Environmental and Experimental Botany 104 (2014) 9–15

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Photoperiodic effects on short-pulse ^{14}C assimilation and overall carbon and nitrogen allocation patterns in contrasting quinoa cultivars

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ARTICLE INFO

Article history:
Received 29 November 2013
Received in revised form 10 March 2014
Accepted 12 March 2014

Keywords:
Chenopodium
Crop adaptation
Source–sink relationship
Resource allocation
Day length
Yield potential

ABSTRACT

Further understanding of the range of environmental influence on source–sink relationships in quinoa is important to streamlining future crop improvement and efforts concerning geographic expansion of cultivation areas. In the present study a photoperiod sensitive quinoa cv. 'Achachino' and photoperiod neutral cv. 'Titicaca' were studied under short (10 h) and long (17.5 h) days, with respect to C and N distribution as well as partitioning of newly assimilated C to plant organs. An extended photoperiod resulted in ^{14}C decreasingly being allocated to stem growth and lower leaves in 'Titicaca', but increasingly in 'Achachino'. Both cultivars increased biomass accumulation under extended photoperiod, but in the short day cultivar 'Achachino' the extension mostly favoured stem and lower leaf growth and resulted in deteriorated seed development. In contrast, 'Titicaca' responded to extended photoperiod with an immediate increase in carbon allocation to upper leaves, and over time to the reproductive structures, resulting in a more than 50% increase in final yield. Collectively the results indicate that even though the photoperiod sensitive cultivar flowered under long photoperiod it did not develop seeds, whereas the photoperiod neutral cultivar in comparison has a wider range in photoperiod plasticity and ability to specifically utilize additional light towards reproductive growth, resulting in an increased yield potential in regions outside of the tropical zone.

1. Introduction

As a high value crop with natural tolerance for saline soil and drought conditions, Quinoa (*Chenopodium quinoa* Willd.) is an excellent candidate for improving agricultural diversification and crop production, as well as economic conditions, in regions where production of other crops is severely limited by drought, poor soil quality, or increasingly unstable growing conditions (Jacobsen et al., 2003a,b; Jacobsen, 2012) that are now exacerbated by anthropogenic activity, driving climatic changes further and faster (Craufurd and Wheeler, 2009). However, the majority of quinoa cultivars, particularly those with greater drought and salt tolerance, are short day plants and exhibit high sensitivity during seed development to photoperiods longer than 12 h (Fuller, 1949; Galwey, 1993; Bertero et al., 1999; Jacobsen et al., 2003a,b; Bertero et al., 2004; Christiansen et al., 2010; Jacobsen, 2012). Crop production is naturally sensitive to variation in climate, and both regional and seasonal determined shifts in day length can have radical effects on yield potential (Lawn, 1989). With definite permanent alterations and severe short term variations in the global climate firmly established as the reality (IPCC, 2007a,b), farmers will be faced with having to accommodate shifts in photoperiod and temperature conditions that divert from the established farming calendar (Craufurd and Wheeler, 2009). Therefore, crop selection and management practices will have to quickly adapt and remain flexible. Quinoa as a crop, with potential uses for both human and animal consumption, is undergoing a rapid rise in popularity worldwide (Jacobsen, 2012). The heightened interest warrants further research into specific aspects of quinoa cultivation, particularly with regards to how photoperiod effects on plant development may currently be limiting yield potentials and further geographic expansion (Christiansen et al., 2010). Determining the phenological plasticity, carbon (C) and nitrogen (N) allocation patterns under different photoperiods for differently adapted quinoa cultivars will be essential in further assessment of the adaptive potential of the crop. The establishment of future germplasm improvement strategies

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http://dx.doi.org/10.1016/j.envexpbot.2014.03.002
0098-8472/

and management recommendations, to assist future geographic expansion of quinoa cultivation in South America and other regions, may also be dependent on this.

Previous studies involving quinoa have indicated highly differentiated photoperiod dependent growth responses of short day adapted cultivars compared to day length neutral cultivars (Christiansen et al., 2010; Bendevis et al., 2013). Until now, photoperiod induced changes in C and N allocation, in contrasting quinoa cultivars, have not been studied in detail, nor have they been related to any differences in physiologically adaptive response mechanisms as those suggested between two different day length adapted cultivars (Bendevis et al., 2013). Previous studies have observed and described the high sensitivity in quinoa to extended photoperiods in phenological terms (Fuller, 1949; Bertero et al., 1999; Christiansen et al., 2010), but only a few recent studies have compared the responses to long photoperiods for contrasting quinoa cultivars and related it to photoperiod adaptation (Christiansen et al., 2010; Bendevis et al., 2013) and only one study (Bendevis et al., 2013) has thus far attempted to elucidate aspects of the physiological basis and a possible photoperiod induced phytohormone response as a link to further explain the resulting growth and development differences of the contrasting cultivars. Previous observations have alluded to important cultivar (Christiansen et al., 2010; Bendevis et al., 2013; Gutjahrn et al., 2013) and species differentiation (Dorais et al., 1996), in adjustment of source–sink relationships as a response to both photoperiod and plant development stage. In the present study we sought to further assess the impact of an extended photoperiod on the distribution patterns of newly incorporated C as well as the influence the light environment will have on whole-plant N and C allocation and how it may impact quinoa yield potentials.

