compounds of this group has been reported (Yokota, 1999a).

BRs are derived from the 5-cholestane skeleton and their structural variations come from the type and position of functionality in the A/B rings and the side chain (Fig. 1) (Yokota, 1995, 1997).

With respect to the A-ring, BRs having vicinal hydroxyl groups at C-2α and C-3α. BRs with an α-hydroxyl, β-hydroxyl or ketone at position C-3 are precursors of BRs having 2α,3α-vicinal hydroxyls. On the other hand, BR with 2α,3β-, 2β,3α- or 2β,3β-vicinal hydroxyls probably may be metabolites of 2α,3α-vicinal hydroxyls. The two 2α,3α-vicinal hydroxyl groups at the A-ring represent a general structural feature of most active BRs, such as BL and CS. Decreasing order of activity 2α,3α > 2α,3β > 2β,3α > 2β,3β shown by structure-activity relationship suggests that the α-oriented hydroxyl group at C-2 is essential for greater biological activity of BRs in plants. Biogenic precursors, like typhasterol (TY) and teasterone (TE), have only one hydroxyl group in the A-ring. Also BRs with an 2,3-epoxide group in the A-ring — secasterone (SE) and its 24-epimer (24-*epi*SE) have been found. Furthermore,

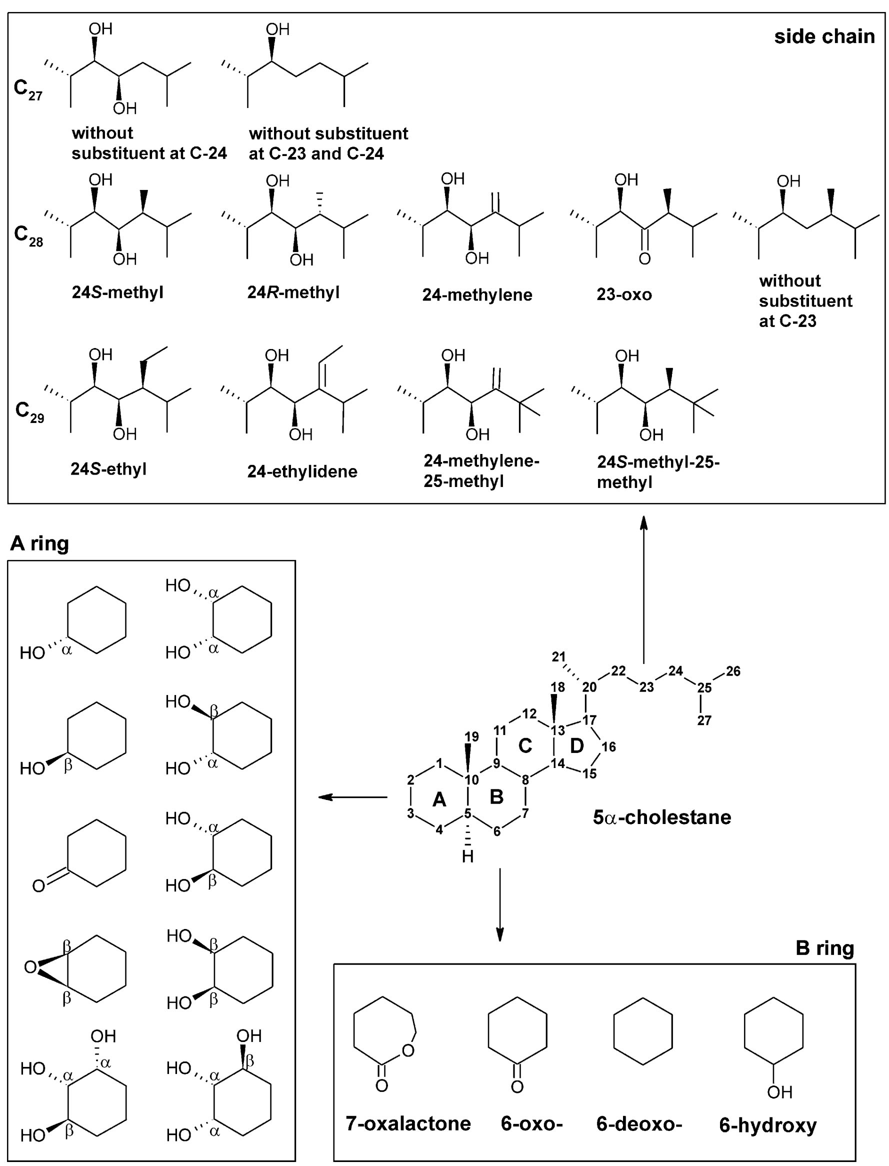


Fig. 1. Different substituents in the A- and B-rings and side chain of naturally occurring brassinosteroids.

Table 1
Division of brassinosteroids according to the B-ring and orientation of hydroxyl, ketone and epoxide groups at position C-1, C-2, C-3 and C-6 in the A-ring

Type of brassinosteroids				
Carbon position	7-Oxalactone	6-Ketone (6-oxo)	6-Deoxo (non-oxidized)	6α-Hydroxy
C(2α,3α)[a]	Brassinolide (BL) 24-*epi*BL 28-NorBL 28-HomoBL Dolicholide (DL) 28-HomoDL 23-DehydroBL	Castasterone (CS) 24-*epi*CS 28-NorCS 28-HomoCS 25-MethylCS (25-MeCS) Dolichosterone (DS) 28-HomoDS 25-MeDS 23-*O*-β-D-Glucopyranosyl-25-MeDS (25-MeDS-Glu)	6-DeoxoCS 6-Deoxo-24-*epi*CS 6-Deoxo-28-norCS 6-DeoxoDS 6-Deoxo-28-homoDS 6-Deoxo-25-MeDS	
C(2α,3β)[a]	3-*epi*BL 3-*epi*-23-dehydroBL	3-*epi*CS 3,24-Di*epi*CS	3-*epi*-6-DeoxoCS	
C(2β,3α)[a]	2-*epi*-23-dehydroBL	2-*pi*CS 2-*epi*-25-MeDS 23-*O*-β-D-glucopyranosyl-2-*epi*-25-MeDS (2-*epi*-25-MeDS-Glu)		
C(2β,3β)[a]	2,3-Di*epi*-23-dehydroBL	2,3-Di*epi*CS 2,3-Di*epi*-25-MeDS		
C(3α)[a]	2-DeoxyBL	Typhasterol (TY) 28-HomoTY 28-NorTY 2-Deoxy-25-MeDS	6-DeoxoTY 6-Deoxo-28-norTY 3-*epi*-6-DeoxoCT	
C(3β)[a]		Teasterone (TE) 28-HomoTE TE-3-myristate (TE-3-My) TE-3-laurate (TE-3-La) TE-3-*O*-β-D-glucoside (TE-3-Glu) 3-*epi*-2-Deoxy-25-MeDS Cathasterone (CT)	6-DeoxoTE 6-DeoxoCT 6-Deoxo-28-norCT	
C(1α,2α,3β)[a]		3-*epi*-1α-OH-CS		
C(1β,2α,3α)[a]		1β-OH-CS		
C(2α,3α,6α)[a]				6α-OH-CS
C3[b]		3-DehydroTE (3-DT)	3-Dehydro-6-deoxoTE	
C(2β,3β)[c]		Secasterone (SE) 24-*epi*SE		

[a] Hydroxyl group.
[b] Ketone group.
[c] Epoxide group.

