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Effect of plant growth temperature on membrane lipids in strawberry (*Fragaria* × *ananassa* Duch.)

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Abstract

Changes in membrane lipid composition are important in the acclimation of plants. The influence of four day/night growing temperature combinations (18/12, 25/12, 25/22, and 30/22 °C) on membrane lipids of 'Earliglow' and 'Kent' strawberry (*Fragaria* × *ananassa* Duch.) were studied. The monogalactosyl diglyceride (MGDG) and digalactosyl diglyceride (DGDG) were the major galactolipids in the strawberry leaves. 'Earliglow' contained a higher amount of galactolipids in the leaves than 'Kent'. The major phospholipids in the strawberry leaves, roots, and fruit were phosphatidylcholine (PC), phosphatidylinositol (PI), phosphatidylglycerol (PG), and phosphatidylethanolamine (PE). PC and PE were the two predominant phospholipids in the strawberry. The leaves and fruit of 'Earliglow' contained higher amounts of phospholipids compared to those of 'Kent', whereas 'Kent' strawberry roots had higher phospholipids. Palmitic (C16:0), stearic (C18:0), oleic (C18:1), linoleic (C18:2), and α-linolenic (C18:3) acids were major fatty acids in galacto- and phospholipids of the 'Earliglow' and 'Kent' strawberry. PC is very rich in linolenic acid in leaves compared to the fruit and root tissues. PC had the highest ratio of unsaturated to saturated fatty acids among all phospholipids. There was a significant increase in the content of galactolipids (MGDG, DGDG) and phospholipids (PC, PI, PG and PE) and unsaturation of their fatty acids in the cool day/night growth temperature. Increasing day/night growth temperatures decreased MGDG/DGDG ratios. The shifts in saturation and composition of fatty acids observed with strawberry may be an adaptation response of plants to the temperature changes.
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Keywords: *Fragaria* × *ananassa*; Galactolipid; Phospholipids; Fatty acids; Temperature

1. Introduction

Growth temperature has a profound influence on membrane fatty acid composition and degree of unsaturation (Lyons, 1973). Changes in the composition of fatty acid components of membrane lipids are important in the acclimation of most types of plants (Martin et al., 1976). The physical state of the membrane lipids and the ratio of unsaturated to saturated fatty acids play an important role in determining the physiological function of the plant tissue (Brenner, 1984). Lipid molecules are essential building blocks for every membrane of a living cell, and membranes are sites for many specific enzymatic activities, transport ions and metabolites, and hormonal receptors. The composition of membrane lipids may also be a factor in determining major biological properties of membranes that in turn may influence biological changes, such as the growth of plants (Brenner, 1984).

Different growing temperatures, low or high air temperatures, during the growing season are a common occurrence in many strawberry production regions. Extreme temperatures reduce photosynthetic rate and increase transpirational water loss that may exceed the plant's ability to replenish. High temperature stress can result in reduced growth, diminished yields and poor fruit quality (Hellman and Travis, 1988). Our previous studies showed that 25/12 °C (day/night) was the optimum temperature to grow strawberry (Wang and Camp, 2000). Higher growth day/night temperatures enhanced the development of fruit color more rapidly than lower growth temperatures. When the day/night temperature became higher, the fruit surface and flesh colors became redder and darker. On the other hand, leaf color was brighter and greener as day/night temperatures decreased (18/12 °C). Increased growth temperatures resulted in decreased fruit soluble solids (SSC), titratable acids (TA), SSC/TA ratio, and ascorbic acid (AA) content in the fruit. Plants grown at 18/12 °C contained high amounts of

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fructose, glucose, citric acid and total carbohydrates in fruit. Temperatures of 30/22 °C inhibited plant and fruit growth, and reduced fruit quality. Cooler day/night temperature (18/12 °C) shifted biomass from leaves to roots (Wang and Camp, 2000). Growth temperatures also affected phenolic acid, flavonol, and anthocyanin content and antioxidant capacity. The concentration of flavonoids in strawberry juice was correlated with oxygen radical absorbance capacity against $ROO^{\bullet}$, $O_2^{\bullet -}$, H_2O_2, $OH^{\bullet}$, and $^1O_2$ radicals. Strawberry grown under high day/night (30/22 °C) temperature conditions contained enhanced levels of flavonoids and antioxidant capacities in the fruit (Wang and Zheng, 2001). However, little information is available about the effect of the growth temperature on membrane lipids in strawberry. The objectives of this research were to quantify the changes in the degree of unsaturation of fatty acids in galactolipids and phospholipids of leaves, roots and fruit of strawberry as affected by day/night growing temperatures.

