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Review article

Phytohormones as targets for improving plant productivity and stress tolerance

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ABSTRACT

In this review, we summarize the results of experiments that lead to altered levels of phytohormones in transgenic plants to improve plant productivity. The available data indicate that manipulating the level of phytohormones might also be a promising way to enhance the environmental stress tolerance of crop plants. In the regulation of the level of phytohormones, both biosynthesis and their catabolism pathways can be targeted for engineering purposes. Moreover, the signaling pathways of phytohormones should explored in this respect. In genetic modifications, conditional promoters must be developed to avoid undesired effects on growth. In order to find a practical application, the effects of genetic modifications should be further verified under field conditions and over a longer time scale.

1. Introduction

Plant productivity, yield and resistance to environmental stresses are currently the main points of interest for agriculture and plant biotechnology. Biotic and abiotic stresses cause huge losses in crop yield. An increasing human population and food demand necessitate the creation of plant varieties with improved traits. One of the approaches for achieving this goal is the metabolic engineering of phytohormones (Bartwal et al., 2013; Wani et al., 2016).

Phytohormones (plant growth regulators) are compounds that act at very low concentrations and regulate various cellular processes and plant responses to changing environmental conditions (Fahad et al., 2015; Wani et al., 2016). The plant hormones that have been most investigated include cytokinins (CK), auxins (Aux), gibberellins (GA), abscisic acid (ABA), ethylene (ET), brassinosteroids (BR) and jasmonates (JA). Representative examples of plant hormone groups are shown in Fig. 1. It is traditionally assumed that JA and ET are involved in plant defense, while Aux, CK, GA and BR are associated with plant development. ABA is the key hormone that regulates plant responses to abiotic stresses (Kazan, 2015). Therefore, the engineering of phytohormones might be a promising tool for biotechnologists to improve plant productivity and stress tolerance. The level of phytohormones is affected both by anabolic (biosynthesis) and catabolic pathways. Enzymes of both pathways have been used as targets in transgenic approaches (Fig. 2). Other potential targets are components of the signal transduction pathways of phytohormones. In this review, we present the results of experiments that focus on the engineering of phytohormones that lead to elevated plant productivity and stress resistance, as well as reports that take advantage of phytohormone mutants when investigating the stress tolerance of crop plants.

2. Manipulation of the level of phytohormones as a way of improving plant productivity and resistance to stress

During their lifetimes, plants are exposed to multiple environmental stresses, both abiotic and biotic, influencing their growth and development, which also affects their productivity. Among abiotic factors, the most important are climatic factors, including water availability, light intensity, temperature or others (e.g. salinity). Biotic factors, i.e. interactions of other organisms, could have a beneficial influence on plant growth, such as symbiosis, but also negative effects, such as herbivory, pathogen infection or allelopathy. In response to these factors, plant growth regulators play a crucial function. Phytohormones regulate the majority of processes associated with growth, development and response to external stimuli, and thus the targeted control of hormone biosynthesis, metabolism and signaling could significantly affect plants' productivity.

Below, we describe examples of experiments that lead to an altered level of phytohormones, especially in crop plants, and the results of these manipulations, which are intended to enhance stress tolerance,

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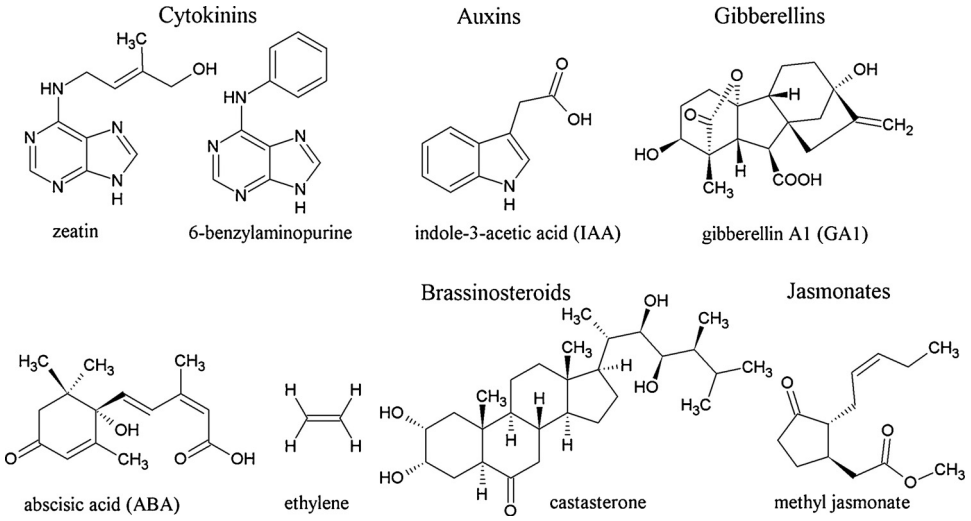

Fig. 1. Structure of representatives of the main groups of phytohormones.

