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Research article

Drought tolerance of selected bottle gourd [*Lagenaria siceraria* (Molina) Standl.] landraces assessed by leaf gas exchange and photosynthetic efficiency

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ABSTRACT

Successful cultivation of bottle gourd in arid and semi-arid areas of sub-Saharan Africa and globally requires the identification of drought tolerant parents for developing superior genotypes with increased drought resistance. The objective of this study was to determine the level of drought tolerance among genetically diverse South African bottle gourd landraces based on leaf gas exchange and photosynthetic efficiency and identify promising genotypes for breeding. The responses of 12 bottle gourd landraces grown in glasshouse under non-stressed (NS) and drought-stressed (DS) conditions were studied. A significant genotype x water regime interaction was observed for gs, T, A, A/C_i, IWUE, WUE_{ins}, F_m', F_v'/F_m', Φ_{PSII}, qP, qN, ETR, ETR/A and AES indicating variability in response among the studied bottle gourd landraces under NS and DS conditions. Principal component analysis identified three principal components (PC's) under drought stress condition contributing to 82.9% of total variation among leaf gas exchange and chlorophyll fluorescence parameters measured. PC1 explained 36% of total variation contributed by gs, T, F_0', F_m', F_v'/F_m' and qN, while PC2 explained 28% of the variation and highly correlated with A, A/C_i, IWUE, WUE_{ins} ETR/A and AES. PC3 explained 14% of total variation contributed by Φ_{PSII}, qP and ETR. Principal biplot analysis allowed the identification of drought tolerant genotypes such as BG-27, BG-48, BG-58, BG-79, BG-70 and BG-78 which were grouped based on high gs, A, $F_m'F_v'/F_m'$, qN, ETR/A and AES under DS condition. The study suggests that the identified physiological traits could be useful indicators in the selection of bottle gourd genotypes for increased drought tolerance.

1. Introduction

Drought is a major constraint affecting global production of major and minor crops (Cattivelli et al., 2008). This has a significant effect on agriculture and food security, especially in regions that depend on rain as their primary source of water (Bray et al., 2000). In particular, subsistence and small-scale farmers, living in the semi-arid areas of sub-Saharan Africa and Asia, are vulnerable to the impacts of drought as they often lack essential resources for additional agricultural inputs and irrigation systems (Leichenko and O'Brien, 2002). The cultivation of drought-tolerant crops has been proposed as a solution for successful production in semi-arid areas.

Abbreviations: gs, stomatal conductance; T, transpiration rate; A, net CO_2 assimilation rate; A/C_i, CO_2 assimilation rate/intercellular CO_2 concentration; C_i, intercellular CO_2 concentration; C_i/C_a, ratio of intercellular and atmospheric CO_2; IWUE, intrinsic water use efficiency; WUE_{ins}, instantaneous water-use efficiency; F_0', Minimum fluorescence of light-adapted leaves; F_m', maximum fluorescence of light-adapted leaves; F_v'/F_m', maximum quantum efficiency of photosystem II photochemistry; Φ_{PSII}, the effective quantum efficiency of photosystem II photochemistry; qP, photochemical quenching; qN, non-photochemical quenching; ETR, electron transport rate; ETR/A, relative measure of electron transport to oxygen molecules; AES, alternative electron sinks.

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In order to maintain normal plant function and metabolism, plants have evolved physiological mechanisms to maintain tissue turgor and stomatal opening so as to maximize photosynthetic efficiency. Generally, as water stress increases, stomatal conductance and net photosynthesis decline (Singh and Raja Reddy, 2011). The decrease in stomatal conductance result in a low internal leaf CO_2 concentration and consequently, a decrease in CO_2 concentration at the carboxylation site of ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco), thereby decreasing net photosynthetic rate (Flexas et al., 2004). By limiting transpiration, stomatal closure can also improve plant water use efficiency (WUE) and therefore indirectly influence productivity under water stressed conditions (Flexas et al., 2012). Therefore, assessment of leaf gas exchange parameters such as stomatal conductance, transpiration rate, photosynthetic rate, intercellular CO_2 concentration and water-use efficiency can be indicative of drought tolerance characteristics among closely related genotypes (Anyia and Herzog, 2004; Souza et al., 2004; Cruz de Carvalho et al., 2011; Erice et al., 2011; Singh and Raja Reddy, 2011).