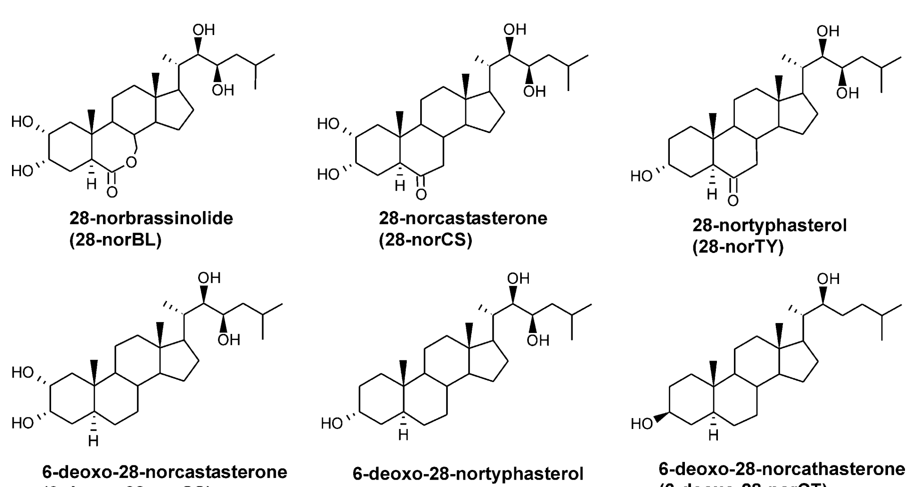


Fig. 2. Chemical structures of C_{27} brassinosteroids.

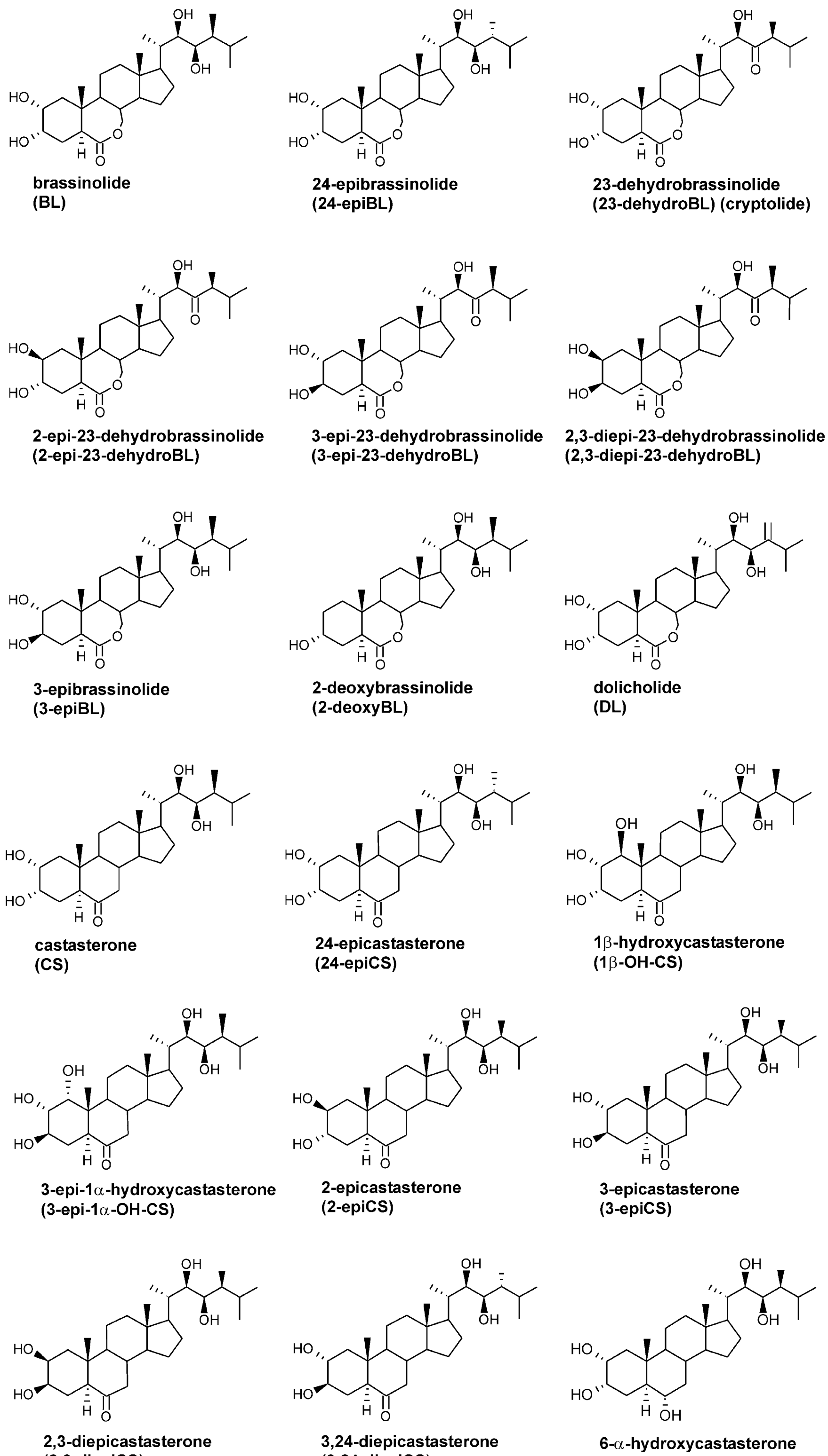
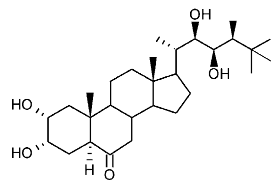
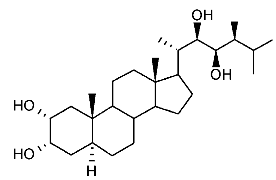


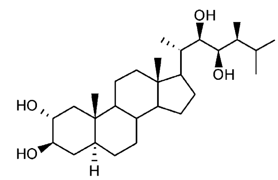
Fig. 3. Chemical structures of C_{28} brassinosteroids.



