



Research article

Wheat and rye genome confer specific phytohormone profile features and interplay under water stress in two phenotypes of triticale



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ARTICLE INFO

Article history:

Received 5 June 2017

Received in revised form

17 July 2017

Accepted 18 July 2017

Available online 19 July 2017

Keywords:

Abscisic acid

Auxins

Cytokinins

Gibberellins

Jasmonic acid

Salicylic acid

Water stress

ABSTRACT

The aim of the experiment was to determine phytohormone profile of triticale and quality-based relationships between the analyzed groups of phytohormones. The study involved two triticale phenotypes, a long-stemmed one and a semi-dwarf one with *Dw1* gene, differing in mechanisms of acclimation to drought and controlled by wheat or rye genome.

Water deficit in the leaves triggered a specific phytohormone response in both winter triticale phenotypes attributable to the dominance of wheat (semi-dwarf cultivar) or rye (long-stemmed cultivar) genome. Rye genome in long-stemmed triticale was responsible for specific increase (tillering: gibberellic acid; heading: N6-isopentenyladenine, *trans*-zeatin-9-riboside, *cis*-zeatin-9-riboside; flowering: N6-isopentenyladenine, indolebutyric acid, salicylic acid) or decrease (heading: *trans*-zeatin) in the content of some phytohormones. Wheat genome in semi-dwarf triticale controlled a specific increase in *trans*-zeatin content at heading and anthesis in gibberellin A1 during anthesis. The greatest number of changes in the phytohormone levels was observed in the generative phase. In both triticale types, the pool of investigated phytohormones was dominated by abscisic acid and gibberellins. The semi-dwarf cultivar with *Dw1* gene was less sensitive to gibberellins and its mechanisms of acclimation to water stress were mainly ABA-dependent. An increase in ABA and gibberellins during drought and predominance of these hormones in the total pool of analyzed phytohormones indicated their equal share in drought acclimation mechanisms in long-stemmed cultivar.

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1. Introduction

Phytohormones are plant growth and development regulators that at low concentrations modify plant physiological functions (Tarkowská et al., 2014). Basic plant hormones include auxins, cytokinins, gibberellins, abscisic acid, salicylic acid, ethylene, brassinosteroids or jasmonic acid (Pan et al., 2008). Their regulatory role consists in stimulating or inhibiting such processes as seed germination, cell division, root formation, plant movements, formation of lateral buds or organ and tissue aging (Landjeva et al., 2008; Mueller-Roeber and Balazadeh, 2014; Navarro-León et al., 2016). However, their biological activity is much more diverse and it usually depends on interactions with other phytohormones, which means that disturbing biosynthesis of one phytohormone

may activate or deactivate the functioning of another phytohormone (Letham, 1969; McAtee et al., 2013). Therefore, changes in specific plant hormone levels induced by stress factors affect also the levels of other phytohormones (Tarkowská and Strnad, 2016).

Plant hormones affect multiple physiological and biochemical processes, such as transportation and accumulation of assimilates, synthesis of nucleic acids, enzymatic activity, chlorophyll and carotenoid levels, lignification of leaf tissues, stomatal opening, photosynthesis intensity, chloroplast division and their ultrastructure formation and synthesis of photosynthetic proteins (Fosket and Short, 1973; Volfová et al., 1978; Pospíšilová, 2003; Denness et al., 2011; Bajguz and Piotrowska-Niczyporuk, 2014; Piotrowska-Niczyporuk and Bajguz, 2014). They also induce gene expression (Michael et al., 2008; Song et al., 2009). This is why the mechanisms of acclimation to environmental stresses, including drought, may be modified by plant hormones (Iqbal and Ashraf, 2013; Iqbal et al., 2014; Li et al., 2016; Buchner et al., 2017).

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Abbreviations

ABA	Abscisic acid
A	Anthesis
cZ	Cis-zeatin
cZR	Cis-zeatin-9-riboside
GA1	Gibberellin A ₁
GA3	Gibberellic acid
GA4	Gibberellin A ₄
GA6	Gibberellin A ₆
H	Heading
IAA	Indole-3-acetic acid
IBA	Indole-3-butyric acid
IPA	N6-isopentenyladenine
JA	Jasmonic acid
K	Kinetin
KR	Kinetin-9-riboside
RWC	Relative water content
SA	Salicylic acid
T	Tillering
tZ	Trans-zeatin
tZR	Trans-zeatin-9-riboside

Triticale is a laboratory bred inter-generic hybrid of wheat and rye. It has been introduced as a commercial crop in the end of 1970s, so it is a relatively young cereal (Lorenz and Pomeranz, 1974). A lack of natural evolution resulted in the lack of inherent genetic diversity of triticale. This is one of the reasons for ongoing research aimed at enhancing genetic diversity and thus crop improvement (Mergoum et al., 2004). An important aspect of such research are studies on physiological, biochemical and molecular mechanisms of acclimation to environmental stresses, including soil drought stress, and verification of these mechanisms against wheat and rye genome of triticale (Hura et al., 2017a).

