



# Physiological factors affecting intrinsic water use efficiency of potato clones within a dihaploid mapping population under well-watered and drought-stressed conditions



Henrik Bak Toppbjerg<sup>a</sup>, Kacper Piotr Kaminski<sup>b,c</sup>, Bo Markussen<sup>e</sup>, Kirsten Kørup<sup>b</sup>, Kåre Lehmann Nielsen<sup>c</sup>, Hanne Grethe Kirk<sup>d</sup>, Mathias Neumann Andersen<sup>b</sup>, Fulai Liu<sup>a,\*</sup>

<sup>a</sup> University of Copenhagen, Faculty of Science, Department of Plant and Environmental Sciences, Højbakkegaard Allé 13, DK-2630 Taastrup, Denmark

<sup>b</sup> Department of Agroecology, Faculty of Science and Technology, Aarhus University, Blichers Allé 20, 8830 Tjele, Denmark

<sup>c</sup> Department of Biotechnology, Chemistry and Environmental Engineering, Aalborg University, Sohngaardsholmsvej 49, DK-9000 Aalborg, Denmark

<sup>d</sup> Danish Potato Breeding Foundation, Grindstedvej 55, DK-7184 Vandel, Denmark

<sup>e</sup> Department of Mathematical Sciences, Faculty of Science, University of Copenhagen, Universitetsparken 5, DK-2100 Copenhagen Ø, Denmark

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## ABSTRACT

Optimizing crops water use is essential for ensuring food production under future climate scenarios. Therefore, new cultivars that are capable of maintaining production under limited water resource are needed. This study screened for clonal differences in intrinsic water use efficiency (WUE<sub>i</sub>) within a dihaploid potato (*Solanum tuberosum* L.) mapping population under well-watered (WW) and drought-stress (DS) conditions. The factorial dependency of WUE<sub>i</sub> on several plant bio-physiological traits was analyzed, and clonal difference of WUE<sub>i</sub> was compared. Significant differences in WUE<sub>i</sub> were found among the clones within the population. Under WW the two clones showing the highest WUE<sub>i</sub> were significantly different from the two lowest WUE<sub>i</sub> performing clones. This could only be seen as a trend under DS. Under WW, WUE<sub>i</sub> differences were closely associated to net photosynthetic rate (A<sub>n</sub>) and nitrogen isotope composition (δ<sup>15</sup>N) in the leaf biomass, but did not relate to stomatal conductance (g<sub>s</sub>) and carbon isotope composition (δ<sup>13</sup>C) in the leaf biomass. A<sub>n</sub> was found to correlate significantly with leaf nitrogen concentration ([N]<sub>leaf</sub>) and chlorophyll content index (CCI) under WW. Leaf abscisic acid concentration did not correspond to the changes in g<sub>s</sub>, indicating that other factors might have been involved in controlling g<sub>s</sub> among the different clones. Collectively, the clonal differences in WUE<sub>i</sub> were attributed mainly to the variation in A<sub>n</sub>, which in turn was influenced by plant N metabolism. Clones with high WUE<sub>i</sub> could be potentially used as material in future breeding programs. Furthermore CCI seemed to be a reliable tool in estimating the clonal A<sub>n</sub> and thereby WUE<sub>i</sub>.

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## 1. Introduction

The current world population is expected to nearly double by 2050 (Wallace, 2000). In order to feed this ever growing population, crop production should consequently be increased by about 70% (Bruinsma, 2009). One of the major challenges confronting agricultural production is the shortage of freshwater resource for irrigation, as agriculture utilizes more than 70% of the world's freshwater withdraws today (Döll, 2009). Thus, to produce more food with each drop of water, increase of water use efficiency (WUE) is of primary importance for sustaining food production in a future drier climate.

Potato (*Solanum tuberosum* L.) is the fourth most important cultivated food crop globally with an overall production of ca. 324 million tons per year (FAOSTAT, 2013). Apart from being a source of carbohydrates, it also contains a variety of important dietary compounds as fibers, carotenoids, antioxidant phenols, minerals and vitamins (Burlingame et al., 2009). Potato is known to have a high water demand and as being sensitive to low soil water potentials (Lynch et al., 1995), particularly during the tuber bulking period (van Loon, 1981). The low drought tolerance has mainly been attributed to the shallow and sparse root system (van Loon, 1981), and irrigation is needed for potato production in order to achieve acceptable yield (Liu et al., 2006). Therefore, to sustain the crop yield, new potato cultivars with higher WUE under varied environmental conditions are needed.

