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Review

Metabolism of brassinosteroids in plants

Andrzej Bajguz*

University of Bialystok, Institute of Biology, Swierkowa 20 B, 15-950 Bialystok, Poland

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Abstract

Brassinosteroids represent a class of plant hormones. More than 70 compounds have been isolated from plants. Currently 42 brassinosteroid metabolites and their conjugates are known. This review describes the miscellaneous metabolic pathways of brassinosteroids in plants. There are some types of metabolic processes involving brassinosteroids in plants: dehydrogenation, demethylation, epimerization, esterification, glycosylation, hydroxylation, side-chain cleavage and sulfonation. Metabolism of brassinosteroids can be divided into two categories: i) structural changes to the steroidal skeleton; and ii) structural changes to the side-chain.

Keywords: Brassinosteroids; Metabolism; Plant hormones

1. Introduction

Brassinosteroid (BR) metabolism pathways produce structural modifications to the natural BRs that affect their activity, function and transport in plants. Discoveries about BR biosynthesis, catabolism and signal transduction have generated excitement and significantly increased the level of our knowledge about BRs [18,39,55,59]. In the area of BR metabolism, genes coding for BR conjugation and other biotransformation enzymes are just beginning to be discovered. Since 1979, when the first BR has been isolated from the pollen of rape plant (*Brassica napus*), the chemical structures of most BRs, their biosynthesis, function and their signal transduction have become well known [3,9,15,18,31,34,46]. BRs are hydroxylated derivatives of cholestane and their structural variations comprise substitution patterns on rings A and B as well as the C-17 side-chain. These compounds can be classified as C_{27}, C_{28}, or C_{29} BRs, depending on the length of the side chain. Till now, 65 free BRs and five BR conjugates have been characterized from the plant kingdom. BRs are considered the plant analogues of steroid hormones in the animal kingdom [9].

BRs are important plant growth regulators in multiple developmental processes at nanomolar to micromolar concentration, including cell division, cell elongation, vascular differentiation, reproductive development and modulation of gene expression. BRs also influence various other developmental processes like germination of seeds, rhizogenesis, flowering, senescence, abscission and maturation. They also confer resistance to plants against various abiotic and biotic stresses [34,42,59]. Observed physiological responses to BR application include ethylene biosynthesis through activation of 1-aminocyclopropane-1-carboxylic acid synthesis [5,44], membrane hyperpolarisation through enhanced proton extrusion [6,12], enhanced DNA, RNA and protein synthesis [8,22], increased invertase activity [43], stimulation of photosynthetic activity [7,11,21], and changes in the balance of other endogenous phytohormones [16]. Key observations in BR's interaction with other hormones in stem elongation include a synergistic response with auxins and an additive effect with gibberellins [32,62]. BRs inhibit root elongation [40] that may be the consequence of BR-induced ethylene synthesis [4]. Although, BRs can promote the development of crown roots, primary and secondary branched roots, and the extension of thin primary branched roots [42].

Abbreviations: BL, brassinolide; BR, brassinosteroid; CS, castasterone; 3-DT, 3-dehydroteasterone; TE, teasterone; TY, typhasterol.

* Tel.: +48 85 745 7334; fax: +48 85 745 7302.
E-mail address: abajguz@uwb.edu.pl

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A detailed study of the biosynthesis of brassinolide (BL) in *Catharanthus roseus* and *Arabidopsis thaliana* revealed that two parallel routes, the early and late C-6 oxidation pathways, are connected at multiple steps and are linked to the early and late C-22 oxidation pathways. Moreover, surprising similarities exist between the BRs and animal steroid hormone biosynthetic pathways [18,46]. Several *Arabidopsis* mutants with lesions in BR signal transduction have been characterized and the corresponding genes cloned and studied [10,13,14,33,39,47,52,53,54,55].