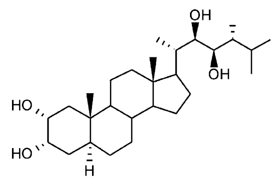
25-methylcastasterone (25-MeCS)



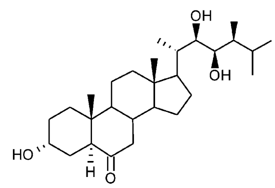
6-deoxocastasterone (6-deoxoCS)



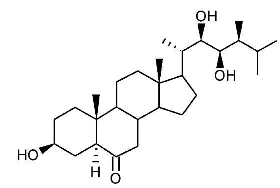
3-epi-6-deoxocastasterone (3-epi-6-deoxoCS)



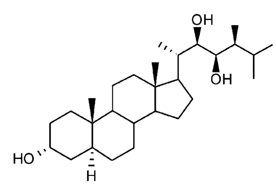
6-deoxo-24-epicastasterone (6-deoxo-24-epiCS)



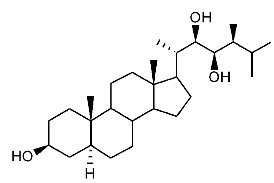
typhasterol (TY)



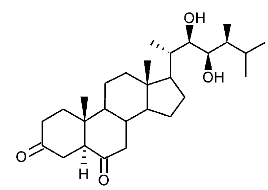
teasterone (TE)



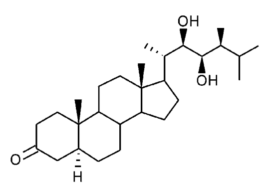
6-deoxotyphasterol (6-deoxoTY)



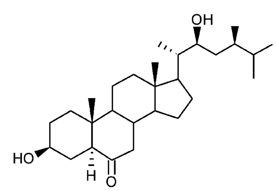
6-deoxoteasterone (6-deoxoTE)



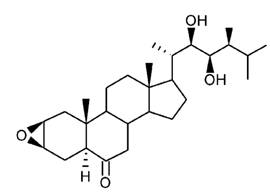
3-dehydroteasterone (3-DT)



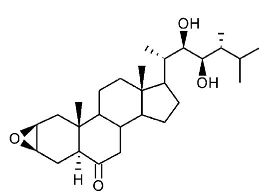
3-dehydro-6-deoxoteasterone (3-dehydro-6-deoxoTE)



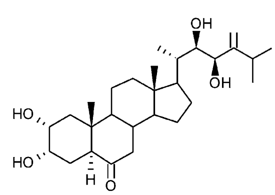
cathasterone (CT)



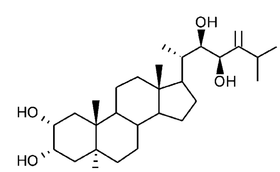
secasterone (SE)



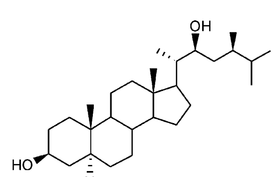
24-episecasterone (24-epiSE)



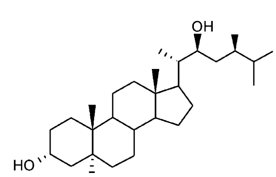
dolichosterone (DS)



6-deoxodolichosterone (6-deoxoDS)

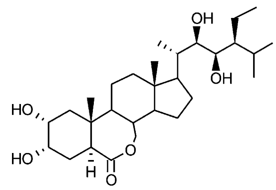


6-deoxocathasterone (6-deoxoCT)

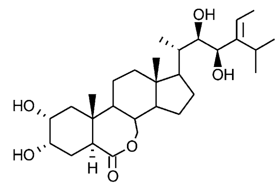


3-epi-6-deoxocathasterone (3-epi-6-deoxoCT)

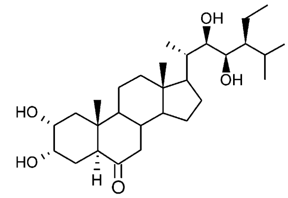
Fig. 3 (*continued*).



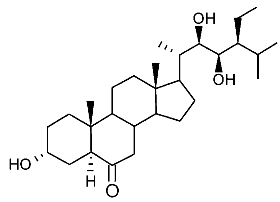
28-homobrassinolide (28-homoBL)



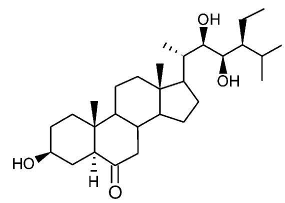
28-homodolicholide (28-homoDL)



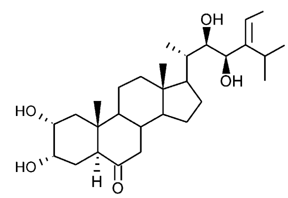
28-homocastasterone (28-homoCS)



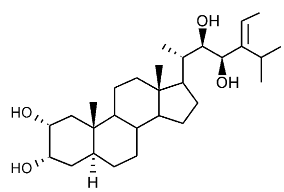
28-homotyphasterol (28-homoTY)



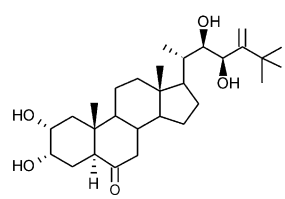
28-homoteasterone (28-homoTE)



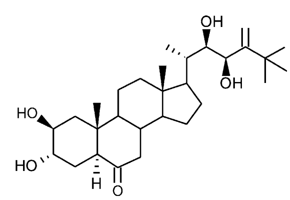
28-homodolichosterone (28-homoDS)



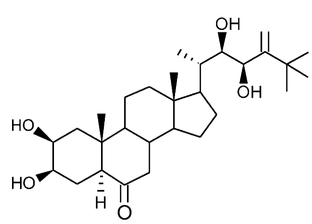
6-deoxo-28-homodolichosterone (6-deoxo-28-homoDS)



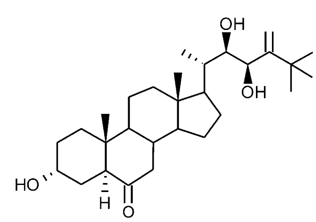
25-methyldolichosterone (25-MeDS)



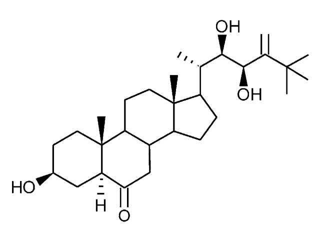
2-epi-25-methyldolichosterone (2-epi-25-MeDS)



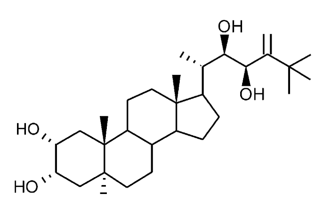
2,3-diepi-25-methyldolichosterone (2,3-diepi-25-MeDS)



2-deoxy-25-methyldolichosterone (2-deoxy-25-MeDS)



3-epi-2-deoxy- -25-methyldolichosterone (3-epi-2-deoxy-25-MeDS)



6-deoxo-25-methyldolichosterone (6-deoxo-25-MeDS)

Fig. 4. Chemical structures of C_{29} brassinosteroids.

there are two BRs having a 3-keto group, such as 3-dehydroteasterone (3-DT) and 3-dehydro-6-deoxoteasterone (6-deoxo-3-DT) but also BRs having additional hydroxyl group in the A-ring at position C-1α or C-1β, such as 3-*epi*-1α-hydroxycastasterone (3-*epi*-1α-OH-CS) and 1β-hydroxycastasterone (1β-OH-CS) (Table 1) (Mandava, 1988; Kim, 1991; Adam and Petzold, 1994; Yokota, 1995; Bishop et al., 1999; Fujioka, 1999; Schmidt et al., 2000).

