



Hydraulic and photosynthetic compensation versus fruit yield of red raspberry following partial leaf defoliation



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ABSTRACT

This study investigated if removal of floricanes leaves from the inner non-fruiting canopy portion would improve the photosynthesis of the remaining leaves only through raising their daily light sum, or if it would do so also through the ameliorated hydraulic parameters. From the beginning to the end of the fruiting season, the integrated daily light transmission decreased linearly from 36% to 23% vs. 18% respectively for the partially defoliated (42% floricanes leaf removal) vs. control treatments. This resulted in an estimated average daily leaf PPFD available across the mid-canopy that was 40% greater in the partially defoliated treatment. However, modeled net photosynthetic productivity of the partially defoliated floricanes canopy around mid-height was essentially equivalent to that of the control. Although, in the morning measurement period, significant up-regulation of $K_{\text{soil-leaf}}$, g_s and A_{sat} was observed in partially defoliated plants throughout the fruiting period, the overall fruit yield obtained was similar in both treatments. We demonstrated that red raspberry plants are capable of sustaining substantial up-regulation of their leaf specific hydraulic/photosynthetic capacity throughout the fruiting season in response to LAI reduction, thereby partially buffering against the ensuing reduction of current photosynthate supply.

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1. Introduction

Crop yields, whether dry matter or fruit, are usually found to be well correlated with canopy leaf area index (LAI) due to enhanced light interception (Monteith, 1977; Gallagher and Biscoe, 1978; Jackson, 1980; Bavec and Bavec, 2002). However, this positive relationship holds only up to an optimal LAI above which net productivity reaches a plateau or even declines due to high respiratory costs and to excessive shading of a large proportion of leaves and fruiting sites (Watson, 1958; Weber et al., 1966; Corley, 1973; Wünsche and Lakso, 2000). In conventional red raspberry (*Rubus idaeus* L.) soil cultivation where the available rooting volume is considerable and the hedgerow canopy height and width are controlled for ease of manipulation, the canopy LAI and fruit yield are optimized through increasing the number of canes per linear meter (Granger, 1972; Raymond-Bayne et al., 2012). The optimum cane density at which fruit yield is reported to reach its maximum varies among studies depending on the raspberry cultivar and cultural

conditions used, but optimal densities in excess of 20 canes per linear meter are not uncommon (Oliveira et al., 2004; Landry, 2011). Comparatively, in soilless raspberry production where operational and cost considerations lead to a significant reduction of the rooting volume, the potential for maximizing yield by increasing the linear density of canes in the row crop may be more limited than in conventional soil cultivation. A successful strategy that has been developed for increasing canopy LAI and crop yields particularly in soilless raspberry cultivation is the so-called long-cane production system whereby taller canopies holding long fruiting laterals are produced (Sønsteby et al., 2009).

The overall increase in crop yield achieved through canopy densification is usually concurrent with a reduction of fruit size and yield per unit fruiting lateral length (Wright and Waister, 1982; Lawson and Wiseman, 1983; Heuvel et al., 2000), a phenomenon usually associated with increased intra-canopy competition for limited resources. For example in dense biennial summer-fruiting raspberry canopies, the simultaneous existence of vegetative primocanes and fruiting floricanes on the same plant results in strong competition for light between cane types (Wright and Waister, 1982; Fernandez and Pritts, 1996). Based on the yield potential indicated by flower numbers, Wright and Waister (1984) concluded

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that heavy mutual leaf shading among canes was the main cause leading to a reduction of fruit yield per unit fruiting lateral. Aside from its well-known negative effect on gross photosynthesis, insufficient canopy light penetration may result in greater respiration losses from heavily shaded leaves, most especially during periods of high temperatures and vapour pressure deficit (VPD) (Hogg and Hurdle, 1997; Oren et al., 1999).

Another possible reason for the aforementioned reduction of fruiting branch vigor in dense raspberry plant canopies is hydraulic coordination. As reviewed in Meinzer (2002), a number of studies have shown that stomata adjust dynamically to changes in leaf area-specific plant hydraulic properties. For example, in sugarcane, when the leaf-specific hydraulic conductance of a plant (hydraulic conductance per unit leaf area) decreases as the plant builds up its LAI during growth, the stomatal conductance of the canopy leaves gradually adjusts negatively to achieve leaf water status homeostasis (Meinzer and Grantz, 1990; Meinzer et al., 1992). Conversely, when a plant leaf-specific hydraulic conductance is increased through partial defoliation, the stomatal conductance of the remaining leaves usually increases (Meinzer and Grantz, 1990; Reich et al., 1993; Pataki et al., 1998; Hart et al., 2000). Similar dynamic stomatal-hydraulic coordination responses have also been reported in cases where the overall plant transpiration was modulated through partial canopy shading (e.g. Whitehead et al., 1996; Pepin et al., 2002).

