Phenological and physiological responses to drought stress and subsequent rehydration cycles in two raspberry cultivars

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\textbf{A B S T R A C T}

Raspberry (\textit{Rubus idaeus} L.) is a deciduous plant with perennial roots, 75\% of which are concentrated in the upper level of the soil. Its shallow rooting system requires a regular water supply; a water deficit can affect fruitification as well as cane growth and yield for the following season. Despite the demonstrated drought stress impact on the raspberry, there is little information about the phenological and physiological responses to drought stress. The main goal of this study was to evaluate the effects of drought stress on the phenological phases, physiological parameters and yield of two raspberry cultivars: Heritage (remontant type) and Meeker (non-remontant type). All plants were grown in pots under greenhouse conditions, and the following watering treatments were applied: (T1) well-watered, 100\% irrigation and (T2) a controlled drought-stress cycle. The volumetric soil water content (θ), phenological phases, leaf net photosynthetic rate (A), transpiration rate (T), and stomatal conductance (gs) were registered periodically. The free proline and total soluble sugars were also determined. Based on the phenological study, Heritage under drought-stress (T2) showed earlier flowering and a shorter fruit production period in relation to well-watered plants (T1). In Meeker, T2 extended the cane and summer lateral elongation, showing earlier senescence. Leaf gas exchange decreased with drought stress, A declined after 28-day period under drought stress, from 9.2\,μmol CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1} to 3.0\,μmol CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1} in Heritage, and from 12.2\,μmol CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1} to 3.0\,μmol CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1} in Meeker. In both cultivars, the free proline and total soluble sugars increased with drought stress. The fruit production was also affected in the next season under T2 condition, decreasing in 34 and 38\% in relation to well-watered plants.

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1. Introduction

Raspberry (\textit{Rubus idaeus} L.) is a deciduous plant with perennial rhizomes. The plant’s shallow rooting system requires a regular and uniform water supply, particularly in the period from fruit set to harvest (\textit{Razeto}, 1993; \textit{Crandall}, 1995). In Mediterranean environments raspberry is grown under irrigated conditions, however water for irrigation is not always available at the time and amount needed by the crop. Furthermore, dry years are occurring more frequently during the last decade probably due to climate change, and the probability of water deficit for raspberry is increasing, particularly in Central Chile (\textit{CONAMA}, 2008).

\textit{R. idaeus} shows moderate tolerance to short drought stress periods; however, prolonged water deficits result in negative impacts on plant growth and fruit production. The phenological timing and yield for the following season are also affected (\textit{Crandall}, 1995; \textit{Percival et al.}, 1998; \textit{Privé and Janes}, 2003). During a water deficit, overall plant development is delayed, and leaf size is reduced; anatomical changes due to modifications in cell size, senescence and, ultimately, plant death are also observed in several species (\textit{Aion et al.}, 2004; \textit{Jaleel et al.}, 2008). The low water availability in the soil decreases photosynthesis and carbohydrate accumulation, limiting overall plant growth (\textit{Chaves}, 1991; \textit{Chaves et al.}, 2003; \textit{Chaves and Oliveira}, 2004; \textit{Flexas et al.}, 2004). In addition to affecting stomata closure, drought stress decreases gas exchange in plants by reducing transpiration and the photosynthetic rate (\textit{Chaves}, 1991; \textit{Ekayake}, 1994; \textit{Dalla Costa et al.}, 1997; \textit{Deblonde and Ledent}, 2001; \textit{Glass et al.}, 2003; \textit{Kiziloglu et al.}, 2006). It has been reported in Heritage that transpiration and photosynthesis are sensitive to water stress, decreasing gradually after two days under drought stress until rehydration (\textit{Percival et al.}, 1998). Other studies in \textit{Rubus} species have concluded that soil water depletion decreases

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leaf cell turgor, reducing stomatal conductance (Stoll et al., 2002; Jaleel et al., 2009). Water content in the leaves, stomatal conductance and transpiration under drought stress are highly correlated (Chaves et al., 2003; Flexas et al., 2004).

