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Physiological and growth responses to water deficits in cultivated strawberry (*Fragaria* × *ananassa*) and in one of its progenitors, *Fragaria chiloensis*

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Cultivation of strawberry (*Fragaria* × *ananassa*) requires irrigation. Improving crop water use efficiency (WUE) is important for future production. *Fragaria chiloensis*, a progenitor of cultivated strawberry, grows in sandy soils, and may prove useful in breeding for improved WUE. Little, however, is known about variation in drought tolerance within this species. This research explores drought tolerance in a range of *F. chiloensis* and *F.* × *ananassa* genotypes. Four cultivars of *F.* × *ananassa* and four accessions of *F. chiloensis* were compared when well watered, and when subjected to a water deficit (65% of evapotranspiration). New leaf production, stomatal conductance, and photosynthetic rate were significantly reduced under water deficit, and also significantly differed between genotypes. A significant interaction of genotype and irrigation was found for transpiration rate, leaf area and dry mass, production of runners, predawn water potential, a measure of transpiration efficiency (shoot biomass produced per litre water transpired), and carbon isotope composition, indicating that some genotypes were more severely affected by water deficit than others. The South American *F. chiloensis* accession 'Manzanar Alto' had a similar rate of transpiration to the commercial cultivars, but the remaining (North American) *F. chiloensis* accessions used far less water than the *F.* × *ananassa*. Well-watered *F. chiloensis* plants used less water than water-limited plants of the *F.* × *ananassa* cultivar 'Florence'. Transpiration efficiency of the *F. chiloensis* accession 'BSP14' was improved by water deficit: this was the only genotype not to show a reduction in leaf area and dry mass under water deficit. Greater drought resistance in three *F. chiloensis* accessions compared to *F.* × *ananassa* results from a conservative vegetative growth strategy, reducing loss of water.

1. Introduction

Worldwide, crop production is limited by drought more than by any other environmental stress (Cattivelli et al., 2008). Mean global temperatures are expected to rise over the next few decades, leading to increased evaporation rates (Houghton et al., 2001; European Environment Agency, 2004), which will result in increased crop demand for water. For long-term agricultural sustainability, crops with greater water use efficiency (WUE) are required (Cattivelli et al., 2008).

The commercial strawberry *Fragaria* × *ananassa* Duch. is a hybrid between *Fragaria chiloensis* (L.) Duch. and *Fragaria virginiana* (L.) Duch. The shallow root system, large leaf area, and high water content of fruits of *F.* × *ananassa* means that it uses large quantities of water (Klamkowski and Treder, 2006). Commercially, strawberry plants are usually grown on raised beds covered with impermeable polythene mulch and rely entirely on water provided by trickle irrigation beneath the polythene. A rapid decline in leaf water potential (Ψ_l) was found when watering was withheld from pot-grown strawberry (Blanke and Cooke, 2006), and, in field studies, yield was reduced as a result of soil water deficit (Savé et al., 1993; Yuan et al., 2004; Liu et al., 2007; Li et al., 2010). Klamkowski and Treder (2008) found differences between three strawberry cultivars in yield and root development during drought stress. More recently, Grant et al. (2010) have shown substantial variation amongst ten cultivars in physiology and morphology both when well watered and when subjected to deficit irrigation. In that study, responses to water deficits were not uniform across cultivars, with a significant interaction of cultivar and irrigation for stomatal conductance (g_s), midday osmotic potential at full turgor (ψ_s^{100}), marketable yield, and berry mass. On the other hand, variation between cultivars in plant canopy structure and growth and transpiration efficiency was

Abbreviations: *A*, assimilation rate; CWSI, crop water stress index; °C h, degree hour; $\delta^{13}C$, carbon isotope composition; *E*, transpiration rate; ET_p, evapotranspiration; g_s, stomatal conductance; I_G, index of stomatal conductance derived from leaf and reference temperatures; Ψ_l, leaf water potential; ψ_s^{100}, osmotic potential at full turgor; T_{dry}, dry reference temperature; TE, transpiration efficiency; T_{leaf}, leaf temperature; T_{wet}, wet reference temperature; WL, water-limited; WW, well-watered; WUE, water use efficiency; WUE_i, instantaneous water use efficiency.

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not strongly influenced by irrigation. Screening the cultivars under both well-watered and water-limited conditions for variation in g_s and instantaneous water use efficiency (WUE_i), using thermal imaging and carbon isotope composition ($\delta^{13}C$) respectively, indicated substantial intrinsic variation between the cultivars. In general, however, all cultivars responded to limited water availability in a similar manner, reducing their g_s, which resulted in increased WUE_i (Grant et al., 2012). This suggests that a substantial improvement in WUE is unlikely to be achieved using existing *F.* × *ananassa* genetic material. Thus WUE of related species needs to be explored, with a view towards introgression of desirable traits into cultivars of *F.* × *ananassa*.