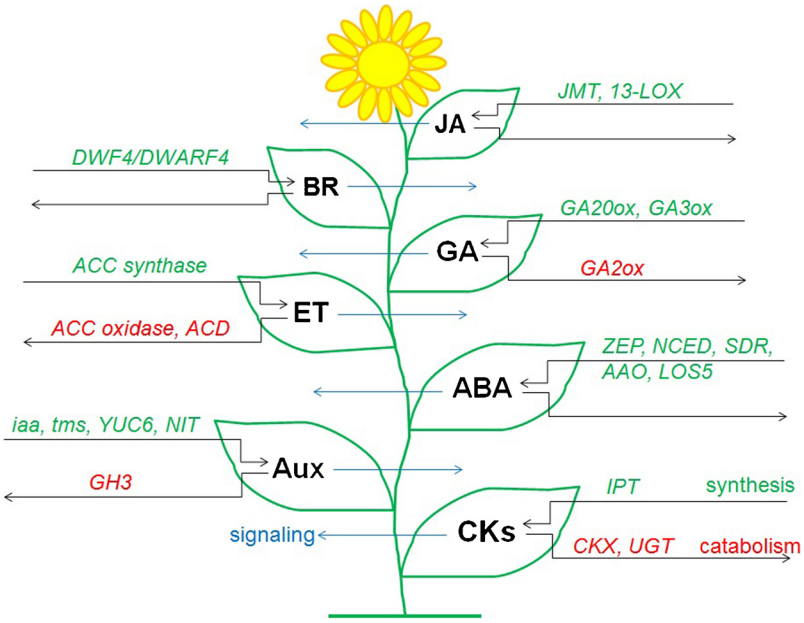

Fig. 2. Target genes of phytohormones anabolism (green) or catabolism (red) whose expression was modified in transgenic approaches. AAO, aldehyde oxidase; ACC, 1-aminocyclopropane-1-carboxylic acid; ACD, 1-aminocyclopropane-1-carboxylate deaminase; CKX, cytokinin oxidase/dehydrogenase; *DWF4/DWARF4*, gene encoding steroid 22α-hydroxylase (CYP90B1); GA20ox, GA 20-oxidase; GA2ox, GA 2-oxidase; GA3ox, GA 3-oxidase; GH3, proteins responsible for conjugation of Aux to amino acids; *iaaM*, bacterial gene encoding tryptophan monoxidase; IPT, isopentenyl transferase; JMT, jasmonic acid carboxyl methyltransferase; LOS5, molybdenum cofactor required for AAO activity; 13-LOX, 13-lipoxygenase; NCED, 9-*cis*-epoxycarotenoid dioxygenase; NIT, nitrilase converting indole-3-acetonitrile to IAA; SDR, short-chain alcohol dehydrogenase/reductase; *tms1*, agrobacterial gene encoding tryptophan monooxygenase; UGT, UDP-glycosyltransferase; *YUC*, gene encoding enzyme converting tryptamine to N-hydroxyl-tryptamine; ZEP, zeaxanthin epoxidase.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

improved yield and productivity.

2.1. Cytokinins

CK regulate a number of aspects of plant growth and development, such as cytokinesis, cell differentiation, growth, quiescence, and the transport of assimilates or senescence. These phytohormones are also involved in abiotic stress responses. Therefore, they have been long considered to be connected with plant yield and productivity. The main biotechnological targets are genes involved in CK synthesis (isopentenyl transferase *IPT*) and metabolism (cytokinin oxidase/dehydrogenase *CKX*, glucosyltrasferases).

Adenosine phosphate-isopentenyl transferase (IPT) is the key enzyme in CK biosynthesis and catalyzes transfer of the isopentenyl moiety of dimethylallyl pyrophosphate or 1-hydroxy-2-methyl-2-(*E*)-butenyl 4-diphosphate to ATP, ADP or AMP. The isopentenyl-ATP, -ADP and -AMP that form are the precursors of biologically active CK (Zalabák et al., 2013). Irreversible degradation of CK is catalyzed by cytokinin oxidase/dehydrogenase CKX, cleaving N^6 side chain of CK, which results in the formation of adenine (or its corresponding derivative of N^9 - substituted CK) and the unsaturated aldehyde 3-methyl-2-butenal. CKX have been found in many plant species and have a high level of sequence homology (Frébort et al., 2011). In *Arabidopsis*, seven *CKX* members have been identified. AtCKX1 and AtCKX3 are vacuolar, while AtCKX2 is an extracellular protein (Werner et al., 2003).

CK activity can also be affected by their conjugation with sugar or alanine moieties. Glycosylation of CK is catalyzed by UDP-glycosyltransferase (UGT). The most common types of CK glycosylate are *O*- and *N*-glycosides at positions 7 and 9 in the purine ring (Zalabák et al., 2013). Glycosyltransferases are a large group of enzymes which recognize various substrates. In *Arabidopsis*, only five UGT are able to glucosylate CK: UGT76C1 and UGT76C2 glucosylate CK at the N^7 and N^9 positions, UGT85A1, UGT73C5, and UGT73C1 form the *O*-glucosides of *trans*-zeatin and dihydrozeatin (Hou et al., 2004). Less common is conjugation with alanine at N^9 position of adenine moiety, whose products are characterized by low activity because of the absence of those enzymes responsible for the hydrolysis of conjugates to the active form (Bajguz and Piotrowska, 2009).

CK have been found as key factors in the regulation of plant senescence. Controlling the senescence is one of the strategies for improving a plant's yield and extend vitality. Gan and Amasino (1995) were the first to use the senescence-specific promoter, SAG12, from