Synthesis of compatible solutes such as proline, soluble sugars, glycine betaine and others seems to have a central role in osmotic adjustments, preventing or reducing the loss of turgor. Proline has been associated with drought tolerance and other abiotic stresses in several plant species (McCue and Hanson, 1990; Andrade et al., 1995; Kavi Kishor et al., 1995; Wang et al., 2003; Chaves and Oliveira, 2004; Kavi Kishor et al., 2005; Chaman, 2007). In fact, studies on several fruit species have shown that the free proline concentration increases in leaves with water stress. This phenomenon has been demonstrated in citrus (Nolte et al., 1997), blackberry (Parra et al., 1999), tomato (Claussen, 2005) and olives (Ahmed et al., 2008). A recent study evaluating induced in vitro drought-stress effects on raspberries and blackberries reported a sustained increase in free proline content with progressive drought in the majority of evaluated clones (Orlikowska et al., 2009).

Raspberries are classified as remontant and non-remontant types, according to their production season. The remontant cultivars flower and bear fruit twice a year, at the beginning of spring (on floricanes from the previous growing season) and at the end of summer (on primocanes from the same year). Non-remontant cultivars bear fruit only once a year on floricanes, from the end of spring until the beginning of summer. In accordance with these productive characteristics, the phenological and physiological responses during drought stress can be expected to differ between the two types of cultivars. Only two studies have addressed these effects in raspberry: those by Percival et al. (1998) and Privé and James (2003). In this work, it was hypothesized that remontant and non-remontant raspberry cultivars have different phenological and physiological responses to drought stress.

The main goal of this study was to evaluate the effect of a controlled water deficit on the phenological phases, physiological parameters and yield of the Heritage and Meeker raspberry cultivars.

2. Materials and methods

2.1. Material vegetal and growth conditions

This study evaluated two raspberry cultivars: Heritage (remontant type) and Meeker (non-remontant type). The plant materials used during this experiment were two-year-old plants and were produced by a nurseryman certified by the Agricultural and Livestock Service (SAG). They were obtained from etiolated shoots. All plants during the growing season were grown in 25 L pots under greenhouse conditions (25 °C ± 3, 16/8 h day/night photoperiod, 400–480 μmol m⁻² s⁻¹ light intensity), spacing 1.5 m × 0.5 m. After summer, the greenhouse temperature acclimation system was turn-off to allow cold acclimation. Plants were grown in a mixture of peat Sunshine Mix #6 (Sun Gro Horticulture Inc., Bellevue, WA), compost and sand (3:3:1), supplemented with 3N, 3P and 1K every season. Plants were watered with well water using drip irrigation, one dropper of 4 L h⁻¹ per pot.

2.2. Watering treatments

The following watering treatments were applied to plants: (T1) well-watered, with 100% irrigation and (T2) a controlled drought stress cycle consisting of a 28-day period without watering, until the soil water decreased close to the permanent wilting point, a 7-day period of recovery (100% irrigation) and another 28-day period without watering. In the well-watered treatment (T1), the water supplied was equal to the transpiration losses, as determined by differences in pot-weight between successive waterings. The watering treatments were applied from early summer to early autumn, when raspberry plantations are naturally affected by drought stress. Visual phytosanitary inspections did not uncover pests, fungal or bacterial problems.

2.3. Soil water status

The soil water content was measured as the volumetric water content (θ), defined as the ratio of the volume of the water in the soil to the total volume of soil (m⁻³). θ was measured 15 cm below the soil surface by using ECH2O probes and Em50 data loggers (Decagon Devices, Inc., Pullman, WA). Data points were automatically recorded every 30 min. Two soil moisture sensors (ECH2O probes) per experimental unit were installed during all experiment.

2.4. Phenological phases in raspberry

The phenological stages (sprouting/bud development, lateral cane elongation, flowering, fruiting—ripening, plant senescence or beginning of dormancy) were evaluated using the protocol described by the Centre Technique Interprofessionnel des Fruits et Légumes – Le Francia CITIFL (Granier et al., 2006). The readings were taken every two days from winter (2009) to the autumn of the next season (2010), in all plants under all experimental conditions.

