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Leaf development, net assimilation and leaf nitrogen concentrations of five *Prunus* rootstocks in response to root temperature

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Abstract

Rootstocks differentially influence tree physiology and these differences may be due to varying responses to root zone temperature (RZT). To determine if this is the case, the physiology, leaf development and nitrogen relationships of five different *Prunus* rootstocks with chill requirements between 100 and 1100 h were examined during and after growth at RZTs of 5, 12 and 19 °C for 6 weeks. RZT correlated positively with leaf numbers, expansion rates and final leaf area, and significant differences existed among the rootstocks in the magnitude of these parameters at different RZTs. In particular, leaf expansion and area were less affected at low RZT in the low chill varieties. Net assimilation (A_n), leaf nitrogen ($N\%$) and photosynthetic nitrogen use efficiency (A_n/N) also correlated positively with RZT: again, there were differences in the magnitude of these parameters among the rootstocks. No associations amongst A_n, $N\%$ or A_n/N could be found for the rootstocks; hence, they all differed in their physiological responses to RZT. Low RZT alone was sufficient to reduce A_n and decreased both leaf area and photosynthetic activity. Leaf expansion was related to $N\%$, as the varieties with the lowest $N\%$ also had the lowest expansion rates. Infrared thermography of the cv. Golden Queen showed a negative correlation between RZT and leaf temperature with leaves of plants at the lowest RZT being 2 °C warmer than ambient whilst those at the highest RZT were 2 °C cooler than ambient. These differences were due to transpiration, as transpiration for the variety used decreased with reducing RZT. Transpiration from the other rootstock varieties was lowest at the 5 °C RZT but, depending on variety, at 12 °C was either higher, lower or the same as that from plants whose roots were at 19 °C. Together, the results of this study explain some of the rootstock-induced changes in tree growth and suggest the need to incorporate seasonal changes in RZT into development models for peaches.

Keywords: Infrared thermography; Leaf area; Leaf temperature; Photosynthetic nitrogen use efficiency; *Prunus persica*; Transpiration

1. Introduction

Rootstocks differentially influence the growth and vigour of stonefruit trees (Rom and Carlson, 1987; Layne, 1994; Moreno et al., 1994). A number of studies have shown that rootstocks affect leaf area development (Yadava et al., 1980; Yadava and Doud, 1989; Malcolm et al., 1999), transpiration rates (Natali et al., 1985) and certain leaf nitrogen relationships (Couvillon, 1982; Knowles et al., 1984; Caruso et al., 1996). However, the authors of these studies did not claim that these were the mechanisms by which rootstocks have their effects on growth. Malcolm et al. (2006) demonstrated that root zone temperature (RZT) influenced growth, leaf development and physiological indices such as net assimilation and transpiration of the peach rootstock, Green Leaf Nemaguard. Further, Malcolm et al. (2007) showed that rootstocks differ in their growth responses to RZTs. Therefore, it is possible that the responses of individual rootstocks to RZT may also affect the growth and development of the scions grafted onto them.

Varietal differences in sensitivity to RZT have been reported in lettuce (Lee and Cheong, 1996; He and Lee, 1998), cucumbers (Kleinendorst and Veen, 1983) and in maples (Wilkins et al., 1995). In apples (Gur et al., 1976), tolerance to high RZTs was found to vary among different rootstocks. Peach rootstocks differ in the magnitude of their growth and biomass partitioning in response to RZT (Malcolm et al., 2007). This study of Malcolm et al. (2007) also showed that the changes in partitioning caused by RZT resulted in differences in leaf, stem and root mass ratios and that these differences in partitioning were greatest at low RZTs and became less as RZT increased.

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The study also showed that the response to RZT was related to a variety's chill requirement.

Varietal and species differences in growth responses to RZTs can also be reflected in the plant's physiology. For example, leaf nitrogen concentrations in peppers (Gosselin and Trudel, 1986) were reduced by low RZTs whereas in tomatoes, concentrations are raised (Gosselin and Trudel, 1983b). For stone fruit, there are few published studies examining the potential relationships among RZTs, growth and physiology. However, it is known that there are strong correlations between leaf nitrogen concentration and net assimilation (De Jong, 1982) and between shoot productivity and leaf nitrogen content (De Jong and Day, 1991). Nevertheless, it is not known if RZT affects these correlations nor whether rootstocks change their comparative leaf development, net assimilation and leaf nitrogen responses when grown at different RZTs.