2. Materials and methods

2.1. Plant material and growing conditions

Two cultivars of quinoa (*C. quinoa* Willd.), cv. 'Titicaca' and cv. 'Achachino', were grown from seeds in controlled environment walk-in growth chambers (Conviron, Winnipeg, Canada) at the University of Copenhagen Faculty of Science, Taastrup, Denmark. 'Titicaca' (previously Q52) is a day length neutral cultivar developed at the Faculty of Science, Taastrup, Denmark (55°40′ N, 12°18′ E, 28 m above sea level). 'Achachino' is a short day cultivar of the real type from southern Bolivia (20°28′ S, 66°50′ W, 3653 m above sea level). The air temperature in the growth chambers was set to 22/15 °C day/night air temperature. The photosynthetic photon flux density (PPFD) for all the chambers, for the duration of the study, was approximately 600 μmol m^{-2} s^{-1}, at upper plant height, provided by metal halide lamps (Osram, HQI 400W). Four seeds were sown directly into each of the 2 L pots used in this study. Plants were thinned to one per pot after two leaves had fully emerged. The pots were moved every couple of days within each growth chamber to avoid positioning effects. Peat based potting soil (Substrate No. 1, Pindstrup A/S, Ryomgaard, Denmark) was used as growth medium. For the duration of the study, all pots were kept adequately watered by drip irrigation and supplied with a standard fertilizer solution (Pioner NPK Makro, 14-3-23+Mg combined with Pioner Mikro+Fe (Azelis, Lyngby, Denmark); EC 1.3 mS cm^{-1}; pH 5.5).

Two photoperiod treatments were managed in two growth chambers as integrals of uninterrupted full light. The treatment of continuous short photoperiod (S) was 10 h of light (with a daily light integral of 21.6 mol m^{-2} day^{-1}), which is sufficiently below the 12 h required for optimum reproductive development of short day quinoa cultivars. The short to long day treatment (SL), started with short photoperiod during pre-flowering bud development stages (stage 2–6 as classified by Jacobsen and Stølen (1993), which was then extended to long photoperiod (17.5 h, daily light integral 37.8 mol m^{-2} day^{-1}) until plant harvest at the completion of the study period. The long day treatment of 17.5 h reflects the maximum day length under Danish field conditions during the growing season (Christiansen et al., 2010). Plant data was collected in short day (S1 and SL1) 35 days after sowing (DAS). The same day, SL1 plants were transferred to long photoperiod. Data was collected again (S2 and SL2) at 42 DAS, one week after transfer. All plants were at the same developmental stage at the time of the transfer for SL1. There were no visible morphological differences between cultivars at this point. The difference in photoperiod between the S and SL treatments was estimated to create a sufficient gradient to quantify a shift in plant growth and C allocation within a relatively short period of time. The increase in photoperiod for the SL2 treatment was implemented to trigger internal adaptive mechanisms, in order to measure subsequent changes in the distribution pattern of new uptake of C, as well as possible alterations in allocation of C and N resources. The data points from S1 to S2 provides a measure of the 'normal' growth pattern, whereas the difference between S2 and SL2 treatments enables a direct comparison of how plant growth and C and N allocation are affected by extended photoperiod. Different resource distribution in the two contrasting quinoa cultivars used in this study, have been implied through observations in previous experiments with similar photoperiod design (Bendevis et al., 2013).

2.2. ^{14}C labelling and analysis

On two occasions, separated by one week, 16 plants (four of each cultivar for each treatment) were labelled with short ^{14}C pulses. The labelled plants were harvested and processed for analysis of distribution patterns of newly assimilated C, as well as redistribution and allocation of C and N pools in relation to both normal plant development and extended photoperiod influence. Additionally, four plants of each cultivar for both the S and SL treatments were left unlabelled and grown to maturity, beyond the designated study period, to obtain final yield for both S2 and SL2. In total 48 plants were used, whereof 32 were labelled with ^{14}C and 16 grown to maturity. The plants used for ^{14}C labelling were randomly selected out of the total plant population. The S1 ^{14}C labelling was carried out 35 DAS and the S2/SL2 label was applied one week later at 42 DAS. Each plant was enclosed in 30 L transparent plastic bags with 150 μl of $NaH^{14}CO_3$ carrying a specific activity of 278 kBq (7.6 μCi) in a glass vial. 2 ml of 5 M HCl was injected with a syringe through the plastic and into the glass vial with the $NaH^{14}CO_3$ to release $^{14}CO_2$. The syringe holes were sealed with airtight tape and after 4 h of exposure to the labelled CO_2, 2 ml of NaOH was added to the solution in the vial to trap the remaining $NaH^{14}CO_3$ in the enclosed space (Hansen, 1967; Carvalho et al., 2006; Nkurunziza and Streibig, 2011). Labelling was carried out between 09:00 and 11:00 to ensure adequate photosynthetic activity. S1/S2 photoperiod started at 07:00 and SL2 at 05:00. To further ensure complete photosynthate distribution throughout the plants, while also minimizing the amount of ^{14}C lost through respiration, labelled plants were harvested the morning following each of the two ^{14}C applications (viz. 24 h after labelling).

Final ^{14}C activity and oxidizer efficiency (E) was determined following the same protocol as detailed by Nkurunziza and Streibig (2011) using a sample oxidizer (307 Sample Oxidizer, Packard) for complete combustion of the samples to release ^{14}C into vials with scintillation liquid, and liquid scintillation counter (WALLAC Win Spectral 1414). All of the above-ground plant organs were separated into stems, lower leaves, upper leaves, and buds dried to constant weight at 70 °C and weighed. The leaf canopy height of each plant was halved and leaves separated into lower and upper