2.5. Leaf gas exchange parameters and fruit yield

The leaf gas exchange was evaluated according to Seppänen and Coleman (2003) and Schnittenhelm et al. (2004) by using a Li-6400XT Portable Photosynthesis System (LICOR Biosciences, Inc. Lincoln, Nebraska, USA) with an automatic leaf chamber (6 cm² leaf area, 25 °C constant air temperature, 600 ppm of external leaf CO₂ concentration (Ca) and a 1000 μmol saturation point m⁻² s⁻¹ PAR). We evaluated the photosynthetic rate (A, μmolCO₂ m⁻² s⁻¹), transpiration rate (T, mmolH₂O m⁻² s⁻¹), stomatal conductance (gs, mmol m⁻² s⁻¹) and the A/CI ratio (CO₂ assimilation rate/intercellular CO₂ concentration). gs was also followed with a porometer Decagon Device (Leaf Porometer model, USA). Leaf gas exchange measurements were taken weekly throughout the assay in completely expanded leaves located in the middle portion of the cane in each cultivar, watering treatment and replication. A total of three readings were taken per plant, daily at midday. The total fruit yield was determined during the second season of evaluation (2010–2011) considering the production of 5 plants for each cultivar, treatment and replication. Yield was express in g plant⁻¹.

2.6. Proline and sugar analysis

The total soluble sugars and free proline contents were determined using fully expanded leaves for the two watering treatments (T1 and T2). Samples were taken weekly during the first drought-stress cycle from completely expanded leaves (young and mature) located in the middle portion of the canes for each cultivar, watering treatment and replication. Young leaves and mature leaves were taken from the apical and basal part of the shoot, respectively. A total of three samples were taken for each plant. Leaf tissue was collected, pulverized in liquid N₂ and stored at −80 °C. Proline analyses were conducted as in Gilmour et al. (2000), using 20 and 30 mg lyophilized tissue per sample for the T1 and T2 conditions, respectively. Total soluble sugars analysis was performed using the phenol-sulfuric acid method as in Pino et al. (2008). The absorbance was determined at 515 nm for proline and at 492 nm for total.
soluble sugars using a UNICO SpectroQuest-2800 spectrophotometer (USA).

2.7. Experimental design and statistical analysis

A randomized complete block experimental design with three replications was used. Each block had five plants per cultivar and treatment. The statistical differences among treatment and cultivars was determined through variance analysis (ANOVA), and the statistical software SAS Program Version 9.1.3 (2003) (SAS Institute Inc., Cary, NC, USA), the Duncan test ($p < 0.05$) was used for separation of the means.

3. Results

3.1. Soil water content

In well-watered plants from the T1 group, the soil water content ($\theta$) was close to 50% during the entire period of the experimental period in both raspberry cultivars. In plants from T2 conditions, the $\theta$ decreased to 16% in Heritage plants and to 35% in Meeker plants during the first drought-stress cycle. After 7 days under recovery conditions (100% irrigation), the soil water content ($\theta$) returned to the initial level (50%) in both raspberry cultivars. After the second drought-stress cycle, the $\theta$ dropped to 28% and 34% in Heritage and Meeker plants, respectively (Fig. 1).

3.2. Phenological responses

Under drought-stress cycle conditions (T2), the Heritage plants showed earlier flowering and earlier fruiting in December, than well-watered plants (T1), but not in April were fruiting was few days later (Fig. 2). In December flowering and fruiting occurred on stalks from the previous growing season, and in April from stalks from the same growing season. However, the fruits did not reach maturity. After the second drought-stress cycle, the majority of plants showed leaf wilting and canes were brownish; after the subsequent rehydration (100% irrigation), however, plants were able to gradually activate buds.

Well-watered Meeker plants (T1) showed constant primocanes development and elongation of lateral stems until the fall, when low temperatures inhibited plant growth (Fig. 2). During the first drought-stress cycle (T2), Meeker did not show leaf wilting or any drought stress signs until after 2 weeks; the plants started to show evident signs of dehydration, such as basal leaf wilting and altered leaf growth patterns. After irrigation recovering, and in the beginning of the second drought-stress cycle, the plants showed primocane elongation, and the new leaves in the floricanes wilted.

