



Photosynthetic response of bottle gourd [*Lagenaria siceraria* (Molina) Standl.] to drought stress: Relationship between cucurbitacins accumulation and drought tolerance

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ARTICLE INFO

Keywords:

Cucurbits
Drought stress
Drought tolerance
Physiology

ABSTRACT

Cucurbitacins are a group of secondary metabolites produced by cucurbits including bottle gourd [*Lagenaria siceraria* (Molina) Standl.]. The role of cucurbitacins in plant responses to drought stress is not well-determined. The objective of this study was to investigate the response of bottle gourd to drought stress and to establish the relationship between cucurbitacins accumulation and drought tolerance. Leaf gas exchange, chlorophyll fluorescence and level of cucurbitacins production were investigated on 12 bottle-gourd landraces grown under drought-stressed (DS) and non-stressed (NS) conditions. Results showed that stomatal conductance (g_s), transpiration (T) rate, net CO_2 assimilation rate (A), the ratio of CO_2 assimilation rate and intercellular CO_2 concentration (C_i/C_a), intrinsic and instantaneous water-use efficiencies declined in landraces that were subjected to drought stress. Intercellular CO_2 concentration, the ratio of intercellular and atmospheric CO_2 concentration increased significantly in response to drought stress. The maximum quantum efficiency of photosystem II photochemistry (F_v'/F_m'), the effective quantum efficiency of photosystem II photochemistry, photochemical quenching (qP) and non-photochemical quenching (qN) were not affected by drought stress; whereas, electron transport rate, electron transport to oxygen molecules (ETR/A) and alternative electron sink (AES) declined. Cucurbitacin E and I were detected under NS and DS conditions in some of the tested bottle gourd landraces. Significant and positive correlations were observed between cucurbitacin I content with ETR/A and AES. The current study identified drought tolerant bottle gourd landraces namely: BG-48, BG-58, BG-70, BG-78 and BG-79 based of high values for g_s , T , A , F_v'/F_m' and qN under DS condition. These selections may be useful for drought tolerance breeding in bottle gourd or related cucurbits. There is a need for a further investigation whether cucurbitacin I accumulation may be involved in the regulation of the physiological processes evaluated in the present study.

1. Introduction

Drought is one of the leading constraints affecting global crop production and productivity (Cattivelli et al., 2008). Drought tolerant crop genotypes have varied adaptation and survival mechanisms and physiological responses under drought stress condition. Under drought stress, key physiological responses include synthesis and accumulation of compatible solutes which are referred to as osmoprotectants or osmolytes responsible in lowering of the cell water potential and enhancing water extraction capacity in water-limited environments

(Ramanjulu and Sudhakar, 2000). Blum and Sullivan (1986) reported that plants constantly experiencing drought stress may possess or develop some unique physiological drought adaptation mechanisms.

Plants in the *Cucurbitaceae* family produce a bitter secondary metabolite commonly referred to as cucurbitacins (Sharma et al., 2006; Sharma et al., 2012; Sukhlecha, 2012). The biosynthesis of cucurbitacins is initiated with the cyclization of 2, 3-oxidosqualene to cucurbitadienol. Cucurbitadienol is then metabolized into different cucurbitacins by subsequent hydroxylation, acetylation and glucosylation (Chen et al., 2005). Cucurbitadienol, a triterpene synthesized from

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oxidosqualene, is the first precursor of cucurbitacins produced by a specialized oxidosqualene cyclase called cucurbitadienol synthase. Cucurbitacins are classified into 12 types namely: A, B, C, D, E, F, I, L, 23, 24-dihydrocucurbitacin F, and hexanorcucurbitacin F. Cucurbitacins differ from each other by the presence of hydroxylation at C-2, -3, -19, -24 (cucurbitacins A, B, C and D), the presence of ketone function at C-3 (cucurbitacins A, B, C and D), double bond between C-23 (cucurbitacins B, D, E and I) and C-24 (B, D, E and I), and by the acetylation of the C-26 hydroxy group (B, D, E and I) (Greige-Gerges et al., 2007).

Cucurbitacins are generally toxic to many organisms and therefore, their natural role in plants is probably to act as a defense mechanism against pathogens and pests (Davidovich-Rikanati et al., 2015; Dube and Mashela, 2016; Shadung and Mashela, 2016). Cucurbitacins contents are reported to accumulate in response to environmental stresses including heat and drought stress (Haynes and Jones, 1975; Kano and Goto, 2003). However, the level and role of cucurbitacins content in plants to drought stress are not well-documented. Knowledge on their role and importance in drought adaptation may contribute to the development of reliable selection criteria for drought tolerance breeding. Therefore, the objective of this study was to determine the relationship between accumulation of cucurbitacins with leaf gas exchange and chlorophyll fluorescence parameters in bottle gourd under drought stress condition in order to establish the relationship between cucurbitacins accumulation and drought tolerance.

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 used due to their varied response to drought stress (Mashilo et al., 2017) and variation in fruit characteristics such as fruit colour, shape and texture (Mashilo et al., 2015, 2016).