Drought adaptation in crop plants is generally associated with the induction of defense mechanisms for the protection of the photosynthetic apparatus. Photosynthetically active radiation (PAR) in plants is absorbed by chlorophyll and accessory pigments of chlorophyll-protein complexes, and it migrates to the reaction centers of photosystem II (PS II) and photosystem I (PS I), where the conversion of the quantum photosynthetic process takes place (Horton et al., 1996). Photosystem II is highly sensitive to light and a reduction in photosynthesis under drought stress causes an energy imbalance in the PSII reaction centers leading to photo-damage (Pastenes et al., 2005). Chlorophyll fluorescence of light or dark adapted leaves is a direct indicator of the photosynthetic activity (Lichtenthaler and Babani, 2000; Baker and Rosenqvist, 2004) and gives an indication of status of photosynthetic apparatus (Maxwell and Johnson, 2000). The measurement of this parameter allows estimation of the degree of injuries and their place in photosystem II and to study the protection mechanisms involved in the removal of the excess of excitation energy through the emission of heat/fluorescence from the photosynthetic apparatus (Araus et al., 1998; Lu and Zhang, 1999). The analysis chlorophyll fluorescence parameters such as F_0 (initial fluorescence), F_m (maximum fluorescence), F_v/F_m (maximum quantum yield of PS II photochemistry), qP (photochemical quenching) and NPQ (non-photochemical quenching) are considered as an important approach for evaluating drought tolerance in crops (Maxwell and Johnson, 2000; Baker and Rosenqvist, 2004; Li et al., 2006).

Bottle gourd [*Lagenaria siceraria* (Molina) Standl.] is a diploid ($2n = 2x = 22$) vine crop of the *Cucurbitaceae* family mainly grown for its fruits (Beevy and Kuriachan, 1996; Achigan-Dako et al., 2008). Sub-Saharan Africa where the species is cultivated for diverse uses such as for food, medicine, decoration, household utensils and musical instruments is thought to be the centre of origin and genetic diversity (Jeffrey, 1976). Fresh bottle gourd fruit juice is used as medicine for treatment of non-communicable diseases such as diabetes mellitus, hypertension, liver diseases (Ghule et al., 2007). The seeds are rich in essential amino acids and oil (Achigan-Dako et al., 2008). Bottle gourd is also used as a rootstock in watermelon breeding to control soil-borne diseases and to manage low soil temperature stress (Lee, 1994; Yetisir and Sari, 2003).

Bottle gourd is an important crop in arid and semi-arid tropics of SSA where recurrent drought is the major constraint to crop production but is one of the most neglected and under-researched food crops (van Rensburg et al., 2007). In sub-Saharan Africa bottle gourd is commonly grown by smallholder farmers predominantly using unimproved and genetically diverse landrace varieties (Mashilo et al., 2017a) often under water-limited conditions. Neglected and underutilized crops such as bottle gourd are thought to be drought tolerant (Zeven, 1998). This is probably through many years of selection by famers living in marginal and drought prone areas. This might have led to the development of drought resilient landrace varieties that are unique and adapted to their local conditions. According to Blum and Sullivan (1986), farmers' local varieties or landraces may possess some unique genetic and physiological attributes that may not be present in modern varieties. Landrace varieties are believed to be tolerant to abiotic stress (e.g. heat and drought stresses) making these material potentially key genetic resources for crop improvement. Bottle gourd is reportedly adapted to dry environments with limited rainfall and has been reported to possess some degree of drought tolerance (Park et al. 2014; Sithole and Modi 2015). The existence of genotypic variability in yield performance of bottle gourd under field conditions with tolerance to high temperatures and water stress has been reported (Samadia, 2002). Bottle gourd has also been reported to grow well with annual rainfall ranging from 400 to 1500 mm per annum (Haque et al. 2009). Mashilo et al. (2017b) further reported that diverse bottle gourd genotypes produced a mean fruit yield of 8.75 t ha^{-1} with a rainfall of 262 mm, indicating the capacity of the crop to grow in dry environments. Identification of drought tolerant bottle gourd genotypes is fundamental to enhance productivity in SSA and for effective breeding and conservation. However, the underlying genotypic variability of bottle gourd with respect to physiological responses is not well understood and has not been well-documented. Understanding physiological adaptive responses will assist breeders to identify key physiological process for drought tolerance breeding in this crop. Studying the genotypic variability in bottle gourd with respect to physiological mechanisms such as changes in stomatal conductance and photosynthetic efficiency in response to drought stress could provide useful stress indicators that may explain the physiological basis for drought adaptation in bottle gourd. The objective of this study was to determine the level of drought tolerance among a diverse set of selected South African bottle gourd landraces based on leaf gas exchange and photosynthetic efficiency and identify promising genotypes for drought tolerance enhancement in bottle gourd improvement programmes.

2. Material and methods

2.1. Plant materials

Twelve bottle gourd landraces namely, BG-27, BG-31, BG-48, BG-52, BG-58, BG-67, BG-70, BG-78, BG-79, BG-80, BG-81 commonly grown under dryland conditions in the Limpopo Province, South Africa, and a standard check landrace "GC" were used in this study (Table 1). The landrace GC was used as a comparative control. This landrace is widely grown and marketed at various retail outlets and fruit and vegetable stores in KwaZulu-Natal and Gauteng Provinces in South Africa. The remaining landraces were selected based on their variation in fruit characteristics such as fruit colour, shape and texture.

2.2. Experimental design and crop establishment

Pot experiments were conducted under glasshouse conditions at the Controlled Research Facility (CEF) of the University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°37′37.77″S; 30°24′13.25″E). The study was designed using a 12 × 2 factorial experiment laid out in a completely randomized design with three replications giving a total of 72 experimental units (2 L polyethylene pots). The 12 levels denominated bottle gourd landraces,