

Photosynthetic Responses of Two Groundnut Cultivars with Contrasting Drought Tolerance

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Abstract

Groundnut is frequently constrained by environmental conditions such as drought. Within this context, it is crucial to understand physiological mechanisms and identify specific physiological traits conferring drought tolerance. The objective of this study was to investigate photosynthetic responses and physiological changes of two groundnut cultivars (drought tolerant cv. K-134 and drought sensitive cv. JL-24) subjected to different regimes of water stress conditions for a duration of 12 days. A gradual reduction in leaf water potential (Ψ_L), leaf area, leaf dry mass accumulation (LDW), total chlorophyll (Chl) content, net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration rate (E) was observed. The magnitude of reduction was comparatively greater in sensitive cultivar (JL-24). In both cultivars, intercellular CO_2 concentration (C_i) was unaffected by mild stress but significantly elevated by severe stress. Water use efficiency (WUE) representing the mesophyll efficiency was greater in the tolerant cultivar K-134. The root length and dichlorophenol indophenol (DCPIP) reduction by photosystem II (PSII) were significantly decreased only at a severe stress in both cultivars. Our results indicated the involvement of stomatal and/or non-stomatal components in decline of photosynthesis and differed between cultivars. The relationship between water stress and this metabolism is presented in the light of differential physiological responses of the investigated cultivars.

Key words: Groundnut, Drought, Photosynthesis, Leaf area, Dry weight, P_N , g_s , WUE, PSII

Groundnut or peanut (*Arachis hypogea* L.) is one of the most important edible oil crops, and is also an important source of protein. It is cultivated predominantly in arid and semi-arid regions of the world, and often experiences drought stress conditions during its growth cycle leading to drastic reduction in productivity [1]. Consequently, genetic enhancement to maximize crop production per unit input of water has been major research. Drought stress effects on photosynthesis have been well demonstrated [2]. However, there is still disagreement over whether metabolic dysfunction or stomatal closure are the primary ways that drought reduces photosynthesis [3]. One of the initial responses to drought is stomatal closure, which can limit plant transpiration and CO_2 uptake, resulting in a reduction in photosynthesis [2], [4]. Stomatal closure has been suggested to be the primary factor contributing to reduced photosynthesis during mild to moderate drought [2-3]. Moreover, non-stomatal limitations such as photophosphorylation, RuBP regeneration, and Rubisco activity are impaired under severe stress [3], [5-6]. It has been established that PSII, the first protein complex in light-dependent processes, is susceptible to drought [7]. Investigating these patterns in a range of species may help to shed light on

the relationship between drought tolerance and differential limiting of the stomatal and nonstomatal components of photosynthesis under water stress. Physiological processes like CO_2 assimilation rate, nitrogen absorption, etc. might be better maintained by drought-tolerant cultivars of the same species under water deficit conditions [8]. Since plant photosynthetic activity is mostly responsible for plant growth and yield, several investigators believe that choosing cultivars or varieties based on photosynthetic traits may aid in the development of high-yielding and stress-tolerant crop cultivars [9-10]. Therefore, the aim of this study was to evaluate the effects of water stress on photosynthetic and physiological responses in two cultivars of groundnut, in order to better understand the mechanisms of drought tolerance and indicate promising materials for further use in a groundnut breeding program.

MATERIALS AND METHODS

Experimental design

Seeds of groundnut cultivars namely (K-134 and JL-24) were sown in earthen pots containing 8kg of red loamy soil and farm yard manure (3:1 proportion). Pots were maintained

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for one month in the departmental botanical garden under natural photoperiod of 10-12 h and temperature 28 ± 4 °C. One-month-old plants were then divided into four-sets and arranged in randomized complete block design. One set of pots received water daily to field capacity and served as control (100%). The remaining three sets received water daily to 75, 50 and 25% of the field capacity and were characterized as mild, moderate and severe stresses, respectively. Leaf samples were collected on day-12 after stress induction for analysis of various parameters.

Growth parameters

For the determination of dry mass, the leaves were dried at 80 °C in a hot air oven until a constant mass was formed. The length of the root was measured after inducing water stress. The leaf area of the expanding leaf (second leaf from the apex) was measured in a leaf area meter (*Licor* Li. 3000) in control and water stressed plants.

