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Improving agronomic water use efficiency in tomato by rootstock-mediated hormonal regulation of leaf biomass

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ABSTRACT

Water availability is the most important factor limiting food production, thus developing new scientific strategies to allow crops to more efficiently use water could be crucial in a world with a growing population. Tomato is a highly water consuming crop and improving its water use efficiency (WUE) implies positive economic and environmental effects. This work aimed to study and exploit root-derived hormonal traits to improve WUE in tomato by grafting on selected rootstocks. Firstly, root-related hormonal parameters associated to WUE were identified in a population of recombinant inbred lines (RILs) derived from the wild tomato species *Solanum pimpinellifolium*. A principal component analysis (PCA) revealed that some hormonal traits were associated with productivity (plant biomass and photosynthesis) and WUE in the RIL population. Leaf ABA concentration was associated to the first component (PC1) of the PCA, which explained a 60% of the variance in WUE, while the ethylene precursor ACC and the ratio ACC/ABA were also associated to PC1 but in the opposite direction. Secondly, we selected RILs according to their extreme biomass (high, B, low, b) and water use (high, W, low, w), and studied the differential effect of shoot and root on WUE by reciprocal grafting. In absence of any imposed stress, there were no rootstock effects on vegetative shoot growth and water relations. Finally, we exploited the previously identified root-related hormonal traits by grafting a commercial tomato variety onto the selected RILs to improve WUE. Interestingly, rootstocks that induced low biomass and water use, 'bw', improved fruit yield and WUE (defined as fruit yield/water use) by up to 40% compared to self-grafted plants. Although other hormonal factors appear implicated in this response, xylem ACC concentration seems an important root-derived trait that inhibits leaf growth but does not limit fruit yield. Thus tomato WUE can be improved exploiting rootstock-derived hormonal signals which control leaf growth.

1. Introduction

The last World Water Development Report [1] observes how the various global crises reported recently–in climate change, energy, food security, economic recession and financial turbulence–are related to each other and have impacts on water. It is expected that 60% more food will be needed between now and 2050 to satisfy the demand of an eventual population of more than 9 billion people. Although the agricultural sector is sometimes viewed as a 'residual' user of water, after domestic and industrial sectors, it accounts for 70% of global freshwater withdrawals, and more than 90% of consumptive use. It is also the sector with the largest scope or potential for adjustment. The net result is that agricultural water use is increasing the severity of water shortage in some areas, and causing water scarcity even in areas that are relatively well endowed with water resources [2]. Only if we act to improve water use in agriculture will we meet the acute freshwater challenges facing humankind over the coming 50 years [3].

Water availability is therefore a major constraint of crop yield [4] and is the single most important factor limiting food production, with significant yield losses reported under water deficit [5–7]. This highlights the urgency in developing new scientific strategies in order to identify important traits associated to water use and biomass production to achieve a more efficient use of water in crop plants. Water use efficiency (WUE) is defined, from a physiological point of view, as the ratio between net photosynthesis and transpiration rate (intrinsic WUE), and, from an agronomical point of view,

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Table 1
Linear correlation coefficients between growth-related, water-related, gas exchange and hormonal parameters of a subset of 34 RILs derived from a cross between *Solanum lycopersicum* and *S. pimpinellifolium* growing hydroponically for 30 days.

	SDW	LA	W	WUEveg	WUEi	ACC	ABA	IAA
SDW		0.91**	0.87**	0.60**	0.28**	−0.21**	0.37**	0.39**
LA			0.82**	0.51**	0.34**	−0.15*	0.26**	0.39**
W				0.16	0.12	−0.15*	0.28**	0.42**
WUEveg					0.38**	−0.22**	0.33**	0.11
WUEi						−0.33**	0.43**	0.04
A	0.38**	0.31**	0.18**	0.54**	0.52**	−0.26**	0.45**	−0.02
g_s	0.18**	0.05	0.17*	0.12	−0.53**	0.11	−0.08	0.12
F_v/F_m	0.20**	0.34**	0.20**	0.10	0.34**	−0.10	0.32**	0.26**

	Z	ZR	CK	SA	JA	ACC/ABA	CK/ACC	IAA/CK
SDW	−0.14*	0.40**	0.01	0.11	0.04	−0.21**	0.05	−0.16*
LA	−0.03	0.44**	−0.11	0.03	0.01	−0.15*	0.14	−0.22**
W	−0.01	0.36**	0.02	0.16*	0.10	−0.17*	0.11	−0.18**
WUEveg	−0.28**	0.22**	−0.27**	−0.04	−0.05	−0.19**	−0.08	−0.04
WUEi	−0.09	0.48**	−0.04	0.12	−0.10	−0.28**	0.19**	−0.25**
A	−0.24**	0.19**	−0.22**	0.08	−0.01	−0.21**	−0.03	−0.06
g_s	−0.17*	−0.24**	−0.19**	−0.07	0.03	0.13	−0.21**	0.20**
F_v/F_m	0.08	0.40**	0.12	0.10	0.01	−0.19**	0.20**	−0.04

