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Variation of photosynthetic characteristics and yield in wild and cultivated species of yams (*Dioscorea spp.)* from Koraput, India

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Abstract

Variations in leaf gas-exchange characteristics, PSII activity, leaf pigments, and tuber yield were investigated in seven wild and one cultivated species of *Dioscorea* from Koraput, India, in order to find out their overall adaptability to the environment. The leaf photosynthetic rate, transpiration, stomatal conductance, water-use efficiency, carboxylation efficiency, and photosynthetic pigments were significantly higher in some wild species compared to the cultivated species. In addition, some wild species showed better photochemical efficiency of PSII, photochemical quenching, and electron transport rate in comparison to cultivated one. Furthermore, leaf dry matter accumulation and tuber yield was also higher in some wild species compared to the cultivated species. Taken together, the wild species, such as *D. oppositifolia, D. hamiltonii*, and *D. pubera*, showed the superior photosynthetic efficiency compared to the cultivated *D. alata* and they could be used for future crop improvement programs.

Additional key words: chlorophyll fluorescence; gas exchange; photosynthesis; tuber yield.

Introduction

Root and tuber crops occupy a remarkable position towards food security of the developing world due to their high caloric value and carbohydrate content (Dansi *et al.* 1999, Kumar *et al.* 2013). Yam (*Dioscorea*) species are an important source of food and medicine in the tropics and subtropics and have a significant place in dietary habits of many rural and tribal communities (Edison *et al.* 2006, Behera *et al.* 2009). *Dioscorea* species are the monocotyledonous tuber crops from family Dioscoreacea; the genus includes more than 600 different species worldwide (Kouakou *et al.* 2010, Amanze *et al.* 2011). However, only few species are commercially cultivated and some wild edible species has not yet been domesticated due to inferior tuber quality, low yield, and transformable poisonous forms of some tubers (Behera *et al.* 2009). There is an enormous diversity in the wild and domesticated species that are being used by tribal communities (Dansi *et al.* 1999, Behera *et al.* 2009). However, systematic characterization of the diversity present in wild species is a major prerequisite for using it in breeding programs. As morphological description of *Dioscorea* plant is well established (Ngo Ngwe *et al.* 2015), its phenotyping based on photosynthetic traits could serve as a potential marker for varietal identification and differentiation in order to integrate them into developmental interventions.

Photosynthesis represents an integral part of the plant metabolism and balance sheet of growth and development, which is known to be regulated by internal and environmental factors (Gupta *et al.* 2002, Mathur *et al.* 2016). Photosynthetic rate of the entire crop canopy depends on

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Abbreviations: Car – carotenoids; CE – carboxylation efficiency (= P_N/C_i); Chl – chlorophyll; C_i – intercellular CO_2 concentration; DM – dry mass; DMA – dry matter accumulation; E – transpiration rate; ETR – electron transport rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_v/F_m – maximal quantum yield of PSII photochemistry; FM – fresh mass; g_s – stomatal conductance; LSD – least significant difference; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; RWC – relative water content; WUE – water-use efficiency (= P_N/E); Φ_{PSII} – effective quantum yield of PSII photochemistry.

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the photosynthesis of individual leaves (Below 2001), which can also be influenced by many plant factors, such as a leaf position and age, sink effects, mutual shading, as well as environmental factors, such as light, temperature, nutrition, and water availability (Rodríguez-Montero 1997, Aighewi and Ekanayake 2004). *In vivo* chlorophyll (Chl) fluorescence has been used frequently in the past as a convenient and nonintrusive method to determine the efficiency and estimate of photosynthetic performance of plants (Kao *et al.* 2003, Sayed 2003, Dudeja and Choudhury 2005). It allows to study functional photosynthesis indirectly at the pigment level, primary light reactions, thylakoid electron transport reactions, dark-enzymatic stroma reactions, and slow regulatory processes (Batra *et al.* 2016). Pulse amplitude-modulated (PAM) fluorometer provides quantitative information about PSII (Souza *et al.* 2004) by measuring Chl fluorescence. The valuable information, such as electron transport rate (ETR), photosynthetic yield (F_v/F_m), and quenching parameters, can be used to assess the performance of plants. The measurement of leaf pigmentation is an important parameter for eco-physiologists, because it is an indirect measure of nutrient status, which provides useful insights into plant–environment interactions (Elfeky *et al.* 2007). Unlike other plants, relatively few information has been published on the physiology and photosynthetic efficiency of tropical root and tuber crops and there is an information gap on photosynthetic differences between wild and cultivated species of *Dioscorea*. These eco-physiological traits of plants can be used to assess reliably the fitness and ecological dominance in plants.