Plant water status

Leaf water potential was measured using a portable PR-55 psychrometer microvoltmeter with C-52 sample chamber. (Wescor, Logan, Utah, USA). The readings were measured between 8.00 to 10.00 AM. The measurements were the average of twenty discs to obtain a mean water potential for the leaf.

Leaf gas exchange measurements

Rate of photosynthesis, stomatal conductance, intercellular CO₂ concentration and the rate of transpiration were monitored by using a portable photosynthesis system (Infrared gas analyzer: LCA-3) equipped with a Parkinson leaf chamber (6.2 cm²), (PLC) (Analytical Development Co., Hoddesdon, U.K.). The measurements were made between 8.00 AM to 10.00 AM at photosynthetic photon flux density of approximately 1100 ± 100 μ mol m⁻² s⁻¹. The leaf temperature was ranged between 30 ± 2 °C. The measurements were done in the second leaf (fully expanded) from the top, since this leaf was found to possess maximum photosynthetic capacity [11]. Water use efficiency (WUE) was calculated as the ratio between net photosynthesis and transpiration [12]. Means of five individual estimations were taken from both control and stressed plants.

Biochemical determinations

The total chlorophyll content was estimated in the leaves according to the method [13], using 80% acetone extracts. The 1,6-dichlorophenol indophenol (DCPIP) reduction in isolated chloroplasts was estimated [14].

Statistical analysis

The data obtained in all parameters were subjected to analysis of variance (ANOVA) and the mean values were compared by Duncan's Multiple Range (DMR) test at 0.05% level as described [15].

RESULTS AND DISCUSSION

Plants that are experiencing a water stress will modify their growth pattern and structural dynamics, decrease transpiration loss by altering the stomatal conductance and distribution, roll their leaves, increase their root length, accumulate compatible solutes, increase transpiration efficiency, and postpone senescence [16]. Water potential can be regarded as an indicator to effectively assess water status of plants. In the present study, Ψ_L significantly declined (more negative values) with increase in stress intensity at all stress levels in both cultivars (Table 1). The Ψ_L of severe stressed

plants dropped to -1.60 and -1.16 MPa in cv. K-134 and cv. JL-24 respectively. Maintenance of low (more negative) Ψ_L in drought resistant cultivars has been reported to be an adaptation to water stress in groundnut [17-18] and other plants [6], [19] and as such K-134 seems to be drought tolerant. These results indicate that drought-tolerant cv. K-134 had some drought tolerance mechanism, such as greater uptake of water through roots or lower loss of water through transpiration, or more retention of water through osmotic adjustment [20]. There were no significant changes in root length of both cultivars during mild and moderate stress treatments (Table 1). However, at severe stress treatments the root length was reduced to 15% and 9% in cultivars JL-24 and K-134, respectively when compared to control. Our findings are consistent with those of a previous study that concluded the root growth of groundnut seedlings can be increased to a certain length by mild drought, but as the duration and intensity of the water stress increases, root growth and development will be severely inhibited [21]. In this study, groundnut may delay dehydration by increasing roots up to mild stress levels, and the crop's capacity to retain a healthy root structure under water stress may be a factor in its resistance to drought [22]. Although severe stress has caused inhibition in root length in both cultivars, cv. K-134 exhibited relatively lesser inhibition. This reduced growth under water stress may be ascribed to the declined Ψ_L as evidenced in our study, sufficiently enough to stop cell elongation or to dry soil conditions [21]. One of the most easily observable characteristics of plant leaves under drought stress is the decrease in leaf area, which directly affects plant photosynthesis and productivity. The values of leaf area decreased in both cultivars as the Ψ_L gradually decreased with the severity of treatment (Table 1-2). Due to slower leaf growth and a lower supply of carbohydrates, drought reduces the leaf area of groundnut leaves [18]. Our findings are consistent with those of a previous study that concluded that the length and width of drought-treated leaves were significantly shorter than that of control leaves, which might be the result of significant decreases in photosynthesis-related parameters, including photosynthetic rate, chlorophyll content and PS II activity [23]. Researchers speculated that water stress-induced inhibition of leaf growth can be viewed as an adaptive response because it limits the production of leaf area and eventually rates of transpiration in plants. Reduced transpiration may then prolong plant survival by extending the period during which essential soil-water reserves are available in the root zone [24]. Though both cultivars registered a decline in leaf area during water stress, the magnitude of inhibition was relatively less in the cultivar K-134 than cultivar JL-24 (Table 1). Similar genotypic variations were also reported [25]. Leaf dry weight can reflect the plant growth condition and can be considered as an indicator of drought degree. In this study, the LDW of cv. JL-24 and cv. K-134, declined significantly in the stress treatments, and the decline became greater with the increase in stress intensity. In mild, moderate and severe stress treatment, LDW decreased by 12.50%, 28.06%, and 49.91%, respectively, for cv. JL-24, and 9.58%, 22.5%, and 32.63%, respectively, for cv. K-134. This result suggested that cv. K-134 is more tolerant to drought than cv. JL-24. Groundnut cultivars with vigorous early growth, a relatively large biomass accumulation and capacity for remobilizing stored assimilates to reproductive sinks may be better adapted to drought stress [26]. The decreased leaf dry mass accumulation as a result of water stress may be attributed to both the reduced leaf area, P_N and chlorophyll content was observed in our investigation (Table 1-2), which is in agreement with earlier results [27-29]. It is well-known that photosynthetic pigments, particularly chlorophyll, are essential for