2. Materials and methods

2.1. Plant materials and experimental designs

Uniform sized plants of approximately 1-year-old 'Earliglow' and 'Kent' cultivars were used. 'Kent' was originally bred in Kentville, Nova Scotia at the Research Station Agriculture Canada, while 'Earliglow' was originally bred in Salisburg, Maryland by ARS, USDA (The Brooks and Olmo, 1997). Thus, the two cultivars were adapted to two different temperature zones. The plants of both cultivars were propagated by runner-tip cuttings in June and plants were grown in 2-l plastic pots (15.0 cm × 12.0 cm, E.C. Geiger Inc., Harleysville, PA) containing Pro Mix BX (Premier Brands Inc., Stamford, CT) in a greenhouse. Radiation sources in the greenhouse consisted of natural daylight and Watt-Miser incandescent lamps (Nela Park, Cleveland, OH) that provided a photosynthetically active radiation (PAR) around 700 μmol m^{-2} s^{-1} for 14 h/d (06:00–20:00 h). Temperatures were set at 25 °C during the day and 20 °C at night. During the growing season, all plants were watered daily and fertilized bi-weekly with 150 ml/plant of Peters fertilizer (20–20–20, N/P/K). Prior to initiation of temperature treatments, plants were exposed to ambient winter temperatures of Beltsville, Maryland, USA in an unheated greenhouse from October to February. Plants were then moved to a heated greenhouse (25 °C during the day and 20 °C at night) for approximately 6 weeks to force flowering. Blossoms were self-pollinated by hand using a small brush. Plants with the most fruit (at least 10 fruits per plant) at their green fruit stage were selected for the growth chamber experiments. Forty plants each of 'Earliglow' and 'Kent' were removed from the greenhouse in March and divided into lots of 10 plants. One lot of each cultivar was randomly placed in four growth chambers set at day/night temperatures of 18/12, 25/12, 25/22 and 30/22 °C. The plants were in growth chambers for 6 weeks. The photoperiod for each growth chamber was 14 h (6:00–20:00 h) with a PAR around 700 μmol m^{-2} s^{-1} at plant height. The ripeness of the fruit was determined by color. Firm red-ripe fruits free from defects or decay were harvested from each growth chamber for each cultivar during the fruiting stage and the berries were cut into small slices, mixed, and then used for membrane lipid analyses. Data for the individual harvests were pooled. Two months after the start of the temperature treatments, the plants were harvested and leaves and roots were separated from plants. Young fully expanded leaves and actively growing roots were used for membrane lipid analyses.

2.2. Extraction, fractionation, and analysis of lipids

Lipid were extracted, fractionated and analyzed according to procedures described by Wang et al. (1988) and Wang and Faust (1990). Triplicate 1.0 g samples of leaves, roots and 30 g fruits were collected from 10 plants of each temperature treatment (18/12, 25/12, 25/22, and 30/22 °C) as described in previous section and extracted with isopropanol containing 4 μg 2,6-di-*t*-butyl-4-methylphenol (BHT). Total lipids were separated into neutral lipid, glycolipid and phospholipid fractions by silicic-acid column chromatography on 100- to 200-mesh Bio Sil A (Bio Rad Laboratories, Richmond, CA). The glycolipid and phospholipid fraction were further separated by chromatography (TLC) on 20 cm × 20 cm glass plates pre-coated with a 250 μm thickness of silica gel 60 (EM Reagents, Darmstadt, FRG) using 100 acetone:2 acetic acid:1 water (by volume) and 85 chloroform:15 methanol:10 acetic acid:3.5 water (by volume), respectively (Wang and Faust, 1990).

Individual galactolipids and phospholipids were identified by cochromatography with authentic standards (Sigma, St. Louis, and Supelco, Bellefonte, PA) and by detection with spray reagents specific for hexose sugars or phosphate. Individual lipid bands were scraped off and eluted with 3 ml of 2 chloroform:1 methanol (v/v) followed by a Folch wash (Folch et al., 1957). Galactolipids were quantified by the method of Roughan and Batt (1968). Phospholipids were quantified by the method of Ames (1966) for organic phosphate. Total fatty acids esterfied to polar lipids from strawberry leaves, roots and fruit were derivatized to fatty acid methyl esters (FAMEs). FAMEs were analyzed and quantified by gas–liquid chromatography with flame-ionization (FID-GC) analysis (Wang and Faust, 1990). *n*-Heptadecanoic acid was included in all samples as an internal standard, methyl heptadecanoate was used as an external standard. Individual FAMEs were identified by a comparison of retention times with those of authentic standards (Supelco). This tentative identification of major polar lipid fatty acids was corroborated by further analysis of FAMEs by gas chromatography–mass spectrometry (GC–MS) (Wang et al., 1988).

2.3. Statistics

Data were analyzed as two-factor general linear models using PROC MIXED (SAS Institute Inc., 2004) with cultivar (CV) and temperature as the factor. When necessary the variance grouping technique was used to correct variance heterogeneity for the means comparisons. The analysis of variance results are given in Tables 1–4. When effect(s) were

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