Koraput is one of the thickly tribal (~ 65%) dominated districts of Odisha state in India, harbouring rich genetic diversity of tropical tuberous plants (Mishra *et al.* 2012); it has been recently declared as one of the agro-biodiversity hot spots in India (Mishra *et al.* 2012). There are seven wild *Dioscorea* species, such as *Dioscorea oppositifolia*, *D. tomentosa*, *D. hamiltonii*, *D. bulbifera*, *D. pubera*, *D. pentaphylla*, and *D. hispida* along with one cultivated species *D. alata*, which have been used as food by the tribal people of Koraput (Mishra *et al.* 2011, Padhan and Panda 2016). For proper utilization and incorporation of these wild *Dioscorea* species from the natural crop resources, identification of the allelic variants is of utmost importance. In this background, there is limited phenotypic knowledge and profiling reports of wild edible *Dioscorea* species in relation to their physiological efficiency. Identification of the variations in the physiological processes, such as leaf photosynthesis, PSII activity, and tuber yield, between the wild and cultivated *Dioscorea* species may help in yam improvement programs.

Material and methods

Plant materials and growth conditions: The study was conducted with seven wild edible *Dioscorea* species, namely *Dioscorea oppositifolia*, *D. tomentosa*, *D. hamiltonii*, *D. bulbifera*, *D. pubera*, *D. pentaphylla*, and *D. hispida* along with one cultivated species, *D. alata* (Mishra *et al.* 2011). The tubers of wild *Dioscorea* species were collected from different forest patches of Koraput, while the cultivated species was collected from local farmer's field.

The experiment was conducted in the campus of Central University of Orissa, Koraput, India (82°44′54″E to 18°46′47″N, 880 m a. s. l.; average rainfall of 1,500 mm) during yam growing season (April–December) of 2015 and 2016. Plants were grown in 30-kg polythene bags filled with mixture of farm soil and farmyard manure in a ratio of 3:1. The soil used for the experiment was deep loamy red and lateritic (pH 6.64, organic C of 0.15 ppm, total N of 0.18 ppm, available P of 0.01 ppm, and available K of 0.84 ppm). Uniform-sized tubers of each species were selected and directly sown into the polythene bags by following the standard agronomic practices (Behera *et al.* 2009). The experimental design was a randomized block design with three replications in each species. Plants were regularly irrigated with tap water and subjected to natural solar radiation, with daily maximum PPFD, air temperature, and relative humidity of being about 1,560 ± 20 μmol(photon) m^{-2} s^{-1}, 33.6 ± 2°C, and 65–70%, respectively. All the measurements were performed three times after 180 d of planting (in the flowering stage). Harvesting of tubers was done after all the vines dried which was around 240 d after planting. Fresh tuber yield of each plant was expressed as kg per plant. The pool data of different physiological and yield parameters of both the years 2015 and 2016 was presented.

Leaf gas exchange: The leaf gas-exchange parameters, such as net photosynthetic rate (P_N), transpiration rate (E), intercellular CO_2 concentration (C_i), and stomatal conductance (g_s) were measured between 10–12 h on fully matured leaves of each plant using an open system photosynthetic gas analyzer (*CI-304, CID*, USA) under normal ambient environmental conditions. The leaf from each plant was selected and kept inside the chamber under natural irradiance until stable reading was recorded. The measurements were carried out at 27 ± 2°C, 60–70% of relative humidity, PPFD of 1,114 ± 33 μmol m^{-2} s^{-1}, 370 μmol(CO_2) m^{-2} s^{-1}, and 21% O_2. Leaf water-use efficiency (WUE, P_N/E) and carboxylation efficiency (CE, P_N/C_i) were calculated following Kiran *et al.* (2013).

Chl fluorescence was measured on the same leaves used for gas-exchange measurements in dark- and light-adapted leaves by using a portable Chl fluorometer (*JUNIOR-PAM, WALZ*, Germany) at midday (12:00 h). Different parameters, such as minimal fluorescence (F_0), maximal fluorescence (F_m), variable fluorescence ($F_v = F_m - F_0$), and maximum photochemical efficiency of PSII (F_v/F_m) were measured in 20-min dark-adapted leaves (Maxwell and Johnson 2000). In light-adapted leaves at a PPFD of 420 µmol m^{-2} s^{-1}, steady-state fluorescence yield (F_s), maximal fluorescence (F_m'), and minimal fluorescence (F_0') were measured. Quenching value due to nonphotochemical dissipation (NPQ), the coefficient for photochemical quenching (q_P), and effective quantum yield of PSII photochemistry (Φ_{PSII}) were also calculated (Maxwell and Johnson 2000). The electron transport rate (ETR) was measured by the light-induction curve with different PAR following the software supplied by the manufacturer.

Chl and carotenoid (Car) contents: After measurement of the Chl fluorescence, the same leaves were pooled together, finely chopped, and used for Chl and Car estimation. Fresh leaves of 100 mg were placed in a 25-ml capped-measuring tube containing 10 ml of 80% cold acetone, and kept inside a refrigerator (4°C) for 48 h. The total Chl and Car were measured spectrophotometrically (*Bio spectrophotometer, Eppendorff*, Germany) by taking absorbance at 663, 645, and 470 nm. The total Chl and Car content were calculated using the equations of Arnon (1949) and Lichtenthaler and Welburn (1983), respectively.