The present study extends the work of Malcolm et al. (2006, 2007), by examining the physiological response to RZT of the rootstocks used in the latter of these two studies. In this present study, two trials, each of 6 weeks duration, were conducted using actively growing plants of five *Prunus* rootstocks grown at constant RZTs of 5, 12 and 19 °C. In this paper, we report on the effects of these RZT treatments on leaf development, net assimilation and leaf nitrogen concentrations. The temperature treatments were chosen to represent the RZTs that the roots of peach trees are likely to experience in winter, early spring and early summer in coastal NSW, Australia at a soil depth of 300 mm.

2. Materials and methods

2.1. Plant material, experimental design and growth analysis

The plant materials and experimental design are as reported in Malcolm et al. (2007) and used seedlings of the rootstocks, Okinawa (OK, 100 h), Flordaguard (FG, 300 h), Green Leaf Nemaguard (GL, 850 h), Fay Elberta (FE, 900 h), and Golden Queen (GQ, 1100 h). The figures within parentheses are the chilling requirements of the rootstocks as defined by Weinberger (1950) with the individual values being taken from Okie (1998). Leaf numbers on each individual plant were counted at the beginning of each trial and subsequently at weekly intervals. To assess the daily rate of leaf expansion, the length of two marked, similarly positioned, young leaves on each plant were measured for 7 consecutive days in the week prior to harvest. At harvest, 6 weeks after the start of the trials, the plants were removed from the cabinets. All the leaves were detached from each plant, counted and the leaf area measured using a Leaf Area Measurement System (ICT Technologies, Narrabri, NSW). The leaves were then dried at 65 °C for 72 h before being weighed. The roots of each plant were washed and removed from the stem, then both the roots and stems were dried for 48 h at 80 °C before being weighed (MacKay and Neal, 1993). The dry mass of the plants was estimated as the differences between the mass of control plants assessed at the start of the experiment and that of the treatment plants assessed at the end of week 6.

2.2. Gas exchange measurements and leaf N

CO_2 assimilation rate (A_n) was measured on the youngest, attached, fully expanded leaf on the main stem of each plant ($n = 4$ for each combination of temperature and rootstock). This was done 7 and 3 days before harvest, using a portable open gas exchange system (LI 6400, LI Cor, Lincoln, USA): an average of the 7 and 3 days data was used for analysis. The leaf temperature inside the 600 mm^2 chamber was set at 26 °C. The vapour pressure deficit at the leaf surface was maintained at approximately 1.4 kPa. Measurements were made in air at a PPFD of 1200 μmol m^{-2} s^{-1} supplied by an in-built LED lamp (670 nm). To assess leaf *N* content at harvest, leaves from each plant were dried, ground and then analysed using complete combustion chromatography at the Waite Institute, University of Adelaide. Photosynthetic nitrogen use efficiency (net assimilation per mass leaf nitrogen on a per unit leaf area, A_n/N) was calculated from net assimilation, leaf area and leaf nitrogen data.

2.3. Infrared thermography

In the week prior to harvest, leaf temperatures of Golden Queen rootstocks held at constant 5°, 12°, or 19° RZTs were measured using an infrared camera (ThirmCAM™ PM 575, Flir Systems). The infrared thermographic images were taken within 15 s of each other in the late morning 3 days before harvest.

2.4. Data analysis

The plants were arranged in a split-plot design within trials replicated over time. The response variables were fitted with a linear mixed model (data = trial + treatment + trial: treatment + rootstock + treatment: rootstock + trial: treatment: rootstock + residual error) as reported in Malcolm et al. (2007) with variance parameters estimated using a residual maximum likelihood method (Patterson and Thompson, 1971) and pairwise treatment differences separated using the least significant difference (LSD) at 5% level. This analysis was performed using Genstat for Windows (VSN International Ltd., 2003). Regression analysis was performed using TABLECURVE 2D Version 5 (AISN Software).

3. Results and discussion

Rootstocks have been shown to influence the growth and vigour of *Prunus* species, and it has been documented that there are varietal differences among peach rootstocks in their effect on leaf area and leaf development (Yadava et al., 1980; Massai et al., 1993) particularly in the spring (Caruso et al., 1997; Malcolm et al., 1999). Leaf area and development are important components of growth, as they correlate positively with peach fruit quality (Weinberger, 1931). In stone fruit, apart from an initial paper by Malcolm et al. (2006), there have been few documented studies examining the relationship between RZT and leaf development, even though in tomatoes (Gosselin and