WUE describes the relationship between unit of biomass produced per unit of water used (Richards, 1991; Rebetzke et al., 2002).

\* Corresponding author. Tel.: +45 3533 3392; fax: +45 3532 9577.  
E-mail address: [fl@plen.ku.dk](mailto:fl@plen.ku.dk) (F. Liu).

In relation to breeding, evaluations of crop water use are known to be influenced by interactions between both genotype and environment (Blum, 2009; Richards et al., 2002). Evaluation of genotypic variation in WUE can be carried out at different scales. At the stomatal level, the intrinsic WUE ( $WUE_i$ ) is derived from the ratio between net photosynthetic rate ( $A_n$ ) to stomatal conductance for water vapour ( $g_s$ ), viz.,  $A_n/g_s$  (von Caemmerer and Farquhar, 1981). The relationship between  $A_n$  and  $g_s$  is often found to be curvilinear, and in potatoes it has been reported that partial closure of stomata and reduced  $g_s$  due to soil drying may not initially affect  $A_n$  and therefore resulting in increased  $WUE_i$  (Liu et al., 2005b; Shahnazari et al., 2007). However, genotypic diversity in the response of leaf gas exchange to soil water availability has been widely documented (Edwards et al., 2012; Monclus et al., 2006; Tomás et al., 2013), and for some species or genotypes WUE may not increase under drought conditions (Liu and Stützel, 2004). Likewise, genotypes having a high WUE under irrigated conditions may respond differently under drought (Blum, 2009), and increases in WUE might not always translate directly to an increase in yield (Condon, 2004; Onder et al., 2005). Thus, for selecting crop species or genotypes of high WUE, it is important to evaluate the WUE under both well-watered and drought stressed conditions.

For screening genotypic diversity in  $WUE_i$  under varied environmental conditions, different plant physiological and biochemical traits that closely associate with the performance of leaf gas exchange have been used. As  $WUE_i$  is the ratio of  $A_n$  to  $g_s$ , factors influencing any of the two variables will have a direct effect on  $WUE_i$ . For a given genotype, a high  $WUE_i$  can be achieved by either a high  $A_n$  or a low  $g_s$  or both under a certain environment. It has been well established that under well-watered conditions  $A_n$  is positively correlated with leaf nitrogen (N) concentration ( $[N]_{\text{leaf}}$ ) (Evans, 1989), genotypes having greater  $[N]_{\text{leaf}}$  is expected to have higher  $A_n$  than those having lower  $[N]_{\text{leaf}}$  (Paponov and Engels, 2003; Cabrera-Bosquet et al., 2009). Thus, measurement of  $[N]_{\text{leaf}}$  could be used as a selection parameter for high  $WUE_i$  in well-watered crops. In addition, natural N isotope composition ( $\delta^{15}\text{N}$ ) is closely associated with N metabolism in the plant, and a link between  $\delta^{15}\text{N}$  and WUE has been reported in different plants though the relationship was not constant (Yousfi et al., 2012; Cao et al., 2014). However, it remains unknown that if such a link between  $\delta^{15}\text{N}$  and WUE could be found in potato clones. While, it is noteworthy that as leaf expansion growth is very sensitive to drought stress an increase in  $[N]_{\text{leaf}}$  was found in moderately drought-stressed plants (Wang et al., 2010); also drought may induce stomatal closure hereby decreasing  $g_s$ , which may in turn limit  $A_n$ . Therefore,  $[N]_{\text{leaf}}$  may not be positively correlated with  $A_n$  under drought conditions.

It has been found that the ratio between the intercellular  $\text{CO}_2$  concentration ( $C_i$ ) and that of the atmosphere ( $C_a$ ), viz.,  $C_i/C_a$ , is determined by the balance between mesophyll demand for  $\text{CO}_2$  ( $A_n$ ) and the  $\text{CO}_2$  supply through the stomata ( $g_s$ ) (reviewed in Farquhar et al., 1989). Furthermore the carbon isotopic composition ( $\delta^{13}\text{C}$ ) in plant dry biomass provides a long term measurement of  $WUE_i$ , which is associated with time integrated  $C_i/C_a$  ratio (Farquhar and Richards, 1984). A robust positive linear relationship between  $\delta^{13}\text{C}$  and  $WUE_i$  has been observed in many crop species (Martin and Thorstenson, 1988). For instance, the selection of high WUE wheat cultivars in Australia has been based on analysing  $\delta^{13}\text{C}$  in the plant biomass, which was found to be highly correlated to  $WUE_i$  (Farquhar and Richards, 1984; Farquhar et al., 1982; Hubick and Farquhar, 1989). However, an earlier study by Deblonde et al. (1999) revealed no differences in  $\delta^{13}\text{C}$  among six potato cultivars grown under varied water regimes.