Relative water content (RWC), dry matter accumulation (DMA) and protein: For RWC, the leaflet of each species from the main shoot apex was collected and immediately weighed for taking the leaf fresh mass (LFM, g), dipped in deionised water, and left in the dark for 48 h. Afterwards, they were again weighed to measure the leaf turgid mass (LTM, g) and then placed in an oven at 70°C for 48 h to determine the leaf dry mass (LDM). The relative water content (RWC) of the leaf was calculated according to Abenavoli *et al.* (2016).

$$\text{RWC [\%]} = (\text{LFM} - \text{LDM})/(\text{LTM} - \text{LDM}) \times 100$$

The leaf DMA was calculated by the following formula

$$\text{DMA [\%]} = (\text{LDM}/\text{LFM}) \times 100$$

For leaf protein estimation, fresh leaf material of 0.5 g was homogenized in 10 ml of 50 mM potassium phosphate buffer (pH 7.8). The homogenate was centrifuged at 0–4°C at 12,000 rpm for 15 min and the supernatant was used for determining of protein content following Lowry *et al.* (1951).

Statistical analysis: Differences between various parameters were compared by one-way analysis of variance (*ANOVA*) using *CROPSTAT* (International Rice Research Institute, Philippines) software. The statistical significance of the parameter means was determined by performing the *Fisher's* least significance difference (*LSD*) test. The standard deviations (SD) and multiple correlation analysis were done by *Microsoft Excel 2007*. The similarity index in different *Dioscorea* species was constructed by dendogram using different photosynthetic parameters and was measured through paired group (*UPGMA*) by Bray-Curtis similarity index using *PAST-3* (*Palaeontological Statistics*) software.

Results and discussion

Variation in leaf gas exchange and photosynthetic pigments: Carbon balancing within the plant species is an important feature for climatic adaptability. Leaf photosynthesis and gas-exchange traits are directly linked to a carbon balance (Kondamudi *et al.* 2016). These features were compared in seven wild and one cultivated *Dioscorea* species. In the present study, wide variations were observed in different *Dioscorea* species for leaf gas-exchange parameters (Table 1). There were significant differences between wild and cultivated *Dioscorea* species with regard to P_N; the range of P_N in wild *Dioscorea* species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, were significantly higher than that of cultivated species (*D. alata*). Similarly, g_s and E were also higher in some wild species than that of cultivated species of *Dioscorea*. Further, the WUE (P_N/E) and CE (P_N/C_i) varied significantly among the wild and cultivated *Dioscorea* species (Table 1). The wild *Dioscorea* species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, showed significantly higher WUE and CE than that of cultivated species (*D. alata*). There have been several reports that wild species are associated with higher leaf P_N and can contribute genes for improving complex traits, such as high biomass and abiotic stress tolerance (Placido *et al.* 2013). This adds important information regarding leaf photosynthetic performance of some wild *Dioscorea* species under the prevailing environmental conditions.

Leaf pigments reflect photosynthetic properties of the plants, as they indicate the amount of light-harvesting capacity (Elfeky *et al.* 2007). Car provide photoprotective functions in photosynthesis, are integral constituents of the photosystems, mostly in xanthophylls. Car protect Chl and thylakoid membranes from the damage by absorbed energy, photooxidation (Bailey *et al.* 2004). The significant difference in Chl and Car contents was observed between the *Dioscorea* species (Table 1). The wild species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, showed significantly more Chl and Car in comparison to other species including cultivated *D. alata*.

Variations in leaf PSII activity and electron transport rate: In addition, Chl fluorescence measurement helps to assess the intrinsic photosynthetic performance of plants, which provides important information regarding PSII, reflecting actual performance of the plant in prevalent environmental conditions (Batra *et al.* 2016). The leaf PSII

Table 1. Variation in leaf photosynthetic characteristics and leaf pigments in wild and cultivated species of *Dioscorea*. P_N – photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; C_i – internal CO_2 concentration; WUE – water use efficiency ($=P_N/E$); CE – carboxylation efficiency ($=P_N/C_i$); Chl – chlorophyll; CAR – carotenoid; CV – coefficient of variance; FM – fresh mass. Data are the mean of three replications ± SD. Means followed by a *common letter* in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test.