With respect to the B-ring oxidation stage, BRs are divided into 7-oxalactone, 6-ketone (6-oxo) and 6-deoxo (non-oxidized) types. As a fourth type, there is only one BR with hydroxyl group at C-6α, namely 6α-hydroxycas-

Table 2
Division of brassinosteroids according to different substituents in the side chain

Type	Representatives	Total number
23-Oxo	23-DehydroBL, 2-*epi*-23-dehydroBL, 3-*epi*-23-dehydroBL, 2,3-di*epi*-23-dehydroBL	4
24*S*-Methyl	BL, 3-*epi*BL, CS, 2-*epi*CS, 3-*epi*CS, 2,3-di*epi*CS, TY, TE, TE-3-La, TE-3-My, 6-deoxoCS, 3-*epi*-6-deoxoCS, 3-DT, SE, 6-deoxoTY, 2-deoxyBL, 3-*epi*-1α-OH-CS, 1β-OH-CS, 6α-OH-CS, TE-3-Glu, 6-deoxoTE, 3-dehydro-6-deoxoTE	22
24*R*-Methyl	24-*epi*BL, 24-*epi*CS, 3,24-di*epi*CS, 6-deoxo-24-*epi*CS, 24-*epi*SE	5
24-Methylene	DL, DS, 6-deoxoDS	3
24*S*-Ethyl	28-HomoBL, 28-homoCS, 28-homoTE, 28-homoTY	4
24-Ethylidene	28-HomoDL, 28-homoDS, 6-deoxo-28-homoDS	3
24-Methylene-25-methyl	25-MeDS, 2-*epi*-25-MeDS, 2,3-di*epi*-25-MeDS, 2-deoxy-25-MeDS, 3-*epi*-2-deoxy-25-MeDS, 6-deoxo-25-MeDS, 25-MeDS-Glu, 2-*epi*-25-MeDS-Glu	8
24*S*-Methyl-25-methyl	25-MeCS	1
Without substituent at C-23	CT, 6-deoxoCT, 3-*epi*-6-deoxoCT	3
Without substituent at C-24	28-NorBL, 28-norCS, 28-norTY, 6-deoxo-28-norCS, 6-deoxo-28-norTY	5
Without substituents at C-23 and C-24	6-Deoxo-28-norCT	1

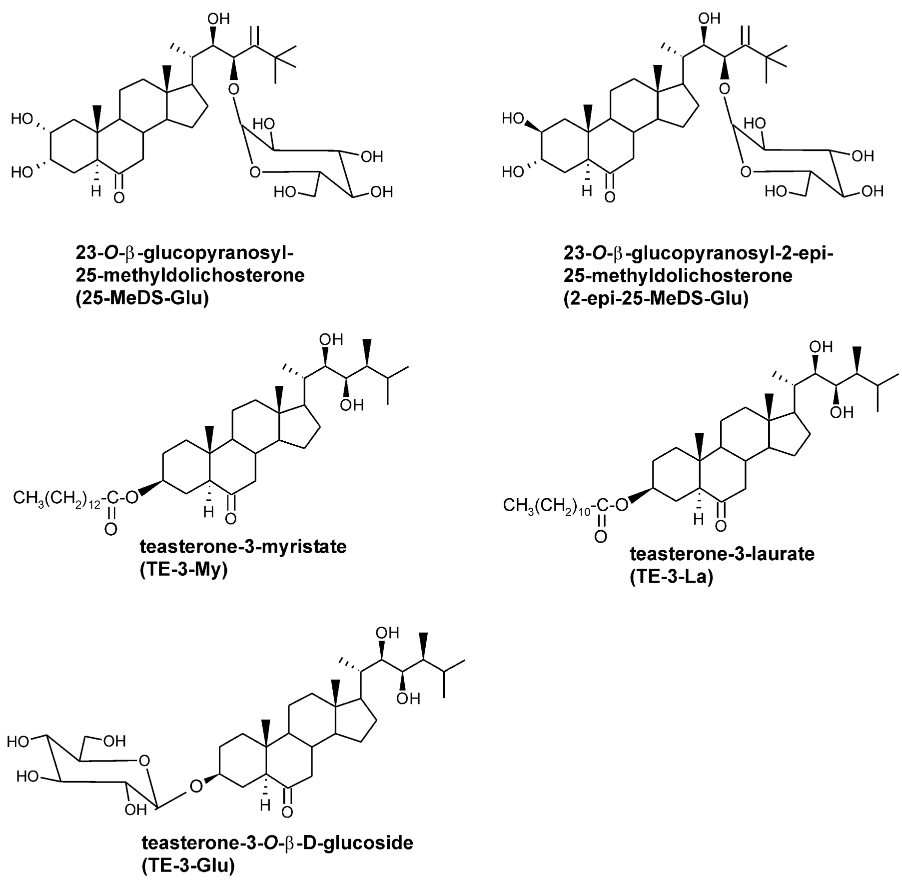


Fig. 5. Chemical structures of brassinosteroid conjugates.

tasterone (6α-OH-CS) (Table 1). In general, 7-oxalactone BRs have stronger biological activity than 6-ketone types, and 6-deoxo types. Sometimes 6-ketone BRs have an activity similar to 7-oxalactone compounds, but non-oxidized BRs reveal almost no activity in the bean internode test, or very weak in the rice lamina inclination test (Kim, 1991; Bishop et al., 1999; Fujioka, 1999).

Furthermore with respect to the A/B ring functionalities the hitherto clarified members can be divided into following groups:

- BRs with 7-membered 7-oxalactone-B-ring and vicinal 2,3-hydroxyl groups;
- 6-oxo compounds with a 6-membered B-ring