In potato, xylem sap ABA concentration ( $[ABA]_{\text{xylem}}$ ) has been shown to regulate  $g_s$  at moderate soil water deficits (Liu et al., 2005b, 2006). ABA induced partial stomatal closure at moderate

drought has been shown potentially to increase  $WUE_i$  for both potato (Liu et al., 2005b) and soybean (Liu et al., 2005a) plants. Although under well-watered conditions, a direct link between endogenous ABA level and  $g_s$  among different genotypes has not been established; however a higher ABA level may associate with low  $g_s$  and consequently results in higher  $WUE_i$ . Nevertheless, when comparing 20 wheat lines with a high ABA concentration with 20 having a low ABA concentration, Read et al. (1991) found that there was no clear relationship between ABA concentration and  $\delta^{13}\text{C}$  and  $WUE_i$ , indicating that plant ABA level may not be directly correlated with  $WUE_i$ .

The aim of the present study was to evaluate clonal variation in  $WUE_i$  of a potato mapping population. A total of 23 clones selected from the population were grown in pots and exposed to both well-watered and drought-stressed conditions. Our purpose was to select promising clones which could be used in breeding for high WUE in potatoes. In addition, the factorial dependency of  $WUE_i$  was analyzed based on regressions between  $A_n$ ,  $g_s$ ,  $[N]_{\text{leaf}}$ ,  $[ABA]_{\text{leaf}}$ , leaf  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ .

## 2. Materials and methods

### 2.1. Plant material

The experiment was carried out from March to August, 2011 in a climate-controlled greenhouse located at University of Copenhagen, Faculty of Science, Taastrup. The potato clones used, belonged to the HCDHDN mapping population produced by a potato breeding company LKF-Vandel (Vandel, Denmark). The population was constructed as two dihaploid backcross populations made by reciprocal crosses between 90-HAF-01 [*Solanum tuberosum* L. (HAP 198.4 × 89-0-08-21)] and 90-HAG-15 [*Solanum tuberosum* (88-0-16-02) × *S. sparsipilum* accession number HHA 6627]. Prior to receiving the tubers, they were pre-sprouted at LKF-Vandel for 14 days at 12–14 °C with a constant overhead dim light. In total 32 clones, varying in number of available seed tubers ( $n = 16\text{--}30$ ), was planted and replicates were later divided equally between treatments. From the original planted clones, nine clones were discarded due to lack of variable replicates or other conditions. In this study, 23 clones were used in the experiment (Table 1).

### 2.2. Growth conditions

The seed tubers were planted at 3 cm depth in 3 L pots (diameter 18 cm) filled with 1.0 kg peat (Pinstруп substrate no. 2, Pindstrup Mosebrug A/S, Pindstrup, Denmark). The peat substrate had been supplemented with clay minerals (40 kg m<sup>-3</sup>), agricultural lime and fertilizers (1.0 kg m<sup>-3</sup> NPK fertilizer and 50 g m<sup>-3</sup> micro fertilizer) by the manufacturer and had a pH of 5.5–6.0 and EC of 1.0 mscm<sup>-1</sup>. The pots were placed in a south facing broad span greenhouse. Curtains provided shading when the solar irradiation was above ca. 2200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Day/night temperatures were set to 14/10 ± 3 °C. At temperatures above 17 °C ventilation was enforced by opening the top and side windows. From planting to two weeks after shoot emergence, the plants were watered manually with tap water when needed. Thereafter the plants were irrigated with nutrient solution (Pioneer NPK Macro 14-3-23 + Mg combined with Pioneer Micro; pH = 5.5; EC = 1.3, Azelis, Antwerp, Belgium) to avoid any deficiency of nutrients. Only one shoot per seed tuber required, hence additional shoots were regularly removed leaving only one shoot per pot. The pots were placed with a distance of 30 cm and were moved randomly from time to time on the table during the experimental period. Aphids were controlled by biological agent (*Aphidoletes aphidimyza*, *Aphidius colemani* and *Aphidius matricariae*) (Borregaard BioPlant Aps, Århus, Denmark).

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