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Phenotypic plasticity of sun and shade ecotypes of *Stellaria longipes* in response to light quality signaling: Cytokinins

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ABSTRACT

From two distinct ecotypes of *Stellaria longipes*, one genotype was chosen from each of two very different locations, an alpine (sun) and a prairie (shade) habitat. Plants were clonally propagated and grown in controlled environment chambers under low and moderate red to far-red (R/FR) ratios. The prairie ecotype plants exhibited increased stem elongation, leaf expansion and flowering (6-fold) in response to a low R/FR ratio, relative to plants grown under the moderate R/FR ratio. In contrast, plants of the alpine ecotype showed no increased growth in response to a low R/FR ratio and their flowering was reduced, all relative to the plants grown under the moderate R/FR ratio. These different phenotypic responses to the reduction in R/FR ratio were associated with very different profiles and concentrations of endogenous cytokinins (CKs) assessed in growing tissues of the upper shoots. Specifically, increased total CKs were associated with the rapid growth of plants of the prairie ecotype under a low R/FR ratio. In particular, concentrations of bioactive *trans*-zeatin and dihydrozeatin, were increased during the period of most rapid shoot growth by 2- to 4- fold for these prairie ecotype plants grown under the low R/FR ratio treatment. In contrast, changes in CK levels for the alpine ecotype plants grown under low R/FR ratios were muted. Of especial interest, plants of the alpine ecotype had a predominance of *cis*-pathway CKs, whereas the low elevation, prairie ecotype plants accumulated predominantly *trans*-pathway CKs. Speculatively, the pattern emphasizing *trans*-pathway CKs may be explained by increased LONELY GUY enzyme activity. This enzyme converts and activates nucleotide CKs to free base CKs (bypassing riboside CKs). It could thus explain, in part, the prairie ecotype's ability to respond to shade light with such a high degree of plasticity if one assumes that high *trans*-CKs levels are causal for the increased shoot growth seen under a low R/FR ratio.

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1. Introduction

Light quality (low red- to far-red [R/FR] ratio) and light quanta (low PAR [photosynthetically active radiation]) are the two main light components of the shade environment (Ballare, 1999; Smith, 2000) which can modify plant growth and development. In general, plants exhibiting the shade avoidance syndrome often exhibit increased stem elongation, reduced leaf expansion and early flowering (Smith, 2000). These morphological changes in plant growth and development are regulated by multiple plant hormones (Franklin, 2008; Stamm and Kumar, 2010). For example, changes in both R/FR ratio and PAR level have been shown to mediate changes in stem elongation and leaf area growth of sunflower seedlings (Kurepin et al., 2007a, 2007b). These changes in growth of sunflower seedlings were regulated by at least four groups of plant hormones: gibberellins (GAs), cytokinins (CKs), auxin and ethylene (Kurepin et al., 2007a, 2007b, 2007c). Brassinosteroids were shown not to be involved in light signaling-mediated growth changes of sunflower seedlings (Kurepin et al., 2012), although abscisic acid (ABA) (Kurepin et al., 2007b) and salicylic acid (Kurepin et al., 2010) may be involved.

Stellaria longipes Goldie s.l. (Caryophyllaceae) is a good model species to study the effects of main shade light components: R/FR

Abbreviations: *c*-Z, *cis*-zeatin; *c*-ZR, *cis*-zeatin riboside; *c*-ZRMP, *cis*-zeatin riboside 5′-monophosphate; CK, cytokinin; DZ, dihydrozeatin; DZR, dihydrozeatin riboside; DZRMO, dihydrozeatin riboside 5′-monophosphate; FB, free base; iP, N^6-(Δ^2-isopentenyl)adenine; iPR, N^6- (Δ^2-isopentenyl) adenine riboside; iPRMP, N^6-(Δ^2-isopentenyl)adenine riboside 5′-monophosphate; LOG, LONELY GUY; LC–MS/MS, liquid chromatography-mass spectrometry/mass spectrometry; MeOH, methanol; NT, nucleotide; PAR, photosynthetically active radiation; R/FR ratio, red to far-red ratio; R, riboside; *t*-Z, *trans*-zeatin; *t*-ZR, *trans*-zeatin riboside; *t*-ZRMP, *trans*-zeatin riboside 5′-monophosphates.

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ratio and PAR quanta, because there are two distinct population ecotypes with varying growth and morphological responses to sun and shade habitats (Emery et al., 1994a, 1994b; Kurepin et al., 2006a). One population of *S. longipes* in Alberta, Canada is from an alpine habitat and grows in the open under bright sun conditions. One genotype from this population, 1D, was chosen as a "sun" plant. In its natural habitat, 1D plants (usually clonal ramets) of the alpine population of *S. longipes* will normally exhibit a dwarf phenotype (shorter ramets with larger leaves) and produce only one flower per ramet (Emery et al., 1994a). Another population grows at a lower elevation in a foothills grasslands "prairie" habitat. Here, mutual shading from neighboring shrubs and grasses modifies both light quality and quanta (Emery et al., 1994a). The genotype chosen to represent this "shade" habitat is 7B. The 7B genotype plant (also usually found as a clonal ramet) exhibits a great degree of phenotypic plasticity, grows tall to compete with taller neighbors and typically produces 5–10 flowers per plant in its natural habitat (Emery et al., 1994a). The alpine 1D plants have a much shorter growth cycle than the plants from prairie population.

