Scientia Horticulturae 180 (2014) 262–267

Contents lists available at ScienceDirect

Scientia Horticulturae

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

Accumulation and remobilisation of sugar and starch in the leaves of young tomato plants in response to temperature

Y. Klopotek*, H.-P. Kläring**

Leibniz Institute of Vegetable and Ornamental Crops Großbeeren/Erfurt e.V., Kühnhäuser Straße 101, 99090 Erfurt, Germany

ARTICLE INFO

Article history:
Received 12 May 2014
Received in revised form 13 October 2014
Accepted 16 October 2014
Available online 21 November 2014

Keywords:
Dry matter content
Glucose
Fructose
Sucrose
Non-structural dry matter
Structural dry matter

ABSTRACT

Temperature integration strategies are a method for decreasing the amount of energy consumed in greenhouse plant production. These strategies are based on the hypothesis that plants can accumulate carbohydrates such as soluble sugars and starch during periods when growth is limited by low temperature for later use when the temperature rises. However, little is known about the storage capacity of non-structural carbohydrates in plants. Therefore, three experiments with tomato plants were carried out in growth chambers where the temperature was changed from warm (dark: 24 °C, light: 26 °C) to cool (dark: 14 °C, light: 16 °C) or from cool to warm. Leaf dry matter content and leaf sugar and starch concentrations were significantly higher when plants were grown at a low rather than at high temperature. Soluble sugar and starch concentrations in the leaves increased or decreased immediately after the temperature was reduced or raised. A strong gradient of changes was observed for up to 36 h and 60 h in soluble sugars and starch, respectively. Over the next four days, sugar concentrations remained in the range observed at 36 h post temperature change; the starch concentration continued to increase or decrease slightly. The time courses of dry matter content corresponded to those of sugar and starch concentrations. Data indicates that young tomato plants can accumulate and store carbohydrates in the form of soluble sugars and starch for at least one week when growth is limited by low temperatures. They can remobilise these carbohydrates when growth is forced again by high temperatures.

1. Introduction

It has become increasingly important in recent years to reduce greenhouse energy consumption in order to cut costs and CO_2 emissions (e.g. Dieleman and Hemming, 2011). Temperature integration strategies are a method for reducing the amount of energy consumed in greenhouse plant production. The principle of this concept is that the set point for heating is lowered in situations where greenhouses have a high heat demand, such as when the outside temperature is low or the wind speed is high. Delayed plant growth is then compensated for by higher temperature under conditions requiring little or no heat demand, such as when the wind speed is low, the outside temperature is high or solar radiation is high (Bailey, 1985; Körner and Van Straten, 2008). The possibility to exploit such temperature integration systems has been published for several ornamental plants and vegetable crops, such as roses (Buwalda et al., 1999), chrysanthemum (Körner and Challa, 2004), cucumber (Slack and Hand, 1983), sweet pepper (Bakker and van Uffelen, 1988) and tomato (De Koning, 1990). These strategies, which are based on a combination of models and empirical knowledge, usually use fixed time periods for achieving a certain average temperature independent of all other micrometeorological variables. However, they do not consider the range of problems associated with storing assimilates under conditions when plant growth is limited by low temperatures and remobilising them under conditions favourable for growth.

A decline in growth-dependent sink demands and a reduced translocation of assimilates to sink organs can be expected at decreasing temperature (e.g. Marcelis, 1996; Gent and Seginer, 2012). This in turn could result in the accumulation of sugars and starch in the leaf (e.g. Venema et al., 2005). However, when the storage capacity for carbohydrates in leaves in the form of sugars and starch is saturated, an increasing fraction of the assimilated carbon may be used to synthesise other substances. These substances, which cannot be remobilised for growth, are summarised in the following under the term 'structural dry matter'.

Several studies have investigated the response of tomato leaves to very low (chilling) temperatures (e.g. Venema et al., 2005). The

* Corresponding author. Tel.: +49 36201 785255; fax: +49 36201 785250.
** Corresponding author. Tel.: +49 33701 78351; fax: +49 33701 55391.
E-mail addresses: klopotek@igzev.de (Y. Klopotek), klaering@igzev.de (H.-P. Kläring).

http://dx.doi.org/10.1016/j.scienta.2014.10.036
0304-4238/

aim of these studies was to improve the low-temperature tolerance of tomato plants by breeding (Venema et al., 1999) or grafting (Venema et al., 2008). Although some data is available on the effect of low temperatures ranging from 12 to 16 °C on contents of leaf dry matter and non-structural carbohydrates of thermophile greenhouse-grown fruit vegetables, there is still much uncertainty regarding the maximum storage capacity of sugars and starch in tomato plants (Seginer and Gent, 2014). In particular, data on the effect of temperature change on the time course of the structural and non-structural carbohydrate contents in plants are lacking. For this reason, the present study focuses on the effect of temperature increases and decreases on leaf carbohydrate accumulation and remobilisation during the early growth phase of tomato plants.