This paper would like to summarize knowledge on BRs metabolism known up to date. Currently 42 BR metabolites and their conjugates are known. The chemical structures of BR metabolites are shown in Fig. 1. Metabolic pathways may vary according to: i) plant species; ii) developmental stages; and iii) BR structures. There are some types of metabolic processes involving BRs in plants: dehydrogenation, demethylation, epimerization, esterification, glycosylation, hydroxylation, side-chain cleavage and sulfonation (Fig. 2). Metabolism of BRs can be divided into two categories: 1)

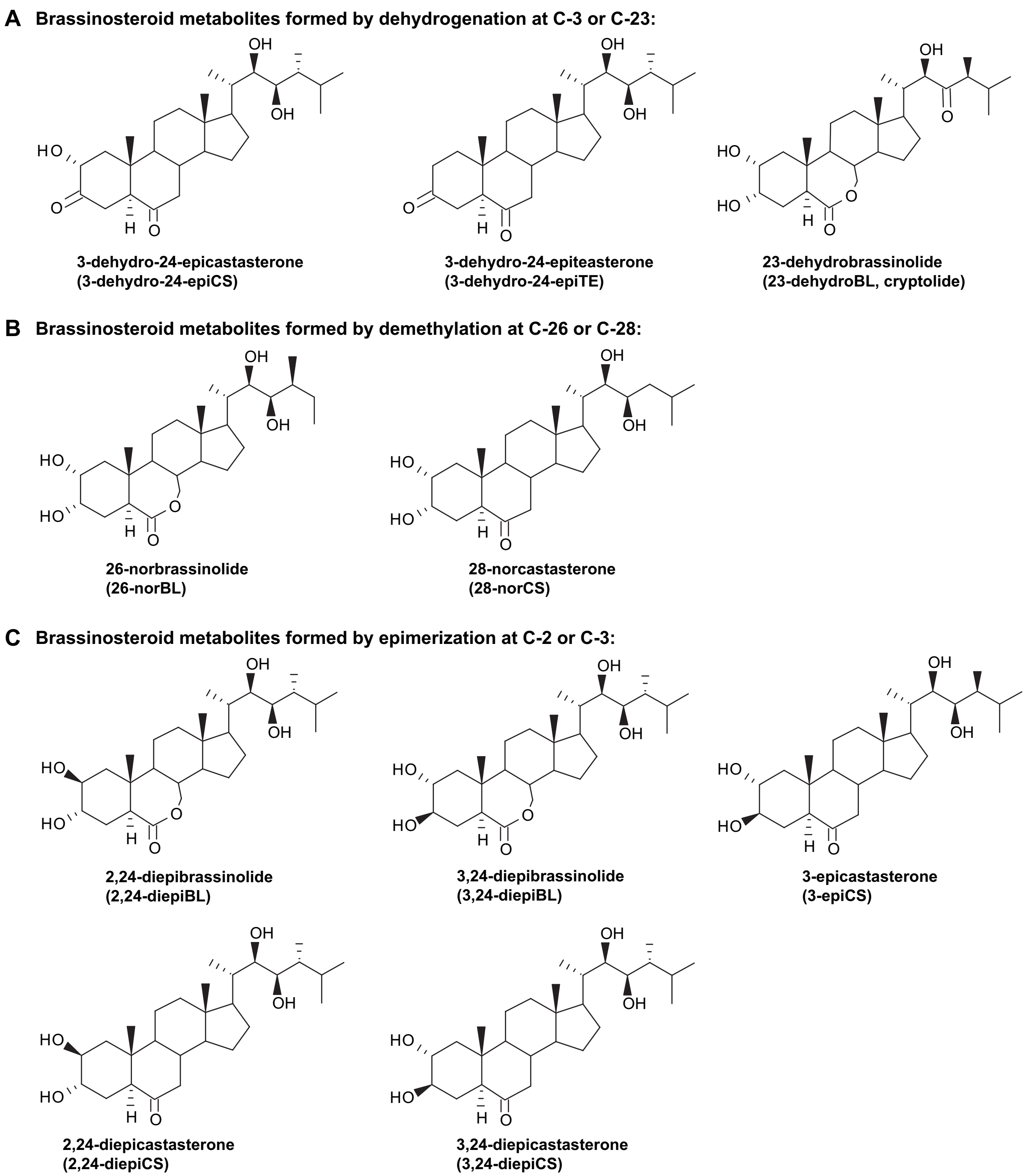

Fig. 1. Chemical structures of brassinosteroid metabolites.