photosynthesis in plants. The decrease in total chlorophyll content (Chl) content is a commonly observed phenomenon under drought [30-32]. Similarly in the present study, the total

chlorophyll content was significantly decreased in mild, moderate and severe stress treatments in both cultivars, but with a greater degree of decline in JL-24 than in K-134 (Table 1).

Table 1 Effect of water stress on leaf water potential (Ψ_L) [-Mpa], root length [cm plant⁻¹], leaf area (cm²), leaf dry weight (LDW) (g plant⁻¹) and total chlorophyll content (Chl) [mg g⁻¹ FW] in two groundnut cultivars

Parameter	JL-24				K-134			
	Control	Mild	Moderate	Severe	Control	Mild	Moderate	Severe
Ψ_L	0.78a	0.87b	0.99c	1.16d	0.87a	1.02b	1.24c	1.60d
	(100)	(111.83)	(126.92)	(148.71)	(100)	(117.24)	(142.53)	(183.90)
	± 0.038	± 0.034	± 0.054	± 0.048	± 0.042	± 0.051	± 0.065	± 0.058
Root length	28.12a	29.09a	26.80a	24.58b	29.94a	31.15a	30.11a	27.47a
	(100)	(100.94)	(94.00)	(85.28)	(100)	(104.05)	(100.57)	(91.78)
	± 0.28	± 0.24	± 0.35	± 0.59	± 0.34	± 0.22	± 0.48	± 0.51
Leaf area	33.21a	32.02a	26.83b	23.12c	31.57a	30.63a	28.89a	25.37b
	(100)	(96.42)	(80.79)	(69.62)	(100)	(97.04)	(91.50)	(80.37)
	± 0.53	± 0.48	± 0.67	± 0.59	± 0.28	± 0.35	± 0.52	± 0.58
LDW	1.078a	0.9432b	0.7755c	0.5400d	0.6872a	0.6214b	0.5326c	0.4217d
	(100)	(87.50)	(71.94)	(50.09)	(100)	(90.42)	(77.50)	(67.37)
	± 0.036	± 0.058	± 0.064	± 0.048	± 0.029	± 0.047	± 0.042	± 0.040
Chl	1.887a	1.636b	1.234c	0.768d	1.692a	1.512b	1.263c	0.938d
	(100)	(86.73)	(65.42)	(40.72)	(100)	(89.37)	(74.67)	(55.47)
	± 0.062	± 0.084	± 0.049	± 0.072	± 0.064	± 0.058	± 0.077	± 0.069

Means from 5 experiments ± SD. The mean values in a row followed by a different letter for each plant species are significantly different ($P \leq 0.05$) according to Duncan's multiple range (DMR) test. Figures in parentheses represent per cent of control

Table 2 Effect of water stress on net photosynthetic rate, (P_N) [μ mol CO₂ m⁻² s⁻¹], stomatal conductance (g_s) [m mol H₂O m⁻² s⁻¹], intercellular CO₂ concentration (C_i) (m mol m⁻² s⁻¹), transpiration rate (E) [m mol H₂O m⁻² s⁻¹], water use efficiency (WUE) [m mol CO₂ mol⁻¹ H₂O] and PS II activity (DCPIP reduction) [mmol kg⁻¹(Chl) s⁻¹] in two groundnut cultivars

