



Yield associated traits correlate with cytokinin profiles in developing pods and seeds of field-grown soybean cultivars



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ABSTRACT

While lab and greenhouse based studies have long indicated that cytokinins (CK) promote yield increases in soybean (*Glycine max* L.), it is not known if the relationship would be valid under more complex field conditions. Thus, an ambitious CK metabolite analysis was undertaken involving long-term field trials of commercial and historical soybean varieties to determine if differences between CK profiles are related to variation in yield performance. Twenty-seven cultivars were evaluated in this study representing a wide range of performance and assessed for 12 agronomically important plant and seed parameters under field conditions. Identification and quantification of 14 forms of CK was undertaken by high-performance liquid chromatography tandem mass spectrometry (HPLC–MS/MS) at three stages of reproductive development that are critical for yield determination (R4–R6). This revealed a substantial increase in CK levels, especially the highly metabolically active free bases, in the high yielding cultivars of soybean. Significant correlations between yield components and the most active CK form, tZ (*trans*-Zeatin), were detected at both R4 and R5 stages. A similar trend was observed for cZ (*cis*-Zeatin), indicating a possible role of both zeatin isomers in pod and early seed development. Positive, significant relationships between yield and cytokinins were maintained also at R6 stage; however, a switch in hormone profiles and increased levels of isopentenyl adenine (iP) types of CK in high yielding cultivars suggested that the presence of iP derivatives allowed developing seeds to maintain their active role in sink organs and attract assimilates during the seed filling phases, when the metabolism of the maturing plant was generally slowing down. Results suggested that cytokinin metabolites or their associated genes, may serve as a valuable, early indicators of yield performance in marker-assisted breeding programs for soybean or be manipulated through gene editing techniques.

1. Introduction

Plant hormones are signal molecules that are produced within the plant and regulate critical developmental processes. A group of hormones, the cytokinins (CKs), play a major role in cell division and differentiation. CKs control a set of metabolic processes like flowering, fruit set, seed filling and many other related functions including inhibition of senescence (Mok and Mok, 2001; Jameson and Song, 2016). In terms of crop plants, they most critically regulate resource partitioning among different plant organs, a phenomenon referred to as source-sink relationships. As the amount of CKs rises in the sink organs, the demand for nutrients increases leading to an increase in sink strength and accumulation of assimilates (Emery et al., 2000; Götz

et al., 2007). Seeds are major organ sinks that impact economic performance since their elevated sink strength leads to a greater seed set and filling that is in turn reflected in higher yields (Brugièrè et al., 2008). Regulation of the source-sink relationship is a major function of CKs that the current research aims to elucidate.

Structurally, CKs are adenine derivatives that are classified as isoprenoid or aromatic depending on the type of side chain substitute at the N⁶ position. Four major types of isoprenoid CKs occur in nature, namely isopentenyl adenine (iP), *trans*-zeatin (tZ), *cis*-zeatin (cZ) and dihydrozeatin (DZ) (Kamada-Nobusada and Sakakibara, 2009; Spichal, 2012; Yamburenko et al., 2017). Although, many of these are generally considered as bioactive CK types (Hirose et al., 2008), the occurrence and the relative physiological activity of the different forms of CKs can

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significantly vary among different plant species and among developmental stages (Emery et al., 2000). For example, *cis*-isomers (cZR (zeatin riboside), and cZRNT (zeatin nucleotide)), along with their isopentenyl precursors were found to be the major CK forms in developing embryos of pea (*Pisum sativum*). Additionally, the total CK quantities peaked during cell division and closely correlated with high rates of sugar metabolism (Quesnelle and Emery, 2007). In barley (*Hordeum vulgare*), Powell et al. (2013) studied field growth of high and low yielding lines and reported highest concentrations for *cis*- and *trans*-forms of zeatin with the former associated with floret setting and the latter during the grain filling stage. Moreover, both endogenous CK levels, and exogenous application of CKs at critical stages of seed development has been shown to have considerable influence on yield. Early studies with lupine (*Lupinus angustifolius*) showed an increased pod initiation upon exogenous CK application during flower initiation (Atkins and Pigeaire, 1993). In cereals, it was firmly established that CKs regulate kernel yields (Ashikari et al., 2005; Zalewski et al., 2010). This appears to be applicable to eudicot crops as well and several strategies have been proposed to target CK accumulation at reproductive phases of growth to enhance yields (Jameson and Song, 2016). Considering the importance of CKs in plant reproductive development, we aimed to identify the forms and abundances of CKs during peak reproductive developmental stages of soybean (*Glycine max* L. Merr.) and to correlate the hormone profiles with selected yield parameters of this economically important legume crop.