Table 3
Brassinosteroids isolated for the first time in plants

No.	Common name	Chemical name	Plant	Reference
1.	Brassinolide	(22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one	*Brassica napus* L.	Grove et al., 1979
2.	Castasterone	(22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Castanea crenata* Sieb. et Zucc.	Yokota et al., 1982a
3.	Dolicholide	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-B-homo-7-oxa-5α-ergost-24(28)-en-6-one	*Dolichos lablab* L.	Yokota et al., 1982b
4.	28-Norcastasterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-5α-cholestan-6-one	*Brassica campestris* var. *pekinensis* L. *Thea sinensis* L.	Abe et al., 1983
5.	28-Homocastasterone	(22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-ethyl-5α-cholestan-6-one	*Brassica campestris* var. *pekinensis* L. *Thea sinensis* L.	Abe et al., 1983
6.	28-Norbrassinolide	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-B-homo-7-oxa-5α-cholestan-6-one	*Brassica campestris* var. *pekinensis* L.	Abe et al., 1983
7.	Dolichosterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-5α-ergost-24(28)-en-6-one	*Dolichos lablab* L.	Baba et al., 1983
8.	28-Homodolichosterone	(22*R*,23*R*,24(28)*E*)-24(28)-ethylidene-2α,3α,22,23-tetrahydroxy-5α-cholestan-6-one	*Dolichos lablab* L.	Baba et al., 1983
9.	Typhasterol (2-deoxycastasterone)	(22*R*,23*R*,24*S*)-3α,22,23-trihydroxy-24-methyl-5-cholestan-6-one	*Typha latifolia* G.F.W. Mey	Schneider et al., 1983
10.	28-Homodolicholide	(22*R*,23*R*,24(28)*E*)-24(28)-ethylidene-2α,3α,22,23-tetrahydroxy-B-homo-7-oxa-5α-cholestan-6-one	*Dolichos lablab* L.	Yokota et al., 1983b
11.	6-Deoxocastasterone	(22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestane	*Phaseolus vulgaris* L.	Yokota et al., 1983c
12.	6-Deoxodolichosterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-5α-ergost-24(28)-ene	*Phaseolus vulgaris* L.	Yokota et al., 1983c
13.	28-Homobrassinolide	(22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-etylo-B-homo-7-oxa-5α-cholestan-6-one	*Brassica campestris* var. *pekinensis* L.	Ikekawa et al., 1984
14.	Teasterone	(22*R*,23*R*,24*S*)-3β,22,23-trihydroxy-24-methyl-5α-cholestan-6-one	*Thea sinensis* L.	Abe et al., 1984a
15.	23-*O*-β-D-Glucopyranosyl-25-methyldolichosterone	(22*R*,23*R*)-2α,3α,22-trihydroxy-23-*O*-β-D-glucopyranosyl-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Yokota et al., 1987a
16.	23-*O*-β-D-Glucopyranosyl-2-*epi*-25-methyldolichosterone	(22*R*,23*R*)-2β,3α,22-trihydroxy-23-*O*-β-D-glucopyranosyl-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Yokota et al., 1987a
17.	24-Epicastasterone	(22*R*,23*R*,24*R*)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Hydrodictyon reticulatum* (L.) Lager.	Yokota et al., 1987b
18.	6-Deoxo-28-homodolichosterone	(22*R*,23*R*,24(28)*E*)-24(28)-ethylidene-2α,3α,22,23-tetrahydroxy-5α-cholestane	*Phaseolus vulgaris* L.	Yokota et al., 1987c
19.	25-Methyldolichosterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Kim et al., 1987
20.	24-Epibrassinolide	(22*R*,23*R*,24*R*)-2α,3α,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one	*Vicia faba* L.	Ikekawa et al., 1988
21.	2-Epicastasterone	(22*R*,23*R*,24*S*)-2β,3α,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
22.	3-Epicastasterone	(22*R*,23*R*,24*S*)-2α,3β,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
23.	2,3-Di*epi*castasterone	(22*R*,23*R*,24*S*)-2β,3β,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
24.	3,24-Di*epi*castasterone	(22*R*,23*R*,24*R*)-2α,3β,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
25.	2,3-Di*epi*-25-methyldolichosterone	(22*R*,23*R*)-2β,3β,22,23-tetrahydroxy-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Kim, 1991
26.	3-*epi*-2-Deoxy-25-methyldolichosterone	(22*R*,23*R*)-3β,22,23-trihydroxy-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Kim, 1991
27.	2-Deoxy-25-methyldolichosterone	(22*R*,23*R*)-3α,22,23-trihydroxy-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Kim, 1991
28.	2-*epi*-25-Methyldolichosterone	(22*R*,23*R*)-2β,3α,22,23-tetrahydroxy-25-methyl-5α-ergost-24(28)-en-6-one	*Phaseolus vulgaris* L.	Kim, 1991

(*continued on next page*)

Table 3 (*continued*)

No.	Common name	Chemical name	Plant	Reference
29.	6-Deoxo-25-methyldolichosterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-25-methyl-5α-ergost-24(28)-ene	*Phaseolus vulgaris* L.	Kim, 1991
30.	3-*epi*-6-Deoxocastasterone	(22*R*,23*R*,24*S*)-2α,3β,22,23-tetrahydroxy-24-methyl-5α-cholestane	*Phaseolus vulgaris* L.	Kim, 1991
31.	3-*epi*-1α-Hydroxy-castasterone	(22*R*,23*R*,24*S*)-1α,2α,3β,22,23-pentahydroxy-24-methyl-5-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
32.	1β-Hydroxycastasterone	(22*R*,23*R*,24*S*)-1β,2α,3α,22,23-pentahydroxy-24-methyl-5α-cholestan-6-one	*Phaseolus vulgaris* L.	Kim, 1991
33.	28-Homoteasterone	(22*R*,23*R*,24*S*)-3α,22,23-trihydroxy-24-ethyl-5α-cholestan-6-one	*Raphanus sativus* L.	Schmidt et al., 1993b
34.	25-Methylcastasterone	(22*R*,23*R*,24*R*)-2α,3α,22,23-tetrahydroxy-24,25-dimethyl-5α-cholestan-6-one	*Lolium perenne* L.	Taylor et al., 1993
35.	3-Dehydroteasterone (3-oxoteasterone)	(22*R*,23*R*,24*S*)-22,23-dihydroxy-24-methyl-5α-cholestan-3,6-dione	*Lilium longiflorum* Thunb.	Abe et al., 1994
36.	Teasterone-3-myristate	(22*R*,23*R*,24*S*)-22,23-dihydroxy-3β-myristate-24-methyl-5α-cholestan-6-one	*Lilium longiflorum* Thunb.	Asakawa et al., 1994
37.	Cathasterone	(22*S*,24*R*)-3β,22-dihydroxy-24-methyl-5α-cholestan-6-one	*Catharanthus roseus* G. Don.	Fujioka et al., 1995
38.	6-Deoxoteasterone	(22*R*,23*R*,24*S*)-2β,22,23-trihydroxy-24-methyl-5α-cholestane	*Catharanthus roseus* G. Don.	Fujioka et al., 1995
39.	3-Dehydro-6-deoxoteasterone	(22*R*,23*R*,24*S*)-22,23-dihydroxy-24-methyl-5α-cholestan-3-one	*Cupressus arizonica* Greene	Griffiths et al., 1995
40.	6-Deoxotyphasterol	(22*R*,23*R*,24*S*)-3α,22,23-trihydroxy-24-methyl-5α-cholestane	*Cupressus arizonica* Greene	Griffiths et al., 1995
41.	6-Deoxo-24-epicastasterone	(22*R*,23*R*,24*R*)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestane	*Ornithopus sativus* Brot.	Spengler et al., 1995
42.	6-Deoxo-28-norcastasterone	(22*R*,23*R*)-2α,3α,22,23-tetrahydroxy-5α-cholestane	*Ornithopus sativus* Brot.	Spengler et al., 1995
43.	Secasterone	(22*R*,23*R*,24*S*)-2β,3β-epoxy-22,23-dihydroxy-24-methyl-5α-cholestan-6-one	*Secale cereale* L.	Schmidt et al., 1995b
44.	2-Deoxybrassinolide	(22*R*,23*R*,24*S*)-3α,22,23-trihydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one	*Apium graveolens* L.	Schmidt et al., 1995c
45.	28-Homotyphasterol	(22*R*,23*R*,24*S*)-3α,22,23-trihydroxy-24-ethyl-5α-cholestan-6-one	*Oryza sativa* L.	Abe et al., 1995a
46.	Teasterone-3-laurate	(22*R*,23*R*,24*S*)-22,23-dihydroxy-3β-laurate-24-methyl-5α-cholestan-6-one	*Lilium longiflorum* Thunb.	Asakawa et al., 1996
47.	23-Dehydrobrassinolide (cryptolide)	(22*R*,24*S*)-2α,3α,22-trihydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6,23-dione	*Cryptomeria japonica* D.Don.	Yokota et al., 1998
48.	24-*epi*Secasterone	(22*R*,23*R*,24*R*)-2β,3β-epoxy-22,23-dihydroxy-24-methyl-5α-cholestan-6-one	*Lychnis viscaria* L.	Friebe et al., 1999
49.	6α-Hydroxycastasterone	(22*R*,23*R*,24*S*)-2α,3α,6α,22,23-pentahydroxy-24-methyl-5α-cholestane	*Lycopersicon esculentum* Mill.	Bishop et al., 1999
50.	2-*epi*-23-Dehydrobrassinolide	(22*R*,24*S*)-2β,3α,22-trihydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6,23-dione	*Cryptomeria japonica* D.Don.	Watanabe et al., 2000
51.	3-*epi*-23-Dehydrobrassinolide	(22*R*,24*S*)-2α,3β,22-trihydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6,23-dione	*Cryptomeria japonica* D.Don.	Watanabe et al., 2000
52.	2,3-Di*epi*-23-dehydrobrassinolide	(22*R*,24*S*)-2β,3β,22-trihydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6,23-dione	*Cryptomeria japonica* D.Don.	Watanabe et al., 2000
53.	Teasterone-3-*O*-β-D-glucoside	(22*R*,23*R*,24*S*)-22,23-dihydroxy-3-*O*-β-D-glucopyranosyl-24-methyl-5α-cholestan-6-one	*Lilium longiflorum* Thunb.	Soeno et al., 2000
54.	28-Nortyphasterol	(22*R*,23*R*)-3α,22,23-trihydroxy-5α-cholestan-6-one	*Arabidopsis thaliana* (L.) Heynh.	Fujioka et al., 2000a
55.	6-Deoxocathasterone	(22*S*,24*R*)-3β,22-dihydroxy-24-methyl-5α-cholestane	*Catharanthus roseus* G. Don.	Fujioka et al., 2000b
56.	3-*epi*-6-Deoxocathasterone	(22*S*,24*R*)-3α,22-dihydroxy-24-methyl-5α-cholestane	*Catharanthus roseus* G. Don.	Fujioka et al., 2000b
57.	6-Deoxo-28-norcathasterone	(22*S*)-3β,22-dihydroxy-5α-cholestane	*Lycopersicon esculentum* Mill.	Yokota et al., 2001
58.	6-Deoxo-28-nortyphasterol	(22*R*,23*R*)-3α,22,23-trihydroxy-5α-cholestane	*Lycopersicon esculentum* Mill.	Yokota et al., 2001
59.	3-*epi*Brassinolide	(22*R*,23*R*,24*S*)-2α,3β,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one	*Arabidopsis thaliana* (L.) Heynh.	Konstantinova et al., 2001