Species	P_N [µmol(CO_2) m^{-2} s^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	g_s [mmol(H_2O) m^{-2} s^{-1}]	C_i [µmol(CO_2) mol^{-1}]	WUE (P_N/E)	CE (P_N/C_i)	Chl [mg g^{-1}(FM)]	CAR [mg g^{-1}(FM)]
D. hispida	14.72 ± 0.81^{ab}	1.73 ± 0.21^{a}	150.5 ± 4.6^{a}	280.5 ± 3.8^{a}	8.51 ± 0.81^{b}	0.052 ± 0.003^{b}	0.637 ± 0.04^{a}	0.17 ± 0.01^{a}
D. pentaphylla	15.36 ± 1.90^{b}	1.76 ± 0.13^{a}	168.9 ± 14.5^{a}	319.5 ± 13.5^{b}	7.84 ± 0.73^{a}	0.048 ± 0.001^{b}	0.527 ± 0.10^{a}	0.15 ± 0.03^{a}
D. bulbifera	12.10 ± 1.50^{a}	1.46 ± 0.31^{a}	199.8 ± 10.6^{b}	302.3 ± 12.3^{b}	7.60 ± 0.82^{a}	0.036 ± 0.002^{a}	0.658 ± 0.10^{a}	0.13 ± 0.03^{a}
D. hamiltonii	18.92 ± 0.42^{c}	1.99 ± 0.20^{b}	280.1 ± 14.9^{e}	306.3 ± 2.5^{b}	9.51 ± 0.91^{b}	0.061 ± 0.001^{c}	0.847 ± 0.10^{b}	0.27 ± 0.02^{b}
D. pubera	17.75 ± 1.01^{c}	1.94 ± 0.15^{b}	246.6 ± 19.6^{d}	303.5 ± 4.5^{b}	9.15 ± 0.72^{b}	0.058 ± 0.003^{c}	0.874 ± 0.04^{b}	0.25 ± 0.01^{b}
D. tomentosa	13.34 ± 0.81^{a}	1.68 ± 0.11^{a}	188.2 ± 10.0^{b}	314.3 ± 4.9^{b}	7.94 ± 0.92^{a}	0.042 ± 0.004^{a}	0.530 ± 0.05^{a}	0.15 ± 0.00^{a}
D. oppositifolia	18.10 ± 1.30^{c}	2.01 ± 0.21^{b}	217.2 ± 16.3^{c}	304.0 ± 1.3^{b}	8.70 ± 0.63^{b}	0.060 ± 0.001^{c}	0.816 ± 0.05^{b}	0.21 ± 0.01^{b}
D. alata	15.92 ± 0.92^{b}	2.39 ± 0.22^{c}	187.1 ± 17.5^{b}	297.8 ± 15.9^{a}	6.83 ± 0.71^{a}	0.053 ± 0.002^{a}	0.677 ± 0.04^{a}	0.14 ± 0.01^{a}
Mean	15.78	1.87	204.8	303.5	8.26	0.051	0.696	0.184
LSD($P<0.05$)	2.7	0.37	20.5	11.04	1.07	0.006	0.156	0.06
CV [%]	9.2	6.3	6.1	3.8	12.9	12.0	4.9	3.5

activity of different *Dioscorea* species was studied by measuring different Chl fluorescence parameters. The F_0, F_m, F_v/F_m, Φ_{PSII}, NPQ, and q_P are widely used Chl fluorescence parameters in plant physiology studies (Murchie and Lawson 2013). These parameters were significantly different between the species (Table 2). In the present study, wild species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, showed better PSII activity under prevalent environmental conditions as evident from the higher value of F_0, F_m, F_v/F_m, Φ_{PSII}, and q_P with less NPQ compared to the cultivated species (Table 2). The result showed that most of the plants were healthy as maximal photochemical efficiency of PSII was in the range of 0.707–0.783 with high q_P and very low NPQ value (Pinnola *et al.* 2013). The parameter Φ_{PSII} gives an approximation of the proportion of absorbed energy being used for photochemistry at a given point in time and reflects the degree of adaptation of plant to its environment (Maxwell and Johnson 2000). Additionally, it has been demonstrated that genotypic differences exist in the composition of NPQ (Müller *et al.* 2001), which relates to the ecology of the plant. Therefore, our result reflected that the degree of adaptation to prevailing environment in some wild species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, was greater than that of cultivated species.

Light-response curves (LCs) reflect intrinsically photosynthetic capacity of plants (Lüttge *et al.* 2007) and can be used to assess the performance of the plants (Batra *et al.* 2016). In the present study, a different range of PAR [65–820 µmol(photon) m^{-2} s^{-1}] was given to measure the ETR of selected *Dioscorea* species for determining the PAR saturation. It was found that with increase in PAR range, the ETR also gradually increased. Maximum ETR was observed in *D. hamiltonii, D. pubera*, and *D. oppositifolia* and showed better photochemical activity in the prevalent environmental conditions compared to the cultivated species *D. alata* (Fig. 1).