LA: leaf area; SDW: shoot dry weight; W: water consumption; WUEveg: vegetative water use efficiency; WUEi: intrinsic water use efficiency; A: photosynthetic rate; g_s: stomatal conductance; F_v/F_m: chlorophyll fluorescence. *$P \leq 0.05$, **$P \leq 0.01$, n = 200.

as the amount of (harvestable) biomass produced per unit volume of water used [8–11]

Tomato is an economically important crop that uses a lot of water. Although the greenhouse tomato crop reduces water consumption by 70% compared to open-field crop, water losses by transpiration are very high in relation to the amount of biomass produced. A tomato plant produces up to 25 g of fruit per liter of water used [10,12]. Any improvement in tomato WUE, considered in terms of harvestable biomass per unit of water used [13,14], would imply significant socioeconomic and environmental benefits (e.g. increasing WUE by 10% within the Mediterranean greenhouse tomato crop would save 1.1 hm^3 of water, the equivalent annual water consumption for a population of 20,000 inhabitants) [15].

Despite this incentive, few studies have aimed to improve WUE in tomato. Some of them have been focused on the control of atmospheric water deficit to reduce transpiration rate [16,17]. However, the genetic variability of wild-relative tomato species to improve WUE still remains unexploited [18], maybe due to the complexity of this character which hinders the selection of lines for commercial purposes. It is known that wild tomato species such as *Solanum pennellii*, *S. cheesmanii* or *S. pimpinellifolium*, growing in extreme conditions of water availability in the soil and moisture in the atmosphere can be an important source to introduce genetic variability of the characters involved in plant water homeostasis and could be exploited to improve WUE in tomato crops [18,19]. Consequently, it is very important to continue exploring the physiological mechanisms (both at root and shoot levels) involved in regulating WUE. Moreover, grafting may provide a more direct and immediate alternative than conventional plant breeding to improve WUE of modern commercial tomato varieties. In woody plants, such as grapevine, it has been already demonstrated that scion transpiration rate and its acclimation to water deficit are controlled genetically by the rootstock, through different genetic architectures [20].

Grafting provides opportunities to exploit natural genetic variability that exists in wild species for interesting root-specific traits by influencing a commercially desirable shoot phenotype [21]. Indeed, the rootstock can affect scion performance by modifying root-to-shoot hormonal relationships. During the last twenty years, several studies have demonstrated the importance of root-to-shoot communication in the control of water relations and the tolerance to abiotic stresses [22], particularly to drought and salinity, where phytohormones seem to play a critical role [23–28].

One of the most direct examples of perceived root-to-shoot communication is related to ABA-mediated stomatal closure limiting water loss [22,23,29]. The reduction of stomatal conductance by ABA seems to be greater than its negative effect on photosynthesis, leading to an increase in WUE [30]. This has been the basis for the successful use in some crops of the irrigation system known as 'partial root-zone drying' [31–33]. ABA can thus affect growth by

Table 2
Linear correlation coefficients between shoot FW, fruit yield, water consumption, water use efficiency and hormone concentrations of the RILs 175 and 38 non-grafted and reciprocally grafted growing in hydroponics for 7 weeks.

	SFW	FY	W	WUEveg	WUEyld	ACC	ABA	IAA
SFW		0.21	0.82**	0.62**	−0.57*	−0.59*	0.53*	0.42*
FY			0.40*	−0.21	0.53*	0.03	0.45*	0.62**
W				0.07	−0.55*	−0.30	0.59	0.47*
WUEveg					−0.27	−0.70**	0.21	0.18
WUEyld						0.36*	−0.28	−0.79**

	Z	ZR	CK	SA	JA	ACC/ABA	CK/ACC	IAA/CK
SFW	0.63**	0.44*	0.62*	−0.22	0.02	−0.59*	0.72*	−0.64**
FY	−0.02	−0.12	−0.02	0.39*	0.33	−0.16	0.06	−0.18
W	0.51*	0.50*	0.52*	−0.30	0.20	−0.35*	0.66**	−0.33*
WUEveg	0.50*	0.17	0.48*	−0.04	−0.22	−0.64**	0.48*	−0.76**
WUEyld	−0.65**	−0.71**	−0.65**	−0.82**	0.01	0.25	−0.72**	−0.21

SFW: shoot fresh weight; FY: fruit yield W: water consumption; WUEveg: vegetative water use efficiency; WUEyld: agronomic water use efficiency. *$P \leq 0.05$, **$P \leq 0.01$, n = 20.