2.2. Experimental design and crop establishment

Controlled pot experiments were conducted under glasshouse conditions at the Controlled Research Facility (CEF), University of KwaZulu-Natal, Pietermaritzburg, South Africa. The study was conducted using a 12 × 2 factorial experiment laid under a completely randomized design with three replications. The 12 levels denominated bottle gourd landraces, while the 2 levels represented watering regimes

(drought-stressed [DS] and non-stressed [NS] conditions).

Plants were grown in drained 2 L polyethylene plastic pots. A loamy soil of known physical properties (Clay% = 31.86; Silt% = 48.94% and Coarse sand = 10.35%) collected from Ukulinga Research Farm (29°39'48.82"S; 30°24'19.89"E), Pietermaritzburg, South Africa was used for the study. Each pot was filled with 2 kg of sieved soil. Fertilizer was applied based on soil fertility analysis using watermelon nutrient requirements as a reference. So far there is no fertilizer recommendation for bottle gourd production in South Africa. Plants under drought-stressed condition were irrigated until the formation of six fully expanded leaves and thereafter irrigation was withheld for 10 days before sampling. Plants in the non-stressed condition were watered daily to maintain soil moisture content at approximately 40% (field capacity). The mean air temperature and relative humidity of the glasshouse were maintained at 25 ± 2 °C and 60 ± 3%, respectively.

2.3. Data collection

2.3.1. Soil moisture content

Volumetric soil water content (%) in the upper 6–10 cm of soil on a percentage by volume were monitored using a soil moisture probe (Type ML2X attached to an HH2 moisture meter, Delta devices, Cambridge, England). Ten pots for drought-stressed and non-stressed treatments were monitored to measure changes in soil water content.

2.3.2. Gas exchange and chlorophyll fluorescence parameters

Leaf gas exchange and chlorophyll fluorescence were measured simultaneously using the LI-6400 XT Portable Photosynthesis System (Licor Bioscience, Inc. Lincoln, Nebraska, USA) fitted with an infrared gas analyzer attached to a leaf chamber fluorometer (LCF) (6400–40B, 2 cm² leaf area, Licor Bioscience, Inc. Lincoln, Nebraska, USA). Leaf temperature was maintained at 25 °C, with external leaf CO₂ concentration (C_a) and artificial saturating photosynthetic active radiation (PAR) fixed at 400 μmol mol⁻¹ and 1000 μmol m⁻²s⁻¹, respectively. The flow rate was maintained at 500 μl and relative humidity maintained at 43%. The leaf-to-air vapor pressure deficit in the cuvette was maintained at 1.7 kPa to prevent stomatal closure due to the low air humidity effect. Measurements were taken between 08h00 to 11h00 h on the third half-fully expanded leaf from the tip of the plant by clamping the leaf inside the sensor head. Measurements were made from three independent plants for each genotype under non-stressed and drought-stressed conditions. Gas exchange parameters such as stomatal conductance (g_s), net CO₂ assimilation rate (A), transpiration rate (T), intercellular CO₂ concentration (C_i) and the ratio of intercellular and atmospheric CO₂ (C_i/C_a) concentrations. The ratio of net CO₂ assimilation rate and intercellular CO₂ concentration (A/C_i) was calculated according to Dong et al. (2016). Two types of water-use efficiencies were calculated, viz: intrinsic water use efficiency (WUE_i) calculated as the ratio A and g_s (Martin and Ruiz-Torres, 1992; Osmond et al., 1999) and instantaneous water-use efficiency (WUE_{ins}),

Table 1

List of bottle gourd landraces used in the study and description of geographic location and coordinates of collection sites.

Landrace	Fruit shape	Collection sites and geographic coordinates	Province in South Africa
BG-27	Cavate	Kgohloane (23°47'39.76" S; 29°22'13.45" E)	Limpopo
BG-31	Cavate	Kgohloane (23°47'39.76" S; 29°22'13.45" E)	Limpopo
BG-48	Cavate	Kgohloane (23°47'39.76" S; 29°22'13.45" E)	Limpopo
BG-52	Cavate	Kgohloane (23°47'39.76" S; 29°22'13.45" E)	Limpopo
BG-58	Cavate	Kgohloane (23°47'39.76" S; 29°22'13.45" E)	Limpopo
BG-67	Cavate	Ga-Rapitsi (23°35'48.37" S; 29°06'25.08" E)	Limpopo
BG-70	Pyriiform Elongated	Ga-Phasa (23°40'57.30" S; 29°15'57.30" E)	Limpopo
BG-78	Cavate	Moletjie-Mabokelele (23°45'14.69" S; 29°17'36.6" E)	Limpopo
BG-79	Pyriiform	Moletjie-Mabokelele (23°45'14.69" S; 29°17'36.6" E)	Limpopo
BG-80	Cavate	Moletjie-Mabokelele (23°45'14.69" S; 29°17'36.6" E)	Limpopo
BG-81	Pyriiform	Moletjie-Mabokelele (23°45'14.69" S; 29°17'36.6" E)	Limpopo
GC	Pyriiform	La Lucia (29°45'19.98" S; 31°04'33.41" E)	KwaZulu-Natal

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