Variations in leaf dry matter accumulation (DMA), relative water content (RWC) and protein: The process of biomass production under changing climate is one of requirements for sustaining global food production (Zhu *et al.* 2008, Kajala *et al.* 2011). Biomass production is mainly a net product of photosynthetic carbon assimilation (Makino 2011). In addition to the leaf P_N, some of the wild species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, showed significantly more DMA (%) compared to the cultivated species (Fig. 2*A*). Higher source size and enhanced photosynthesis was found to be a basis of the increased DMA in wild *Dioscorea* species as reported in other crops (Hayat *et al.* 2012). Some wild species, such as *D. hamiltonii, D. pubera*, and *D. oppositifolia*, showed significantly higher leaf RWC and protein content if compared to the cultivated species *D. alata* (Fig. 2*B,C*). At the same time, the g_s and WUE were also higher in these species than in others (Table 1). In spite of this, not only they preserved their water content effectively but also their

Table 2. Variation in leaf chlorophyll fluorescence parameters in wild and cultivated *Dioscorea* species. F_0 – minimum fluorescence yield obtained with dark-adapted leaf; F_m – maximum Chl fluorescence yield obtained with dark-adapted leaf; F_v/F_m – maximal photochemical efficiency of PSII; NPQ – nonphotochemical quenching; q_P –photochemical quenching; Φ_{PSII} – effective quantum yield of PSII photochemistry; CV – coefficient of variance. Data are the mean of three replications ± SD. Means followed by a *common letter* in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test.

Species	F_0 [rel.]	F_m [rel.]	F_v/F_m [ratio]	Φ_{PSII} [ratio]	q_P [rel.]	NPQ [rel.]
D. hispida	453.5 ± 30.9^{a}	$1{,}810 \pm 194^{a}$	0.709 ± 0.021^{a}	0.131 ± 0.021^{a}	0.298 ± 0.028^{a}	1.81 ± 0.14^{b}
D. pentaphylla	458.5 ± 23.5^{a}	$1{,}892 \pm 175^{a}$	0.705 ± 0.012^{a}	0.129 ± 0.030^{a}	0.294 ± 0.017^{a}	1.43 ± 0.13^{b}
D. bulbifera	422.0 ± 19.4^{a}	$1{,}770 \pm 111^{a}$	0.711 ± 0.022^{a}	0.127 ± 0.018^{a}	0.334 ± 0.021^{a}	2.49 ± 0.26^{c}
D. hamiltonii	578.0 ± 34.3^{b}	$1{,}951 \pm 108^{b}$	0.783 ± 0.012^{b}	0.191 ± 0.014^{b}	0.377 ± 0.020^{b}	1.03 ± 0.03^{a}
D. pubera	567.0 ± 41.3^{b}	$2{,}121 \pm 170^{b}$	0.780 ± 0.011^{b}	0.183 ± 0.033^{b}	0.366 ± 0.027^{b}	1.02 ± 0.05^{a}
D. tomentosa	481.0 ± 31.9^{a}	$2{,}119 \pm 100^{b}$	0.738 ± 0.011^{a}	0.097 ± 0.017^{a}	0.291 ± 0.024^{a}	1.48 ± 0.12^{b}
D. oppositifolia	581.5 ± 33.5^{b}	$2{,}175 \pm 160^{b}$	0.783 ± 0.013^{b}	0.186 ± 0.034^{b}	0.372 ± 0.030^{b}	1.04 ± 0.13^{a}
D. alata	439.5 ± 27.0^{a}	$1{,}705 \pm 136^{a}$	0.742 ± 0.010^{a}	0.159 ± 0.021^{a}	0.335 ± 0.025^{b}	1.48 ± 0.14^{b}
Mean	497.6	1,942.9	0.744	0.151	0.333	1.45
LSD($P<0.05$)	46.3	210	0.035	0.057	0.044	0.41
CV [%]	15.9	18.7	5.7	5.9	5.5	5.1

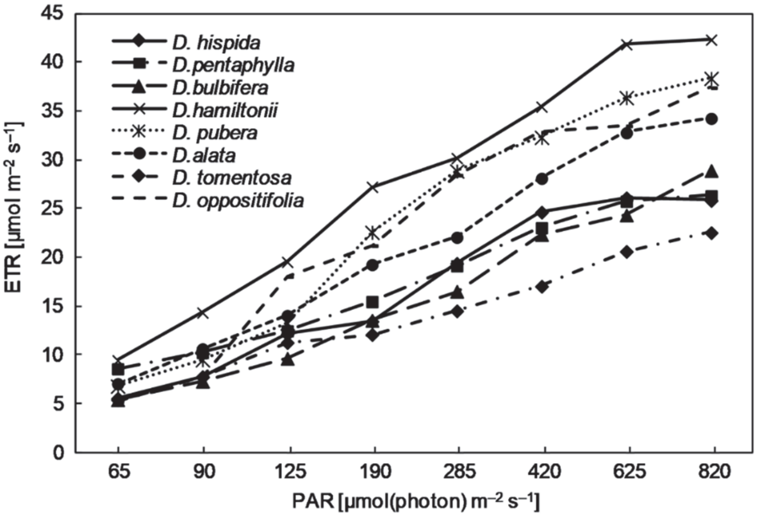

Fig. 1. Electron transport rate (ETR) in different wild and cultivated species of *Dioscorea* under different photosynthetic active radiation (PAR). Data are the mean of three replications ($n = 3$).