Efforts to understand yield responses to defoliation in perennial horticultural crops have focused primarily on characterizing the alteration of source-sink relationships and resulting photosynthate allocation patterns. In plants bearing fruits, partial defoliation effectively increases the fruit load per unit leaf area, thereby increasing the relative sink strength, a well-known correlate to positive photosynthetic compensation (Palmer et al., 1997; Iglesias et al., 2002; Syvertsen et al., 2003). Moreover, ^{14}C -tracer studies performed on partially defoliated vine crops (e.g. kiwifruit, grape) have shown that if the photosynthetic activity of the remaining leaves is not sufficient to support fruit growth, translocation of carbon from other parts of the plants may meet the photosynthetic supply deficit (Lai et al., 1989; Candolfi-Vasconcelos et al., 1994). Hence, partial reduction of the photosynthetically active leaf area may not necessarily affect fruit yield negatively (Scholefield et al., 1978; Millard et al., 2001; Yuan et al., 2005). In fact, in kiwifruit vine canopies, reduction of the canopy leaf area by eliminating emerging vigorous shoots at regular intervals along the center of the vine has been shown to improve overall fruit quality and yields (Cruz-Castillo et al., 2010).

In red raspberry, positive stomatal/photosynthetic compensatory responses have been observed following partial defoliation (Cameron and Hartley, 1989), but unfortunately these were evaluated for only two days after treatment. Although Privé et al. (1994) demonstrated substantial compensatory fruit yield responses in primocane-fruiting red raspberry plants devoid of up to two thirds of their leaf area, they did not evaluate the extent of the potential stomatal/photosynthetic up-regulation that may have contributed to the maintenance of fruit yields following such treatment. Nor did they evaluate the net plant biomass partitioning following cropping, which could have indicated a potential depletion of carbon stores in woody tissues.

The objectives of the present study were to evaluate 1) the extent of potential long-term hydraulic and stomatal/photosynthetic compensatory responses in a biennial summer-fruiting red raspberry canopy following partial defoliation vs. 2) the net plant biomass partitioning at the end of cropping. Specifically, we wished to determine if removal of floricanes leaves from the inner (central) non-fruiting canopy portion would improve the photosynthesis of the remaining leaves from the outer fruiting canopy portion only through raising their daily light sum, or if it would do so also through raising their photosynthetic capacity. We

also wanted to see if the aforementioned partial defoliation of the 1-year-old floricanes would significantly improve the daily light sum and growth of current-year vegetative primocanes trained to remain confined within the central canopy portion. In short, we wished to determine if the inner non-fruiting floricanes leaves thriving in the shade were beneficial at all to the overall carbon budget of the plant, and if these leaves were limiting the water supply to the more distal fruiting portions. We hypothesize that removing the floricanes leaves from the non-flowering center of the canopy would not significantly affect fruit yield and quality, or the carbon stores of the perennial woody tissues (roots and primocane stems).

2. Materials and methods

2.1. Plant material and cultivation

A recently introduced biennial, floricanes-fruiting red raspberry cultivar ('Jeanne d'Orléans' –Khanizadeh et al., 2010) was used for this study. The experiment was conducted in the summer of 2014 on a plot located in the open fields of a commercial farm (Les Fraises de l'Île d'Orléans Inc., Saint-Laurent d'Orléans, Qc, Canada, 71.0262°W, 46.8625°N). The soilless raspberry crop was then in its second (i.e. fruiting) year of production.

In the early spring of the previous year (i.e. the vegetative propagation year), chilled vegetatively propagated canes (Pépinière Lareault Inc., Lavaltrie, Qc, Canada) were planted in 4-l pots disposed in rows spaced at 180 cm from each other. Two primocanes were allowed to grow in each pot. A peat-mixed substrate (Agro mix G7, Fafard et Frères Ltée, Saint-Bonaventure, Qc, Canada) was used as growth medium. Plants were fertigated twice per day via an automatic irrigation system throughout the growing season with a 104–33–125 (ppm of N: P: K) complete fertiliser solution. In the spring of the second year, following the overwintering period under snow cover (approx. 4000 h chilling), canes were transferred into 10-l pots and pruned at 100 cm from the base. In each pot, two additional vegetative primocanes were allowed to develop alongside the two canes from the previous year (now 'floricanes' growing fruiting laterals) –any other vegetative shoots emerging from root suckers were removed weekly. Fruiting lateral branches emerging from the floricanes were attached to the trellis system such that the crop row width was constrained to 60 cm, leaving an inter-row space of 120 cm.

2.2. Experimental design and treatments

Plants were randomly assigned to four blocks disposed in the experimental plot following a completely random block design. Two treatments, control (C) vs. partial defoliation (PD), were included in each block, and twelve pots were used in each treatment (including three pots reserved for biomass sampling at the end of the fruiting season).

Partial defoliation of the floricanes was performed at the beginning of July, once the flowering period was nearly completed. All leaves from the inner, non-fruiting portion of the laterals were cut off from the plant. To determine the lateral branch profile of the floricanes at the time of defoliation as well as the amount of leaf area that was artificially removed, four additional pots of plants were destructively sampled and characterised in detail, including the height of every lateral branch on the main cane, the length of the fruiting vs. non-fruiting branch portions and their respective leaf area (measured with a LI-3100 planimeter, Li-Cor Inc., Lincoln, NE, USA) (see Fig. 1). From these measurements, we determined that on average 42% of the total one-sided floricanes leaf area was removed for the PD treatment.

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