Table 4
The occurrence of brassinosteroids in the monocotyledons

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
Arecaceae				
Phoenix dactylifera L.	Pollen	24-*epi*CS		Zaki et al., 1993
Gramineae				
Lolium perenne L.	Pollen	25-MeCS	0.001	Taylor et al., 1993
Oryza sativa L.	Shoot	CS	0.014	Abe et al., 1984b
		DS	0.008	Abe, 1991
		BL		
	Bran	6-DeoxoCS		Abe et al., 1995a
		28-HomoTE		
		28-HomoTY		
	Seeds	CS		Park et al., 1994b
		TE		
		6-DeoxoCS		
Phalaris canariensis L.	Seeds	CS	5	Shimada et al., 1996
		TE	0.7	
	Seeds	CS		Schmidt et al., 1995b
		TY		
Secale cereale L.	Seeds	CS		
		TY		
		TE		
		6-DeoxoCS		
		28-NorCS		
		SE		
Triticum aestivum L.	Grain	CS		Yokota et al., 1994
		TY		
		TE		
		6-DeoxoCS		
		3-DT		
Zea mays L.				
- Dent corn	Pollen	CS	120	Suzuki et al., 1986
		TY	6.6	
		TE	4.1	
- Sweet corn	Pollen	CS	27.2	Gamoh et al., 1990
		28-NorCS	18.3	
		DS	16.9	
Liliaceae				
Erythronium japonicum Decne	Pollen	TY	5	
	Anther			Yasuta et al., 1995
Lilium elegans Thunb.	Pollen	BL	1–5	Suzuki et al., 1994b
		CS	10–50	Yasuta et al., 1995
		TY	10–50	
		TE	1–5	
Lilium longiflorum Thunb.	Pollen	BL		Abe, 1991
		CS		
		TY		
	Anther	3-DT		Abe et al., 1994
		TE-3-La		Asakawa et al., 1994, 1996
		TE-3-My		Soeno et al., 2000
		TE-Glu	720	
Tulipa gesneriana L.	Pollen	TY		Abe, 1991
Typhaceae				
Typha latifolia G.F.W. Mey	Pollen	TY	68	Schneider et al., 1983
		TE		Abe, 1991

having two hydroxyl groups at position C-2 and C-3;
- 6-oxo compounds with 2,3-oriented epoxide group;
- 6-oxo compounds with an additional hydroxyl group at position C-1;
- BRs without oxygen functions in the B-ring;
- BRs having hydroxyl group at position C-6 (Table 1) (Schmidt et al., 2000).

According to the cholestane side chain, BRs are divided into eleven types with different substituents at C-23,

Table 5
The occurrence of brassinosteroids in the dicotyledons—the Apetalae

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

Table 6
The occurrence of brassinosteroids in the dicotyledons—the Chloripetalae

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
Apiaceae				
Apium graveolens L.	Seeds	2-DeoxyBL		Schmidt et al., 1995c
Daucus carota ssp. *sativus* L.	Seeds	BL		Schmidt et al., 1998
		CS		
		24-*epi*CS		
Brassicaceae				
Arabidopsis thaliana (L.) Heynh.	Shoot	CS	0.75	Fujioka et al., 1996, 1997, 2000a
	Ecotype Columbia	6-DeoxoCS	0.71	
	(wild-type)	TY	0.11	Nomura et al., 2001
		6-DeoxoTY	0.95	
		BL	0.04	
		28-NorCS	?	
		28-NorTY	?	
		TE	0.025	
		6-DeoxoCT	1.96	
		6-DeoxoTE	0.1	
		3-Dehydro-6-deoxoTE	0.13	
	Seeds	BL	0.5–1.9	Fujioka et al., 1998
	Ecotype Columbia	24-*epi*BL	0.22	
	(wild-type)	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-*epi*BL	0.22	Schmidt et al., 1997
		CS	0.36	

(*continued on next page*)

Table 6 (*continued*)