Parameters	JL-24				K-134			
	Control	Mild	Moderate	Severe	Control	Mild	Moderate	Severe
P_N	22.34a	16.76b	10.79c	3.92d	21.86a	18.05b	12.72c	7.70d
	(100)	(75.02)	(48.32)	(17.56)	(100)	(82.57)	(58.16)	(35.23)
	± 1.08	± 1.45	± 0.78	± 1.22	± 1.06	± 1.73	± 1.61	± 1.41
g_s	702a	529b	338c	123d	674a	538b	377c	194d
	(100)	(75.36)	(48.23)	(17.56)	(100)	(79.84)	(55.94)	(28.76)
	± 28.91	± 36.82	± 42.01	± 39.79	± 25.40	± 29.12	± 34.18	± 40.12
C_i	254a	256a	264a	309b	248a	250a	256a	287b
	(100)	(100.79)	(103.94)	(121.65)	(100)	(100.80)	(103.22)	(115.72)
	± 6.5	± 5.8	± 4.2	± 5.9	± 4.6	± 8.2	± 6.9	± 7.8
E	9.2a	7.5b	5.5c	3.3d	8.9a	7.5b	5.9c	4.2d
	(100)	(81.62)	(59.76)	(35.41)	(100)	(84.78)	(66.45)	(46.80)
	± 0.25	± 0.28	± 0.21	± 0.28	± 0.21	± 0.27	± 0.26	± 0.29
WUE	2.42	2.23	1.96	1.18	2.45	2.40	2.15	1.83
	(100)	(92.56)	(80.99)	(48.76)	(100)	(97.96)	(88.55)	(74.68)
	± 0.32	± 0.29	± 0.28	± 0.44	± 0.19	± 0.28	± 0.41	± 0.28
PSII	24.34a	23.04a	22.21a	10.56b	24.96a	24.11a	23.13a	12.01b
	(100)	(94.65)	(91.39)	(43.38)	(100)	(96.59)	(92.67)	(48.12)
	± 0.32	± 0.29	± 0.28	± 0.44	± 0.19	± 0.28	± 0.41	± 0.28

Means from 5 experiments ± SD. The mean values in a row followed by a different letter for each plant species are significantly different ($P \leq 0.05$) according to Duncan's multiple range (DMR) test. Figures in parentheses represent per cent of control

Decrease in Chl content was attributed to suppression of specific enzymes responsible for synthesis of Chl and to disarrangement of pigment-protein complexes, and disruption of fine structure of chloroplasts was reported [33]. The decrease of chlorophyll under water stress may be also due to decreased rate of its synthesis or enhanced chlorophyllase activity [34]. Chlorophyll loss is a negative consequence of plant stress on plants, but it is also viewed as an adaptive feature because it decreases light harvesting and the risk of further damage to the photosynthetic apparatus from activated oxygen radicals in the case of excess excitation energy [35]. Chlorophylls are the most important physiological markers of drought tolerance for the evaluation in groundnut [25], and as such cv. K-134 seems to be relatively drought tolerant. Contrarily, studies have also

demonstrated that plants that the chlorophyll contents of plants with higher drought tolerance increases with increasing severity of stress [36]. Net CO₂ assimilation rate or net photosynthetic rate (P_N) is an important index to measure vegetation photosynthesis and it was almost unaltered and ranged between 21.69 to 22.34 μ mol CO₂ m⁻² s⁻¹ in control leaves of both cultivars. In general water stress caused decrease P_N in both cultivars throughout the experimentation (Table 2). Compared to that of the well-watered group, the P_N values of the mild, moderate and severe stress treatments decreased by 24.98%, 51.68% and 82.44%, respectively for cv. JL-24, and 17.43%, 41.84%, and 64.77%, respectively, for cv. K-134. In several cases the P_N under stress conditions has been suggested as one of the indices to determine the genotypic tolerance to