WUE was high because of their leaf morphology and architecture. This showed some wild species maintaining the leaf vitality and plasticity more efficiently under prevalent environmental condition than the cultivated species (Türkan *et al.* 2005).

Variation in tuber yield: Very little information is available on the yield potential of wild *Dioscorea* species and many wild species could not be domesticated primarily due to their poor yield and tubers of inferior quality (Behera *et al.* 2009). But in the present study, some of the wild species, such as *D. pubera, D. oppositifolia*, and *D. hamiltonii*, showed significantly higher tuber yield compared to the cultivated species *D. alata* (Fig. 3). Although, the wild species *D. tomentosa* showed better leaf photosynthetic performance in the present study, the yield was very low. This is because higher vegetative growth in a tuber crop requires more photosynthates for maintenance of vegetative parts thus resulting in the poor tuber yield (Behera *et al.* 2009). The ability to form tubers is dependent on the genetics of the variety (Martin 1978) and is affected by environmental factors, such as day length, temperature, and cultivation practices (King and Risimeri 1992). However, the yield of tuber is not the only criterion for selection of species, rather the quality of the tuber plays an important role for domestication.

Correlation: Relationships between leaf photosynthetic parameters and dry matter accumulation and tuber yield in different *Dioscorea* species were studied by multiple correlation analysis (Table 3). The results revealed that the P_N was not significantly influenced by leaf Chl and Car contents. A significant positive correlation between P_N and E, g_s, CE, WUE, F_v/F_m, Φ_{PSII}, and q_P was observed, whereas, leaf P_N was negatively correlated with C_i, F_0, and NPQ. This result indicated that the observed variations in

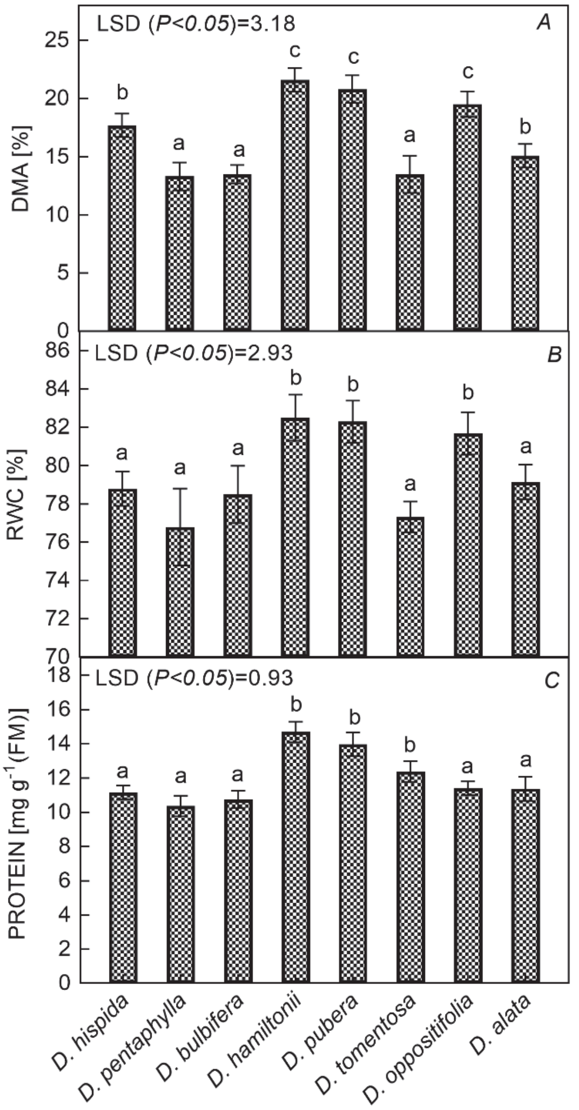

Fig. 2. Leaf dry matter accumulation (DMA), relative water content (RWC), and protein content in different wild and cultivated species of *Dioscorea*. Data are the means of three replications and bars indicate the standard deviation of the means ($n = 3$). Means followed by a *common letter* are not significantly different at the 5% level by *Fisher'*s least significance difference (LSD) test.