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
	Root callus	BL		Konstantinova et al., 2001
		3-*epi*BL		
Brassica campestris var. *pekinensis* L.	Seeds	BL	940	Abe et al., 1982, 1983
		28-NorBL	1300	Ikekawa et al., 1984
		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	
			160	
			50	
			20	
			12	
Dolichos lablab L.	Seeds	DL	160	Baba et al., 1983
		DS	50	Yokota et al., 1982b, 1983b, 1984
		28-HomoDS	20	
		28-HomoDL	12	
		BL		
		CS		
		6-DeoxoCS		
		6-DeoxoDS		
Robinia pseudo-acacia L.	Pollen	CS		Abe et al., 1995b
		TY		
		6-DeoxoCS		
Vicia faba L.	Seeds	BL	190	Park et al., 1987
		24-*epi*BL	5	Ikekawa et al., 1988
		CS		
		28-NorCS		
	Pollen	BL	181	Gamoh et al., 1989
		CS	134	
		28-NorCS	628	
		DS	537	
Psophocarpus tetragonolobus (Stickm.) DC.	Seeds	BL		Takatsuto, 1994
		CS		
		6-DeoxoCS		
		6-DeoxoDS		
Ornithopus sativus Brot.	Seeds	CS		Schmidt et al., 1993a
		24-*epi*CS		
	Shoot	CS		Spengler et al., 1995
		6-DeoxoCS		
		24-*epi*CS		
		6-Deoxo-24-*epi*CS		
		6-Deoxo-28-norCS		
Phaseolus vulgaris L.	Seeds	BL		Yokota et al., 1983c, 1987c
		CS		Kim et al., 1987, 1988, 2000
		2-*epi*CS		Kim, 1991
		3-*epi*CS		Park et al., 2000
		2,3-Di*epi*CS		
		3,24-Di*epi*CS		
		TY		
		TE		

(*continued on next page*)

Table 6 (*continued*)

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
		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-Di*epi*-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		
Pisum sativum L.	Seeds	BL		Yokota et al., 1996
		CS		
		TY		
		6-DeoxoCS		
		2-DeoxyBL		
	Shoot	BL	0.2–0.8	Nomura et al., 1997, 1999, 2001
		CS	0.4–2.4	
		6-DeoxoCS	5.2	
		TY	1	
		6-DeoxoCT	3.75	
		6-DeoxoTE	0.047	
		3-Dehydro-6-deoxoTE	0.074	
		6-DeoxoTY	0.8	
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		Abe, 1991
		CS		
		TY		
		TE		
Citrus sinensis Osbeck	Pollen	BL	36.2	Motegi et al., 1994
		CS	29.4	
Theaceae				
Thea sinensis L.	Leaves	28-NorCS	0.002	Abe et al., 1983, 1984a
		28-HomoCS	<0.001	Morishita et al., 1983
		BL	0.006	Ikekawa et al., 1984
		CS	0.1	
		TY	0.06	
		TE	0.02	

C-24 and C-25: 23-oxo, 24*S*-methyl, 24*R*-methyl, 24-methylene, 24*S*-ethyl, 24-ethylidene, 24-methylene-25-methyl, 24-methyl-25-methyl, without substituent at C-23, without substituent at C-24 and without substituents at C-23, C-24 (Table 2) (Sakurai and Fujioka, 1993; Fujioka, 1999; Watanabe et al., 2000; Yokota et al., 2001).

Unconjugated BRs are grouped into C_{27}, C_{28} and C_{29} steroids whose chemical structures have been presented in Figs. 2–4. These classifications result basically from different alkyl substitutions in the side chain. The presence of a saturated alkyl (a methyl or an ethyl group) at position C-24 and a methyl at C-25 makes BRs biologically more active. Most of BRs carry an *S*-oriented

Table 7
The occurrence of brassinosteroids in the dicotyledons—the Sympetalae

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
Apocynaceae				
Catharanthus roseus G. Don.	Cultured cells	BL	0.4–8.7	Choi et al., 1993, 1996, 1997
		CS	0.6–4.5	Fujioka et al., 1995, 2000b
		6-DeoxoTY	0.76	Park et al., 1989
		6-DeoxoTE	0.047	Suzuki et al., 1993, 1994a, c, 1995
		6-DeoxoCS	5.9–18.9	
		CT	2–4	Yokota et al., 1990
		6-DeoxoCT	30	
		3-*epi*-6-deoxoCT		
		3-DT		
		TY		
		TE		
Asteraceae				
Zinnia elegans L.	Cultured cells	CS		Yamamoto et al., 2001
		TY		
		6-DeoxoCS		
		6-DeoxoTY		
		6-DeoxoTE		
Helianthus annuus L.	Pollen	BL	106	Takatsuto et al., 1989
		CS	21	
		28-NorCS	65	
		BL		
Solidago altissima L.	Shoot	BL		Takatsuto, 1994
Boraginaceae				
Echium plantagineum L.	Pollen	BL		Takatsuto, 1994
Convolvulaceae				
Pharbitis purpurea Voigt	Seeds	CS	1.1	Suzuki et al., 1985
		28-NorCS	0.2	
Cucurbitaceae				
Cucurbita moschata Duch.	Seeds	BL		Jang et al., 2000
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.	Shoot	CS	0.2	Yokota et al., 1997d
		6-DeoxoCS	1.7	
		28-NorCS	0.03	
	Root	6-Deoxo-28-norCT	0.22	Yokota et al., 2001
		6-Deoxo-28-norTY	0.13	
		6-Deoxo-28-norCS	0.09	
- Dwarf mutant	Shoot	6-DeoxoCT	1.1	Bishop et al., 1999
		6-DeoxoTE	0.04	
		3-Dehydro-6-deoxoTE	0.03	
		6-DeoxoTY	0.5	
		6-DeoxoCS	5.2	
		6α-OH-CS		
		CS	0.2	
		BL	< 0.001	
		TY	< 0.001	
		3-DT	< 0.001	
		TE	< 0.001	
		CT	< 0.001	

alkyl group at C-24. Nevertheless, there are five exceptions among BRs which have *R*-oriented alkyl, for example 24-epiBL or 24-epiCS. Also BR without substituents at C-24 have been found (Table 2) (Fujioka, 1999). All of these alkyl substituents are also common structural features of plant sterols. It is suggested that BRs are derived from sterols carrying the same side chain. The C_{27} BRs having no substituent at C-24 may come from cholesterol. The C_{28} BRs carrying either an α-methyl, β-methyl or methylene group may be derived

Table 8
The occurrence of brassinosteroids in gymnosperms

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
Cupressaceae				
Cupressus arizonica Greene	Pollen	6-DeoxoTY	6400	Griffiths et al., 1995
		3-Dehydro-6-deoxoTE	2300	
		6-DeoxoCS	1200	
		CS	1000	
		TY	460	
		TE	5	
		28-HomoCS	4	
		3-DT	2	
		BL	<1	
Ginkgoaceae				
Ginkgo biloba L.	Seeds	TE	15	Takatsuto et al., 1996a
Pinaceae				
Piceae sitchensis Trantv. ex Mey	Shoot	CS	5	Yokota et al., 1985
		TY		
Pinus silvestris L.	Cambial region	BL		Kim et al., 1990
		CS		
Pinus thunbergii Parl.	Pollen	TY	89.5	Yokota et al., 1983a
Taxodiaceae				
Cryptomeria japonica D. Don.	Pollen	TY		Yokota et al., 1998
	Anther	DL		Watanabe et al., 2000
		3-DT		
		28-HomoBL		
		28-HomoDL		
		23-DehydroBL (cryptolide)		
		2-*Epi*-23-dehydroBL		
		3-*Epi*-23-dehydroBL		
		2,3-Di*epi*-23-dehydroBL		