3.3. Physiological responses

The physiological parameters showed significant differences between the watering treatments ($P \leq 0.001$) and between the raspberry cultivars X watering treatments interaction ($P \leq 0.021$). The stomatal conductance (gs) decreased over the course of the first drought-stress cycle, dropping to 21% (Heritage) and 39% (Meeker) compared with well-watered plants. However, at the end of the second drought-stress cycle, the gs value was higher in Heritage than in Meeker plants (Fig. 3a and e). In well-watered plants (T1), the transpiration rates ($T$) decreased gradually throughout the assay, without a significant difference between cultivars (Fig. 3b and f). In contrast, in drought-stressed plants (T2), the $T$ dropped more rapidly in Heritage than Meeker plants after two weeks under drought stress. However, the $T$ readings during recovery (100% irrigation) and the subsequent second drought-stress cycle in both cultivars were similar.

In T1 plants, the photosynthesis rate ($A$) decreased progressively during the experimental period, from 8.8 to 4.7 $\mu$molCO$_2$ m$^{-2}$ s$^{-1}$.
in Heritage and from 10.7 to 5.2 μmol CO₂ m⁻² s⁻¹ in Meeker (Fig. 3c and g). In T2 plants, under the controlled drought-stress cycle, the values of A decreased in Heritage plants to 3.0 μmol CO₂ m⁻² s⁻¹ (41.2% of that of the well-watered plants) during the first drought-stress cycle. A similar response was observed in Meeker in T2: values of A decreased from 12.2 μmol CO₂ m⁻² s⁻¹ to 3.0 μmol CO₂ m⁻² s⁻¹ in the same period. During the subsequent recovery (100% irrigation), A increased from 3.0 to 7.3 μmol CO₂ m⁻² s⁻¹ in Heritage and from 3.0 to 3.6 μmol CO₂ m⁻² s⁻¹ in Meeker but showed a similar response after the second drought-stress cycle. However, in well-watered plants, the leaf photosynthesis rate was consistently higher in Meeker than in Heritage. With regard to the A/Ci ratio during the first drought-stress cycle, the Heritage A/Ci started to drop after 21 days without watering, as compared to well-watered plants, while Meeker did not show significant differences compared to well-watered plants. After the subsequent recovery (100% of irrigation) and during the second drought-stress cycle, only the Meeker showed significant differences in the A/Ci between well-watered and drought-stressed plants.

The analysis of the relationship between gs and the leaf gas exchange parameters (Fig. 4), such as photosynthesis rate, transpiration rate, and the A/Ci ratio, showed a high degree of association (R² ≥ 0.57) in both raspberry cultivars (Heritage and Meeker). The highest determination coefficient (R² ≥ 0.88) was observed between gs and A for Heritage and Meeker, suggesting that gs and the photosynthesis rate under drought stress are highly correlated in both cultivars (Fig. 4a). The regression analyses indicate that Meeker exhibited higher response (slope) in A and A/Ci to gs, compared to Heritage.

### 3.4. Proline and total soluble sugars content

In Heritage, drought-stressed plants (T2) showed significant differences in the concentration of free proline for young leaves after 7 days under water deficit; however, in mature leaves, the proline
Table 1

<table>
<thead>
<tr>
<th>Raspberry cultivars</th>
<th>Well-watered plants (T1)</th>
<th>Controlled drought stress cycle (T2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heritage</td>
<td>1.881a</td>
<td>1.161b</td>
</tr>
<tr>
<td>Meeker</td>
<td>1.810a</td>
<td>1.185b</td>
</tr>
<tr>
<td>CV (%)</td>
<td>9.2</td>
<td></td>
</tr>
</tbody>
</table>

CV: coefficient of variation. Different letters (located above the bars), indicate significant differences (P < 0.05), according to Duncan’s test.

3.5. Drought stress affects the production in the next season

In the season following experimentation (2010–2011), the yield was decreased by almost half in drought-stressed plants (Table 1). Similar results were observed in Meeker, suggesting that severe drought stress may affect fruit production in the next season.