P_N in different *Dioscorea* species were not based on the pigment content, but it was related to the PSII photochemical activity and leaf CE and WUE as it has been reported earlier in other crops (Yeo *et al.* 1994, Kiran *et al.* 2013, Haritha *et al.* 2017). Significant association between leaf P_N with light saturation and carboxylation efficiency was reported in many crops (Ding *et al.* 2014). The leaf Chl content is an important physiological trait, closely associated with photosynthesis, and used to predict a yield potential (Teng *et al.* 2004, Abhilash Joseph *et al.* 2014). But in the present study, Chl was not a determinant for leaf photosynthesis, DMA, and yield in *Dioscorea* species under prevalent environmental conditions. Further, leaf P_N showed significant positive correlation with DMA, which supports the previous reports of Evans (2013) and Puteh *et al.* (2014) for increased biomass in other crops. However, in the present study, no association between P_N and the tuber yield was observed, as it has been reported in other crops, such as rice, wheat, soybean, sugarcane, cotton, and sunflower; thus, the higher yield was not associated with leaf P_N (Richards 2000).

Variations among *Dioscorea* species: Cluster analysis based on the Bray-Curtis paired linkage revealed the percentage of similarity in leaf photosynthetic parameters among wild and cultivated *Dioscorea* species presented in Fig. 4. The dendrogram showing the similarity formed two clusters, such as *D. pubera, D. oppositifolia*, and *D. hamiltonii*, which are in one cluster having 95.6% similarity.

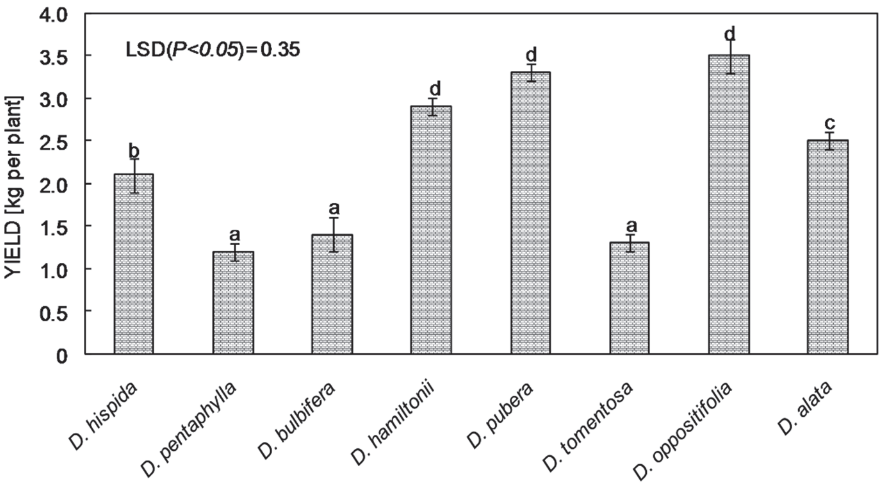

Fig. 3. Fresh tuber yield [kg per plant] in different wild and cultivated species of *Dioscorea*. Data are the mean of three replications and bars indicate the standard deviation of the means ($n = 3$). Means followed by a *common letter* are not significantly different at the 5% level by *Fisher'*s least significance difference (LSD) test.

Table 3. Relationship between leaf photosynthetic parameters with yield and dry matter accumulation in different *Dioscorea* species. P_N – photosynthetic rate; E –transpiration rate; g_s – stomatal conductance; C_i – internal CO_2 concentration; WUE – water use efficiency; CE – carboxylation efficiency; F_0 – minimum fluorescence yield obtained with dark-adapted leaf; F_m – maximum Chl fluorescence yield obtained with dark-adapted leaf; F_v/F_m – maximal photochemical efficiency of PSII; q_P – photosynthetic quenching; NPQ – nonphotochemical quenching; CAR – carotenoid; Chl – chlorophyll; DMA – dry matter accumulation; Φ_{PSII} – effective quantum yield of PSII photochemistry. Degree of freedom (df) = 23; * – $P<0.05$, ** – $P<0.01$, ns – not significant.