Soybean is a species of legume that is widely cultivated across the world. The high oil and protein concentration makes it a valuable crop with multiple uses both in food and biomaterial industry (Nguyen et al., 2016). Despite its importance, a major problem in soybean cultivation is its flower and pod abortion. Soybean in general produces numerous floral buds of which a considerable proportion, 26–72% abscise before fertilization (Abernathy et al., 1977). Linkages between CK and yields of soybean have been suggested for quite some time and a review of the evidence is presented in Kokubun (2011). Among the reproductive stages of soybean, R1–R8, R1 being the flower initiation and R8 being full maturity of pods, studies have shown that stages R3 and R4 which correspond to stages from early pod set until full pod formation are the critical stages for yield determination as most of the abortion occurs during this time (Carlson et al., 1987; Peterson et al., 1990). Earlier studies also reported the role of CKs in regulating the abortion rates and number of pods being set (Carlson et al., 1987; Dyer et al., 1987; Peterson et al., 1990; Nagel et al., 2001). This was later linked to floral positions within the raceme and the probability of abortion at different locations (Kokubun and Honda, 2000). More recently, improved soybean productivity, as measured by the number of seeds per plant, seed weight and seed diameter, was achieved along with reduced abortion rates upon treatment with benzyladenine, a synthetic CK (Larissa et al., 2014).

The sum of all the evidence clearly indicates that increased CK level at critical stages of reproductive development is positively reflected in soybean yield. However: moving the application of this knowledge to cropping conditions requires field-based studies. As pointed-out by Kokubun (2011), simple approaches involving exogenous CK application have only been successful in pot-grown plants, but their effects are obscured in field-grown plants. To verify whether a positive effect of CK on soybean yield can be expected under the complexity of field conditions an approach was used like that undertaken for barley by Powell et al. (2013). To that end, 27 soybean varieties were sampled from long-term field trials. These varieties were selected to represent a wide range of yield performance and were sampled across three reproductive stages. We report profiles of fourteen different CK types that include nucleotide, riboside and free base forms at R4–R6 stages that correspond to full pod, seed initiation and seed filling, stages critical for yield determination. Results provide insight into the clarity of the CK/yield associations and a baseline for further strategies for yield increase such as investigation of spatio-temporal expression patterns of CK gene

family members expressed during seed development (Jameson and Song, 2016) and potential linkages to molecular markers such as has been reported in rice (Ashikari et al., 2005).

2. Materials and methods

2.1. Plant materials

Soybean tissue samples for hormone analysis were collected in 2010 from two sets of soybean cultivars that were part of the long-term field trials conducted by Agriculture and Agri-Food Canada (AAFC). The first set included thirteen varieties developed by the University of Guelph and AAFC and evaluated in the Ontario 2600 CHU Conventional Soybean Variety Trial, while the second set included fourteen varieties evaluated in the Fifty Years Historical Variety Trial. Both trials were grown at the AAFC Ottawa Research and Development Centre (ORDC Central Experimental Farm, Ottawa, Canada (45°23'12.60" N lat, –75°42'12.54" W long)). All the cultivars used in our study had an indeterminate growth habit. Soybean planting, harvest and post-harvest processing of plant materials were performed by ORDC, following their guidelines for soybean cultivation. Five hundred seeds were planted in four row plots (1.8 × 5 m), with four experimental replicated plots per cultivar. To increase the precision of field trials involving large number of entries and to reduce the effect of within complete-block variation, alpha lattice block designs were used.

The 27 cultivars evaluated in this study represented wide range of yield performance and were chosen based on yield data from previous field trials. Twelve agronomically important plant and seed parameters were evaluated in the field trials: yield [kg ha⁻¹], thousand seed weight (TSW, g), days to maturity (DTM; the number of days a cultivar takes for 95% of the pods to ripen, with a moisture content in freshly matured pods of 35%), plant height [cm], lodging score (LS; 1 = completely erect to 5 = completely flattened), seed quality (SQ; 1 = excellent to 5 = poor) and seed composition [%]: protein, oil, sucrose, total sugars, raffinose/stachyose, and total carbohydrates. Seed composition was determined with a near infra-red whole grain analyser, (Infratec 1241, FOSS North America, Eden Prairie, MN, USA). This data was used for drawing statistical correlations with cytokinin levels obtained from hormone profiling by mass-spectrometry. Agronomical and hormone data of the cultivars from both trials were combined and analysed together to increase the sample size and provide a robust model to determine biological correlations. Table 1 includes the list of soybean cultivars and their yield characteristics that were revealed to be associated with cytokinin levels during plant generative development. The values of the remaining eight characteristics of soybean cultivars are presented in Supplementary Table S6.

Three reproductive stages that critically correspond to soybean yield formation, pod and early seed development (Fehr and Caviness, 1977; Pedersen and Lauer, 2004) were identified and sampled in this study. Stage R4 is the latter one of the two stages that describe pod development. It begins about 20 days after flowering, when at least one full pod that is 3/4-in.-long at one of the four uppermost nodes on the main stem with a fully developed leaf. At this stage, rapid pod growth is occurring and seeds are starting to develop while flowering is still present on the upper branch nodes.

At the second analysed stage – R5, seeds are 1/8-in.-long in the pods at one of the four uppermost nodes on the main stem. The R5 stage describes the initiation of seed development where root growth is slowing while rapid seed filling begins and dry weight and nutrients start being redistributed through the plant to the developing seed.

The transition from R5 to R6, the latest stage used for CK profiling in this study, can take up to 15 days. The beginning of the R6 stage (over 40 days after flowering) corresponds to the time when pods contain green seeds that fill the pod to full capacity at one of the four uppermost nodes on the main stem. At that time, seeds of many sizes can be found on the plant. Nitrogen fixation continues all the way through R6 and

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