A genome of hexaploid triticale (AABBRR) contains wheat (A and B) and rye (R) chromosomes (Tyrka et al., 2011). Therefore, acclimation to drought may be controlled separately by either wheat or rye genome or by both genomes simultaneously (Hura et al., 2017a). Our previous studies showed different response of triticale to dehydration of leaf tissues that was due to e.g. differences in the metabolism of carbohydrates and phenolic compounds (Hura et al., 2016). We confirmed that main pathways of carbohydrate utilization in semi-dwarf cultivar included the synthesis of starch and soluble phenolics and accumulation of carbohydrate components of cell wall that improved its flexibility and plasticity. Contrary to that, soluble carbohydrates in long-stemmed cultivar were primarily used for the synthesis of phenolic compounds that were then incorporated into cell wall structures. Increased content of phenolic components improved stiffness and leak tightness of the cell wall (Hura et al., 2016). Observations of morphological, physiological and biochemical mechanisms of adaptation to drought revealed a dominant role of R genome of triticale in long-stemmed cv. (increased content of phenolic components of the cell wall, stiffness and hardness of leaves and lack of leaf curling typical for rye) and of A and B wheat genomes in semi-dwarf cv. (high activity of photosynthetic apparatus, increased content of carbohydrate components of the cell wall, leaf flexibility, leaf curling into a tube typical for wheat) (Hura et al., 2012, 2015a, 2016, 2017a,b). Our last study confirmed that increased level of phenolics in the cell wall was a drought acclimation mechanism associated mainly with the activity of rye genome of triticale (Hura et al., 2017a).

Common ground of the two above described mechanisms of acclimation to water stress is the metabolism of carbohydrates and phenolic compounds that may be also modified by plant hormones (Iqbal and Ashraf, 2013; Denness et al., 2011; Bajguz and Piotrowska-Niczyporuk, 2014). Therefore, the aim of the experiment described in this study was to determine phytohormone profile of triticale and quality-based relationships between and within the most important groups of phytohormones. It was hypothesized that wheat and rye genome confer specific phytohormone profile features and interplay under water stress in two phenotypes of triticale. Two types of response to leaf dehydration may be associated with specific changes in phytohormone profile that will be discussed with reference to wheat (A, B) and rye (R) genome of triticale.

2. Materials and methods

2.1. Plant material, growth conditions and treatments

The experiments included two cultivars of winter triticale differing in their morphological traits, i.e. 'Moderato', a typical long-stemmed cultivar and semi-dwarf 'Woltario' cultivar with *Dw1* gene (Leśniowska-Nowak, 2012).

The experiments were conducted in pots. Seedlings of each genotype were grown in plastic pots 3.7 dm³ in volume, filled with a homogeneous mixture of soil and sand (1:3; v/v). The seedlings at the stage of one leaf were subjected to vernalization in cool chambers for 8 weeks at +4 °C (±1 °C) with 10 h illumination and with a photosynthetic photon flux density (PPFD) of 200 μmol m⁻² s⁻¹. After vernalization, the seedlings were transferred into air-conditioned greenhouse chamber to 16 h light/8 h dark photoperiod, a temperature of 23/18 °C (±2 °C) day/night, 40 ± 5% relative air humidity (RH), and photosynthetic photon flux density (PPFD) of 250–350 μmol m⁻² s⁻¹ (provided by high pressure sodium lamps, 400 W; Philips SON-T AGRO, Brussels, Belgium), at the level of the top leaf. Light intensity at the leaf level was measured with a QSPAR Quantum Sensor (Hansatech Instruments LTD, Kings Lynn, England). The plants were irrigated once a week with a nutrient solution (Hoagland, 1948).

In both cultivars, watering was restricted for 3 weeks at tillering, heading and anthesis, and for two weeks the soil water content in drought stress variant was maintained at 34–37% (75–78% in control). Soil water content was monitored gravimetrically, taking into account the weight of plants growing in the pots.

Measurements were performed on 21st day of limited watering. Such timing for phytohormone content determination was chosen based on our previous experiments on biochemical responses of triticale to water stress (Hura et al., 2007, 2009a,b,c, 2011, 2012, 2013, 2015a,b, 2016, 2017a,b). First top fully developed leaves were collected from plants analyzed at tillering stage, whereas the analyses at heading and anthesis involved flag leaves.

2.2. Relative water content

Relative water content (RWC) was calculated from the following equation: $RWC (\%) = [(fw - dw)/(tw - dw)] \times 100$ (Turner, 1981). The leaves were weighed (fw – fresh weight) and then soaked in distilled water for 24 h in darkness in order to estimate the turgid weight (tw). Then the samples were oven-dried at 80 °C for 24 h and weighed (dw – dry weight).

2.3. Extraction and quantification of phytohormones

Extraction and quantification of phytohormones was performed according to Dziurka et al. (2016). Plant material was lyophilised

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