Parameter	P_N	E	g_s	C_i	WUE	CE	F_0	F_m	F_v/F_m	Φ_{PSII}	q_P	NPQ	CAR	Chl	DMA
E	0.775^{**}														
g_s	0.558^{**}	0.817^{**}													
C_i	-0.362^{*}	0.265^{ns}	0.581^{*}												
WUE	0.491^{**}	-0.121^{ns}	-0.170^{ns}	-0.460^{*}											
CE	0.964^{**}	0.670^{**}	0.371^{*}	-0.309^{ns}	0.570^{*}										
F_0	-0.316^{ns}	-0.269^{ns}	-0.273^{ns}	0.001^{ns}	-0.100^{ns}	-0.295^{ns}									
F_m	0.016^{ns}	0.075^{ns}	0.049^{ns}	0.054^{ns}	0.006^{ns}	-0.008^{ns}	0.689^{**}								
F_v/F_m	0.414^{*}	0.391^{*}	0.358^{*}	0.051^{ns}	0.209^{ns}	0.368^{*}	-0.088^{ns}	0.608^{**}							
Φ_{PSII}	0.906^{**}	0.616^{**}	0.743^{**}	-0.130^{ns}	0.568^{**}	0.866^{**}	0.769^{**}	0.248^{ns}	0.816^{**}						
q_P	0.742^{**}	0.439^{*}	0.861^{**}	-0.049^{ns}	0.540^{**}	0.659^{**}	0.754^{**}	0.308^{ns}	0.856^{**}	0.923^{**}					
NPQ	-0.884^{**}	-0.716^{**}	-0.518^{**}	-0.241^{ns}	-0.475^{*}	-0.858^{**}	-0.781^{**}	-0.570^{**}	-0.781^{**}	-0.661^{*}	-0.486^{*}				
CAR	0.257^{ns}	0.269^{ns}	0.290^{ns}	-0.151^{ns}	0.128^{ns}	0.276^{ns}	-0.375^{*}	-0.098^{ns}	0.297^{ns}	0.802^{**}	0.753^{**}	-0.696^{**}			
Chl	0.194^{ns}	0.233^{ns}	0.285^{ns}	-0.158^{ns}	0.104^{ns}	0.210^{ns}	-0.384^{ns}	-0.102^{ns}	0.282^{ns}	0.930^{**}	0.953^{**}	-0.522^{**}	0.969^{**}		
DMA	0.375^{*}	0.317^{ns}	0.234^{ns}	0.115^{ns}	-0.005^{ns}	0.246^{ns}	-0.098^{ns}	0.111^{ns}	0.388^{*}	0.860^{**}	0.786^{**}	-0.636^{**}	0.018^{ns}	-0.009^{ns}	
Yield	0.086^{ns}	0.150^{ns}	-0.102^{ns}	-0.225^{ns}	-0.082^{ns}	0.140^{ns}	-0.079^{ns}	-0.087^{ns}	0.060^{ns}	0.920^{**}	0.855^{**}	-0.692^{**}	-0.126^{ns}	-0.085^{ns}	0.393^{*}

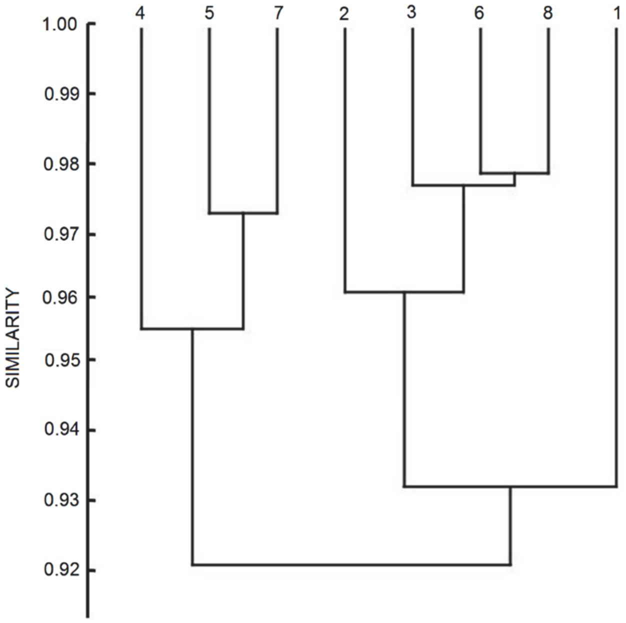

Fig. 4. Dendrogram showing the percentage of similarity between the *Dioscorea* species constructed using different photosynthetic parameters. Data are the mean of three replications ($n = 3$). 1 – *D. hispida*; 2 – *D. pentaphylla*; 3 – *D. bulbifera*; 4 – *D. hamiltonii*; 5 – *D. pubera*; 6 – *D. tomentosa*; 7 – *D. oppositifolia*; 8 – *D. alata.*

The *D. bulbifera, D. pentaphylla, D. tomentosa*, and *D. hispida* were in a separate cluster with the cultivated species *D. alata* and showed 93.7% similarity. The species which are within the same cluster are unique as they showed similar leaf photosynthetic traits. The wild species, such as *D. oppositifolia, D. hamiltonii*, and *D. pubera*, had superior photosynthetic efficiency compared to the cultivated species *D. alata* under prevailing environmental conditions.

Conclusion: The present study on comparative ecophysiological traits between wild and cultivated species of *Dioscorea* revealed that some wild species recorded superior photosynthetic efficiency and yield in comparison to the cultivated species. Environmental adaptation in wild *Dioscorea* species seems to be associated with leaf photosynthetic gas-exchange capacity, PSII activity leading to the better tuber yield. Taken together, the wild species, such as *D. oppositifolia*, *D. hamiltonii*, and *D. pubera*, had superior photosynthetic efficiency and tuber yield potential in comparison to the cultivated *D. alata*, which may determine the ecological dominance and the adaptability of the wild species under the future climate change. Further research is aimed to elucidate the genetic diversity in relation to leaf phenotyping and the use of superior wild *Dioscorea* species for crop improvement programs under a changing climate.

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