2. Materials and methods

2.1. Crop cultivation

Three experiments were carried out on tomato plants (*Solanum lycopersicum* (L.)) cultivar "Pannovy" (Novartis, Basel, Switzerland). Seeds were germinated in sand in February 2011, November 2011 and January 2012 in Expts I, II and III, respectively. Seedlings were pricked out into sand-filled pots and grown in the greenhouse. About 3 weeks after germination, the sand was washed from the roots and the plants were transplanted to 3-L plastic containers with a nutrient solution prepared by mixing deionised water and stock solution according to De Kreij et al. (1997). Each plant was inserted in an expanded polystyrene disc that served as a lid. The nutrient solution of each container was ventilated via flexible tubes and a pump. The nutrient solution was replenished when required. A total of 48 containers were arranged in two growth chambers (Vötsch, Balingen, Germany) in Expts I and III; 24 containers were arranged in one growth chamber in Expt II. The temperature was 26 °C during the 12 h light period and 24 °C during darkness; relative humidity was 75%. Light was provided by high-pressure sodium discharge lamps AGRO SON-T 400W (Philips, Amsterdam, The Netherlands) and krypton bulbs SVA (Osram, Munich, Germany). The photosynthetic photon flux density (PPFD) at plant panel level was approximately 540, 550 and 400 μmol m^{-2} s^{-1} in Expts I, II and III, respectively. The plants were adapted to these environmental conditions for one week prior to commencing the experiment.

2.2. Temperature treatments

In Expt I, the temperature in one growth chamber was kept at 24 °C during the dark and 26 °C during the light period for another two weeks, whilst in the other chamber the temperature was decreased to 14 and 16 °C, respectively. In addition, one week after the temperature treatment had started, six plants were swapped from one growth chamber to another. By the end of the experiment, we therefore had information about tomato plants under the following four conditions: plants grown under warm or cool conditions for two weeks; plants grown under cool conditions for the first week followed by a week under warm conditions and plants grown under warm conditions for the first week followed by a week under cool conditions.

In Expt I, plant samples for growth and carbohydrate analyses were taken at weekly intervals at the end of the dark phase: at the start of the temperature treatment, one week later when some plants were swapped between chambers, and one week later when the experiment was terminated. In contrast, the effects of temperature changes were studied on a short-term basis in Expts II and III. In Expt II, the focus was on plant response to decreasing temperatures; Expt III concentrated on raising the temperature. In Expt II, therefore, the air temperature in the chamber remained high for another week and was then reduced to 14 and 16 °C during the dark and light phase, respectively. The reverse was the case in Expt III: here, plants first adapted to the low temperature, which was raised after one week. The temperature was changed at the start of the dark phase. Plant samples for carbohydrate analyses were taken at short intervals: at the end of the dark phase, 12 h before the temperature was changed, and at the end of the dark phases of the next three days and of the seventh day after the temperature change. Plants for growth analyses were harvested concomitantly, with the exception of on the morning immediately after the temperature change, when no plants were harvested.

2.3. Recording plant biomass characteristics, carbohydrate status

Six plants per treatment in Expts I and II and twelve plants in Expt III were completely harvested on each sampling date stated above. The material collected was divided into shoots and roots, and weighed before and after drying in a ventilated oven at 80 °C for two days. In addition, leaf area was measured in Expt I using a leaf area metre LI 3100 (LI-COR Inc., Lincoln, Nebraska, USA). For Expt I, the relative growth rates were calculated for the one-week periods based on the mean masses of all replications for both fresh and dry matter (difference between the natural logarithm of mass at the start and end of the one-week period divided by seven), and displayed against the masses determined at the start of each period. Thus, two and four growth rates were obtained for the first and second week, respectively, which can be assigned to three different initial masses for each investigated temperature.

Six samples of the third completely unfolded leaf (counted from the top) were taken per treatment in Expts I and II and twelve in Expt III on the sampling dates defined above. Four discs with a diameter of 0.9 cm were sampled per leaf, immediately frozen in liquid nitrogen and stored at −80 °C. The samples were pulverised using a cryomill (Retsch, Haan, Germany). Approximately 30 mg of each pulverised sample was weighed for later measurements. Soluble sugars (glucose, fructose and sucrose) and starch were determined via enzymatic assay in microplates, as described by Stitt et al. (1989), with minor modifications. Samples were extracted twice at 78 °C for 20 min with 80% and 50% ethanol. The supernatant was used for soluble sugar measurement. The residue was dried at 20 °C for 45 min and resuspended in distilled water. After a heating period of 3 h at 120 °C, the samples were cooled down and an enzyme mixture containing 50 mM sodium acetate, amyloglucosidase and α-amylase (Roche D, Grenzach-Wyhlen, Germany) was added for starch hydrolysis. Starch breakdown was conducted three times at a pH of 5.0 and 37 °C. The glucose produced was determined according to Hajirezaei et al. (2000).

In order to assess the effect of temperature on the structural dry matter content of leaves, the difference between the leaf total dry matter content and the leaf non-structural dry matter content, which consists mainly of sugars and starch, was considered.

3. Results

3.1. Plant growth

The growth rate of young tomato plants in Expt I was influenced significantly by temperature (Fig. 1a). In the short period of one week, the relative growth rates based on fresh matter were much higher at a mean daily temperature of 25 compared to at 15 °C (Fig. 1c); these differences were virtually non-existent in the case of dry matter (Fig. 1d). The latter, however, was associated with a marked decrease in leaf area (Fig. 1b) due to increased dry matter content (Fig. 2a).