Changes in R/FR ratio are perceived by plants via phytochromes, a family of photoreceptors which can detect R and FR quanta (Smith, 2000). In Arabidopsis, the phytochrome gene family consists of PHYA, PHYB, PHYC, PHYD and PHYE. These genes can be clustered by similarity of their protein products into three groups: PHYA and PHYC, PHYB and PHYD, PHYE (Clack et al., 1994). From studies with Arabidopsis phytochrome mutants it is now assumed that PHYB mediates plant response to changes in R/FR ratio; i.e. phytochrome B-deficient Arabidopsis plants display increased elongation, decreased leaf expansion, increased apical dominance and early flowering (Devlin et al., 1996). Multiple mutant analyses have also revealed roles for PHYD and PHYE in the PHYB-mediated response to changes in R/FR ratio (Devlin et al., 1998, 1999). In *S. longipes*, the phytochrome gene family consists of PHYA, PHYB and PHYC, and all have shown to alter their gene expression in response to changes in R/FR ratio (Chinnappa et al., 2005; Li et al., 2011).

Shoot morphology of *S. longipes* sun (alpine) and shade (prairie) plants under varying R/FR ratios and PAR settings have been studied extensively (Kurepin et al., 2006a, 2006b, 2007d, 2008). These reports showed that the effects of light quality and light quanta on shoot morphology can be uncoupled in these two ecotypes. Both ecotypes showed increased shoot growth to low PAR treatment, but only plants of the prairie ecotype responded with increased shoot growth to the low R/FR ratio treatment (Kurepin et al., 2006a). Further, the regulatory roles of CKs, GAs, ABA and auxin in shoot growth under varying PAR levels were presented and discussed (Kurepin et al., 2006b, 2008).

It has been suggested that any role for CKs in regulating plant growth in response to changes in the R/FR ratio will be complex and may involve cross-talk with other hormones (Thomas et al., 1997). Fankhauser (2002), and Stamm and Kumar (2010) cite reports which suggest that CKs do play an important role in light quality-mediated plant growth responses. For example, applications of R light or CKs can inhibit seedling growth. Other studies, though, have concluded that there is no direct interaction between R light and CKs (reviewed in Thomas et al., 1997). Further, Arabidopsis mutants with loss-of-function for CK receptors (i.e. AHK2, AHK3, CRE1/AHK4), including triple mutants (ahk, ahk3, cre1), showed no difference from the wild type in hypocotyl elongation when subjected to either continuous R or FR light (Riefler et al., 2006). In another system, sunflower, increases in endogenous CK levels in the shoots of plants grown under a low R/FR ratio treatment have been reported (Kurepin et al., 2007a, 2007b), although the possible role of endogenous CK in shade light-induced growth increases is not clear. Finally, there is a low R/FR ratio-induced increase in hypocotyl elongation in Arabidopsis, which occurs at the expense of cotyledonary leaf growth. This low R/FR-induced growth was shown to involve an auxin-induced degradation of CKs in vein cells of developing leaf primordia, a phenomenon which likely inhibits leaf growth (Carabelli et al., 2007).

We believed that an examination of CK biosynthesis in low R/FR ratio responsive and non-responsive ecotypes of *S. longipes* should provide insight into the possibility that CKs are involved in shade light-induced shoot growth. Herein, we tested hypothesis that increases in bioactive CK concentrations are associated with typically increased growth under low R/FR ratio in plants of prairie, but not alpine ecotype.

2. Materials and methods

2.1. Plants

Individual genotypes from two ecotypes of *S. longipes* were collected. Among them was an alpine genotype (1D) from an open sun-exposed habitat, where vegetation grows in low mats, and also a prairie genotype (7B) from a low elevation foothills grassland habitat. In this lower elevation habitat the *S. longipes* plants are characterized by tall shade-escaping phenotypes which most frequently grow in competition with grasses. The genotypes chosen to represent these two ecotypes were among many originally collected from two populations located on an elevational gradient from near Chain Lakes (1310 m) to Plateau Mountain (2453 m) in S.E. Alberta, Canada and they were judged as being 'typical' of each population (Emery et al., 1994a). Details about propagation of clonal ramets of the alpine and prairie genotypes and growth conditions prior to experimental treatments being initiated are given in Kurepin et al. (2006a).

2.2. Experimental conditions

For light quality experiments Conviron growth chambers equipped with Sylvania cool white 60 W fluorescent bulbs and Philips 60 W incandescent bulbs were utilized. The R and FR light sources were LED (light emitting diode) units with R and FR light emissions that peak at 670 and 725 nm respectively (Quantum Inc., USA). Two R/FR ratios were used, 1.9 (a moderate R/FR ratio that is typical of sunlight, thus emulating the alpine habitat) and 0.7 (FR enrichment, a low R/FR ratio which emulates sunlight found in the shaded, lower elevation grassland habitat). The R/FR ratio was measured as photon quanta between 655 and 665 nm for R and 725 and 735 nm for FR with a LI-COR LI-1800/22 (LI-COR, Inc., Lincoln, Nebraska, USA) quantum sensor. Under both of the above R/FR ratio conditions the PAR level was maintained at a relatively low level of 115 μmol m^{-2} s^{-1} (measured at the soil surface).

2.3. Assessment of plant growth

Stem elongation of each clonal ramet (rooted cutting) was measured from the bottom of the first internode to the shoot tip. Leaf area of the pair of leaves below the third internode from the top was measured with a ΔT Area Meter (Delta-T Services LTD, Cambridge, UK). Stem elongation and leaf area were assessed in three experimental trials (10 ramets each) for each of R/FR ratio treatments and trends were similar for each trial. Thus, individual measurements from 30 ramets were used to calculate the mean and standard error (SE). For assessing the number of flowers produced by each genotype under different R/FR ratios, open blossoms from 50 individual clonal ramets from at least five pots were counted.

2.4. Extraction and purification of cytokinins

CKs were extracted from a separate set of tissue samples and separated under conditions established by Emery et al. (1998)

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