Table 9
The occurrence of brassinosteroids in lower plants

Family/species	Plant parts	Brassinosteroid	Isolated quantity (μg/kg fr. wt)	References
Equisetaceae				
Equisetum arvense L.	Whole plant	CS	0.17	Takatsuto et al., 1990a
		DS	0.75	
		28-NorBL	0.15	
		28-NorCS	0.35	
Hydrodictyaceae				
Hydrodictyon reticulatum (L.) Lager.	Whole plant	24-*epi*CS	0.3	Yokota et al., 1987b
		28-HomoCS	4.0	
Marchantiaceae				
Marchantia polymorpha L.	Cultured cells	TE		Park et al., 1999
		3-DT		
		TY		

from campesterol, dihydrobrassicasterol or 24-methylenecholesterol, respectively. The C_{29} BRs with an α-ethyl group may came from sitosterol. Furthermore, the C_{29} BRs carrying a methylene at C-24 and an additional methyl group at C-25 may be derived from 24-methylene-25-methylcholesterol (Yokota, 1995, 1999b).

In addition to free 54 BRs also 5 sugar and fatty acid conjugates have been identified in plants. 25-Methyldolichosterone-23-β-*D*-glucoside (25-MeDS-Glu) and its 2β isomer from *Phaseolus vulgaris* seeds and teasterone-3β-*D*-glucoside (TE-3-Glu), teasterone-3-laurate (TE-3-La) and teasterone-3-myristate (TE-3-My) from *Lilium* *longiflorum* pollen were isolated as endogenous BRs (Fig. 5) (Abe et al., 2001).

3. Occurrence of brassinosteroids

Since the discovery of BL, 59 BRs, among them 54 unconjugated and 5 conjugated BRs, have been isolated from 58 plant species including 49 angiosperms (12 monocotyledons and 37 dicotyledons) (Tables 4–7), 6 gymnosperms (Table 8), 1 pteridophyte (*Equisetum arvense*), 1 bryophyte (*Marchantia polymorpha*) and 1 chlorophyte, the alga (*Hydrodictyon reticulatum*) (Table 9). Thus the BRs are widely distributed in the plant kingdom, including higher and lower plants. Table 3 summarizes the history (from 1979 to 2001) of isolation for the first time naturally occurring BRs in plants.

BRs were detected in all plant organs such as pollen, anthers, seeds, leaves, stems, roots, flowers, and grain. Other interesting tissues are insect and crown galls, for example the galls of *Castanea crenata*, *Distylium racemosum* or *Catharanthus roseus* where BRs have been found. These plants have higher levels of BRs than the normal tissues. Also, young growing tissues contain higher levels of BRs than mature tissues. Generally, pollen and immature seeds are especially rich source of BRs, while the concentrations in vegetative tissues are very low compared to those of other plant hormones. In the pollen of *Cupressus arizonica* the concentration of 6-deoxoTY can be about 6400-fold greater than BL. Pollen and immature seeds are the richest sources with ranges of 1–100 ng g^{-1} fresh weight, while shoots and leaves usually have lower amounts of 0.01–0.1 ng g^{-1} fresh weight. BRs occur endogenously at quite low levels. Compared to the pollen and immature seeds, the other plant parts contain BRs in the nanogram or subnanogram levels of BRs per gram fresh weight. The highest concentration of BR, 6.4 mg 6-deoxoTY per 1 kg pollen, was detected in *Cupressus arizonica* (Griffiths et al., 1995; Clouse and Sasse, 1998; Fujioka, 1999).

Among the BRs, CS is the most widely distributed (49 plant species), followed by BL (33), TY (24), 6-deoxoCS (19), TE (18), and 28-norCS (11). Furthermore from 2 to 10 BRs are distributed in a limited number of plant species, it means that 24-epiCS was isolated in 8 plant species, DS - 7, 3-DT - 7, 6-deoxoTY - 5, 28-homoCS - 4, 24-epiBL - 4, DL - 3, 6-deoxoTE - 3, 6-deoxoDS - 3, 28-norBL - 2, 28-homoTE - 2, 2-deoxyBL - 2. To the present day 34 other BRs and 5 BR conjugates have been found in only one plant species. Among all naturally occurring BRs, CS and BL are the most important BRs because of their wide distribution as well as their potent biological activity (Kim, 1991; Fujioka, 1999).

Among the plant sources investigated, immature seeds of *Phaseolus vulgaris* contain a wide array of BRs, these are 23 free BRs and 2 conjugates. The wide occurrences of BRs were also found in the dwarf mutant of *Catharanthus roseus* (13 compounds), *Arabidopsis thaliana* (11 compounds), *Cryptomeria japonica* (9 compounds), *Cupressus arizonica* (9 compounds), *Dolichos lablab* (8 compounds), *Oryza sativa* (8 compounds), *Lilium longiflorum* (7 compounds), *Secale cereale* (6 compounds), and *Thea sinensis* (6 compounds).

The occurrence of BRs in monocotyledons has been demonstrated from four families including twelve plant species (Table 4). BRs are represented by 16 various compounds: 7-oxalactone (1, BL), 6-ketone (11), 6-deoxo (1, 6-deoxoCS) types and 3 conjugates. Five BRs such as SE, TY, 3-DT, TE-3-La, TE-3-My were isolated for the first time in this class.

The presence of BRs in dicotyledons has been reported from three subclasses. The first, the Apetalae is represented by 6 families including 8 plant species (Table 5). Total quantity of BRs amount 7 various compounds. The second, the Chloripetalae is represented by 7 families including 20 plant species (Table 6). There are 41 free BRs, among them 25 compounds belong to 6-ketone type, 10 belong to 6-deoxo type and 6 belong to 7-oxalactone type. Furthermore, from immature seeds of *Phaseolus vulgaris* a large quantity of 23 unconjugated and 2 conjugated BRs was isolated so far. Among plants of this subclass, 37 BRs were detected for the first time. The third, the Sympetalae is represented by 7 families including 9 plant species (Table 7). Total quantity of BRs amounts 16 compounds with 7, which were isolated for the first time.

The occurrence of BRs in gymnosperms has been reported from six conifers (Table 8). The presence of new 6 BRs was shown in *Cupressus arizonica* and *Cryptomeria japonica*. Among plant species so far reported, the level of BR in the mature pollen of *Cupressus arizonica* is the highest (6.4 mg/kg 6-deoxoTY).

BRs have been identified in lower plants such as a green alga (*Hydrodictyon reticulatum*), a pteridophyte (*Equisetum arvense*), a bryophyte (*Marchantia polymorpha*) (Table 9). Total quantity of BRs include 9 various compounds, among them 6-ketone type of BRs is dominant (8 compounds). Furthermore, the occurrence of 24-epiCS in algae and the first time in plants has been demonstrated.

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