4. Discussion

Under drought stress, the soil water content (θ) showed a different pattern of water depletion between the two cultivars. This difference could be explained by phenological stages and the raspberry type. While θ in Meeker (non-remontant type) dropped gradually, the θ dropped more rapidly in Heritage plants. This discrepancy could be explained because Meeker plants were undergoing shoot elongation during the watering treatments and, thus, require less water. In contrast, Heritage was in the flowering or fruiting stage during the experiment, requiring more water in these phenological periods. The effects of water stress on fruit quality are complex and unpredictable, with the most common fruit response to water stress being fruit growth reduction (Ebel et al., 1993). Heritage showed accelerated flowering, fruiting, and ripening stages in conjunction with higher watering demand. However, the fruit did not reach complete coloring and ripening; harvested fruits showed malformation and lack of quality. It has been reported that drought stress during the early cell-division period can reduce fruit set and fruit size, affecting the remainder of the season even if water is abundant later (Mpelasoka et al., 2000). In raspberry plantation and primocane fruiting, the water application rates may compensate for 75% of ETC (60% of the evaporation from a Class A pan), avoiding a negative impact on the yield and fruit quality (Koumanov et al., 2006). The fruit size reduction due to drought stress has been reported in several species, such as apple (Mpelasoka et al., 2000) and kiwifruit (Miller et al., 1998), among others.

A study in Heritage cultivar about how to predict drought stress showed that the soil water content (monitored by gravimetric or volumetric methods) was closely associated to early physiological signs of drought stress. The investigators concluded that the best way to detect early drought stress signs in this species is by monitoring leaf water potential, leaf stomata conductance and leaf photosynthesis (Privé and Janes, 2003). Several studies have proposed that stomata closure is the main determining factor in photosynthesis reduction under moderate stress conditions (Chaves, 1991; Cornic and Massicci, 1996; Medrano et al., 2002; Ort et al., 1994; Sharkey, 1990). In Titan and Heritage raspberry cultivars, stomata conductance and the photosynthesis rate dropped as soil water content decreased (Goulart, 1989). In addition, it has been reported that not only was photosynthesis sensitive to water stress in Heritage plants, but transpiration was also affected, decreasing gradually of 2 days under drought stress until rehydration (Percival et al., 1998). Among drought tolerance mechanisms, stomata closure, photosynthetic and water potential adjustments

was significantly higher than in well-watered plants only after 28 days under drought stress (Fig. 5a and b). In Meeker, significant differences in proline were only observed in drought-stressed young leaves at 7 days without irrigation; no further differences were observed between mature leaves in relation to well-watered plants (Fig. 5c and d). For total soluble sugars (TSS), drought-stressed Heritage plants—both young and mature leaves—showed significant differences after 28 days without irrigation (T2) in relation to well-watered plants. In Meeker plants, young leaves show significant differences in TSS in relation to well-watered plants after 28 days without irrigation; however, the TSS were significantly higher in mature leaves when Meeker plants were drought-stressed for one week (Fig. 6).
Fig. 5. Effects of drought stress on free proline in two raspberry cultivars (Heritage and Meeker). Samples were collected from fully expanded leaves (mature and young) after 0, 7, 14 and 28 days during the first-drought stress cycle in T2 and in well-watered plants (T1). During watering experiments, plants were grown in pots under greenhouse (25°C ± 3, 16/8 h day/night photoperiod). The values are the means ± SD. Different letters show significant differences between treatments (P<0.05) according to Duncan's test.

Fig. 6. Effects of drought stress on the total soluble sugars of two raspberry cultivars (Heritage and Meeker). Samples were collected from fully expanded leaves (mature and young) after 0, 7, 14 and 28 days during the first-drought stress cycle in T2 and in well-watered plants in T1. During watering experiments, plants were grown in pots under greenhouse (25°C ± 3, 16/8 h day/night photoperiod). The values are the means ± SD. Different letters show significant differences between treatments (P<0.05) according to Duncan’s test.
play a critical role (Ludlow, 1980). In some plant species, better plant growth has been observed by lowering the water potential in response to decreasing soil water (Wyn Jones and Gorham, 1983).