The progenitors of the commercial strawberry have been reported to show clear differences in their response to water deficits (Zhang and Archbold, 1993a,b). *F. chiloensis* is commonly known as the beach strawberry and often grows in arid coastal environments, although natural populations are also found in woodland environments in North America and at high elevations in Chile (Hancock, 1999). In North America it is found in a narrow band along the Pacific Ocean (Serce et al., 2002). *F. chiloensis* is considered more drought resistant than either *F. viriginiana* or *F.* × *ananassa* (Zhang and Archbold, 1993b). This relates to the species having thick leaves and cuticles, the capacity to adjust osmotically (Zhang and Archbold, 1993b), and relatively sunken stomata, reduced stomatal area per leaf, and greater root growth compared to other *Fragaria* species (Darrow and Dewey, 1934; Hanninen et al., 1999). Little attention has been paid, however, to variation in drought resistance and water use efficiency between *F. chiloensis* accessions, with the exception of a study of clones from California and Oregon (VanDerZanden and Cameron, 1996), in which predawn Ψ_l and biomass production after two cycles of withholding water differed between clones. Comparing two *F. chiloensis* genotypes in the length of time after withholding water that wilting occurred, Archbold and Zhang (1990) suggested that 'CA1466' was less resistant than 'BSP14'. Considerable variation between *F. chiloensis* genotypes exists under optimal conditions in traits such as fruit size, colour, and soluble solids concentration, peduncle length, bloom date, numbers of crowns, and seed set (Hancock et al., 2003), so it may be expected that variation would also exist in responses to water deficit.

The objectives of this study were to characterise the impact of water deficit on the physiology and vegetative growth of diverse accessions of *F. chiloensis*, and to compare the responses of the *F. chiloensis* accessions with that of commercial strawberry cultivars, in order to determine whether any *F. chiloensis* accessions possess WUE-related traits that would be considered desirable in commercial strawberry.

2. Materials and methods

2.1. Plant material

Based on previous work (Grant et al., 2010, 2012), contrasting cultivars of *F.* × *ananassa*, in terms of characteristics that might be beneficial with respect to water use efficiency or drought tolerance, were selected. Independent of irrigation treatment, transpiration efficiency (biomass per litre of water consumed) was found to be low in 'Elvira' but high in 'Totem', and leaf $\delta^{13}C$ also indicated low WUE_i in 'Elvira' (as well as in 'Florence') and high WUE_i in 'Totem'. Thermal imaging indicated low g_s in 'Elsanta' and 'Totem', but high g_s in 'Elvira' and 'Florence', which might suggest greater water requirements in the latter two cultivars. Over a season, 'Totem' showed low transpiration rates, which would indicate relatively low irrigation requirements. 'Elsanta' demonstrated high WUE in terms of marketable yield per unit of water consumed. 'Elvira' and 'Florence' were therefore selected as relatively inefficient in terms of water use or liable to perform poorly under drought, whilst 'Totem' and 'Elsanta' were selected as relatively water use efficient or drought-tolerant.

Since little is known about variation between accessions of *F. chiloensis* in terms of water use efficiency and/or drought tolerance, a genetically diverse range of accessions was chosen. This included three accessions, 'TR4', 'BSP14' and 'ZB4', from natural populations in different locations in Oregon, USA. All three have morphology typical of the species with small, thick, glossy leaves. 'BSP14' was included in this selection on account of existing information regarding its drought tolerance (e.g. Archbold and Zhang, 1990). A cultivated land race from Chile, 'Manzanar Alto', was also selected. This accession differs morphologically from the other three, having larger, less glossy leaves. The cultivars and accessions were propagated by pinning down runners from mother plants. They were grown in a substrate composed of 90% sphagnum peat (60/40 blend), 10% sterilised loam and 2.5 kg m^{-3} controlled release fertiliser (Osmocote Plus [15 + 9 + 11 + 2MgO + trace elements]), in black polyethylene 1 L containers. After three weeks they were transferred to black polyethylene 3 L containers. Plants were allowed to grow for a further month prior to starting the experiment. Both propagation and the experiment took place in a polythene tunnel ('polytunnel') with no supplementary light or heating.

2.2. Experimental design

Initially, two plants per genotype were destructively harvested so as to calculate increases in biomass at the end of the experiment. The remaining plants were placed in a randomised block design on benches under two irrigation regimes – well-watered (WW) or water-limited (WL) – with six replicates of each cultivar in either treatment. The experiment ran from 15 May to 15 August 2008. *F. chiloensis* is dioecious and 'TR4', 'BSP14' and 'ZB4' are all male type. Therefore to avoid confounding differences in water use characteristics with the presence or absence of fruit, flowers were removed from all plants as they were produced.

A separate irrigation line consisting of 13 mm wide LDPE pipe (City Irrigation Ltd., Bromley, UK) was used for each genotype. Two 2 L h^{-1} Netafim drippers (City Irrigation Ltd.) were used to replace 130% of the water lost via evapotranspiration (ET_p) for each plant receiving the WW treatment (drainage from the base of the pots ensured water-logging did not occur). A single dripper on the same line was used to replace 65% of ET_p for each plant in the WL treatment. Stakes were attached to the drippers via 4 mm wide flexible PVC microtube (City Irrigation Ltd.) and placed in the substrate in the pots.

ET_p of each plant was determined on a weekly basis by weighing pots after irrigation (once any excess water had drained through the pot) and the following day before the next irrigation event. An evaporimeter (Evaposensor, Skye Instruments Ltd., Powys, UK) was read daily to determine the accumulated degree hours (°C h) between weighing the pots. One degree hour is a difference in temperature of 1 °C between dry and wet artificial leaves on the Evaposensor; the accumulated °C h is a measure of evaporative demand. Evapotranspiration per °C h could therefore be calculated for each plant. For the well-watered plants, the mean evapotranspiration per °C h was calculated for each genotype. The accumulated °C h over 24 h periods were read daily, and multiplied by the mean evapotranspiration per °C h for each genotype to determine the irrigation requirement of that selection. This was then used to set the length of irrigation run for each genotype. Irrigation was adjusted daily.