In conjunction with stomata conductance reduction, drought stress in fruit species has been associated with transitory soluble carbohydrate accumulation in the leaves and fruit (Miller et al., 1998). A study showed that blackberry plants had decreased stomatal conductance and transpiration after 24 days under dry-out conditions (drought stress), while the leaf turgor did not show variation. This result suggests the occurrence of osmotic adjustment activity. In fact, the researchers reported that blackberry plants without irrigation presented double proline accumulation compared with plants under irrigation (Parra et al., 1999). Recent studies suggest that proline acts as an osmolyte, stabilizing proteins and membranes. In addition, proline has been documented as a source of carbon and energy during cellular rehydration (Kavi Kishor et al., 2005). Another study in raspberry and blackberry under simulated in vitro drought stress (PEG6000) showed that drought-tolerant genotypes presented a higher growth rate and proline accumulation than susceptible genotypes (Orlikowska et al., 2009). Similarly, we observed higher proline and total soluble sugar accumulation with drought stress in both raspberry cultivars, suggesting some degree of osmotic adjustment activity.

The effect of drought stress on fruit quality is complex. The most common response to drought stress is fruit growth reduction (Ebel et al., 1993) because one of the first responses to a water deficit is reduced plant growth due to cell expansion inhibition (Acevedo et al., 1971; Hsiao et al., 1976). Water limitation decreases cell turgor pressure, the force required for cell expansion. This loss of pressure reduces leaf expansion, stem and root growth, also causing leaf senescence (Acevedo et al., 1971; Munne-Bosch and Alegre, 2004). In Heritage cultivar, a study comparing different irrigation methods with non-irrigation showed that drip irrigation increased yield and fruit number up to 106.1% in relation to non-irrigated plants (Parra and Nissen, 1998). Raspberry fruit size is also influenced by irrigation level: plants irrigated at 100% and 150% produced larger fruits than those irrigated at 50% (Bryla et al., 2008).

In the present study, we determined that severe drought stress in conjunction with fruit deformation and fruit size reduction affected the yield in the next season. In both cultivars, the yield decreased 2-fold in relation to well-watered plants.

Global climate projections suggest that the frequency of drought events in many regions will increase, affecting drought-sensitive plant species. In California area for example, is expected that water restriction will limit perennial species production in the arid and semi-arid production regions, unless enough water will be stored for irrigation (Walthall et al., 2012). By the end of the century, short-term droughts are projected to occur as frequently as once per year in the Northeast of the USA, while occasional long-term droughts (>6 month) are projected for Western, where perennial horticulture crops are a major industry (Walthall et al., 2012). In addition, the projected summer heat stress will increase the crop water demands, being particularly detrimental to many cool temperature-adapted species that currently dominate the Northeast agriculture (Wolfe et al., 2005, 2008; Walthall et al., 2012).

In United Kingdom, the climate change effects can have a negative impact on berries, affecting the fruit quality and productivity. Among adaptation strategies to deal with water shortage are; the irrigation scheduling, deficit irrigation techniques, and other techniques to reduce water inputs maintaining yields and high-quality (Else and Atkinson, 2010). In the adaptation strategies is important to increase the irrigation efficiency by implementing different irrigation methods, like drip irrigation or the partial root-zone drying technique. In other species, partial “root-zone drying” can allow a 29–50% of water saving with a similar yield and a concomitant water use efficiency increase (Monneveuxa et al., 2013). Watering restriction during full flowering and fruit raspberry production is particularly harmful. In addition to improve irrigation efficiency, the development of drought tolerant cultivars is the long-term solution to cope drought stress.

5. Conclusions

In conclusion, under controlled drought-stress cycles, Heritage plants showed earlier flowering and a shorter fruiting stage in relation to well-watered plants. In the Meeker plants, drought stress extended cane and summer lateral elongation, with the plants showing earlier leaf senescence. In both raspberry cultivars, the physiological parameters and osmoprotector accumulation showed significant differences. Leaf gas exchange decreased with drought stress, while proline and total soluble sugar increased, particularly after four weeks of water deficit. Yield was also affected, with drought-stressed plants producing significantly less compared with well-watered plants.

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