drought and a positive correlation was established between the better photosynthetic rate and drought tolerance potentials in groundnut [9-10], [37-38] and other plants [7], [29-30], [39]. The drought tolerance was well correlated with their capacity to maintain relatively high P_N under drought stress. Our data suggested that it was the ability of the cv. K-134 to efficiently utilize the available Ψ_L and leaf area to maintain significantly higher P_N during water deficit, which conferred drought tolerance. Similar to the response of P_N to water stress, g_s decreased substantially in both cultivars at all stress regimes (Table 2). The per cent decrease was more in the cultivar JL-24 (82.44%) and less in cultivar K-134 (71.24%) at the end of experiment. Since stomatal closure is one of the early responses to water stress and a key factor in the limiting of photosynthesis, g_s control is thought to be a key mechanism regulating plant responses to water stress. [5]. It was speculated that this may be one of the important reasons why cv-134 was capable of maintaining a higher P_N under drought stress. Under conditions of sufficient water supply, the transpiration rate often correlates with the incident solar radiation. However, drought stressed plants transpire less than unstressed plants. A decrease in transpiration (E) along with increasing in water stress and over time was gradual, and less in the cultivar K-134 than in JL-24 (Table 2). Genotypic variation in stomatal conductance to water stress has been demonstrated by several investigators in groundnut [9-10], [23-25], [38] and other plants [7], [9-10], [29], [39]. Through control of both water vapor loss (transpiration) and CO_2 absorption, or carbon assimilation, stomata play a significant role in photosynthesis. Plants usually show a parallel decrease between g_s and P_N with increased drought [40]. A strong correlation between stomatal conductance and photosynthetic rate seems to represent an adjustment of stomatal conductance to match the intrinsic photosynthetic capacity [41] as showed in the present study in both groundnut cultivars under water stress. The C_i values were almost unaltered under mild stress and only slightly increased (not significant) under moderate stress. However, they were significantly increased under severe stress in both cultivars indicating a decreased carboxylation efficiency. A decline in g_s and P_N without a corresponding decline in intercellular CO_2 concentration normally has been interpreted as a documentation of a non-stomatal effect of water stress on the photosynthetic process [42]. In the present study, partial stomatal closure at moderate water stress did not cause a decline in C_i in both cultivars, which suggested that at this level of drought stress, stomatal constraints prevailed over the non-stomatal effects. Severe stress treatments resulted an increase in C_i in both cultivars; this may indicate a decreased carboxylation efficiency (non stomatal limitation prevailed under severe stress). The increased C_i under water stress might may be due to the effects of stress on the CO_2 fixation machinery or to stomatal control through the alternation in the stomatal aperture [43]. Further, the increase in C_i was relatively less in K-134 (Table 2), reflecting a better maintenance of carboxylation. The most significant element that manifests initially when plants are under drought stress is water use efficiency (WUE) hindrance, which differs for varieties and cultivars [44]. Plants reduce stomatal density and leaf size during drought to minimize water loss and preserve the internal water balance [45] and due to their susceptibility to drought and inability to adapt to their environment, a number of genotypes and cultivars had poor WUE [46]. Difference in water use efficiency were demonstrated among cultivars and within species by many investigators [27-28], [44], [47] and an increase in WUE was evident under water stress conditions, and a better WUE was noticed in the drought tolerant cultivars. The obtained WUE

value in water-stressed groundnut cultivars was lower than controls (Table 2). These results are in agreements with the earlier reports [27-28]. Relatively a better WUE was observed in cultivar K-134 than in JL-24 (Table 2), further supports drought tolerant nature of K-134. The limiting effect on P_N by non-stomatal factors can be attributed to inhibition of the thylakoid-mediated electron transport activity, implicating a decrease in photosystem activities [49] and inhibition of *Ribulose-1,5-bisphosphate carboxylase/oxygenase activity (Rubisco)* [38]. Yet according to previous reports [50] the pattern displayed by the Mehler reactions indicated that, in general, PSII was more affected than PS1, probably because the photosystems are connected to metabolic pathways participating in dissipation of excess energy [51]. Water stress effects directly the photochemical events largely by affecting PS II activity both by degradation of D_1 and D_2 proteins of PS II reaction center and retarded synthesis of these proteins which lead to lowered proteins [52]. However, some investigations confirm the drought tolerant-nature of PSII [39]. In the present study, a significant inhibition of electron transport as evidenced by DCPIP reduction was observed only under severe stress (Table 2), and a greater magnitude of inhibition of PSII activity was noticed in cv. JL-24 than in cv. K-134. These findings indicated that severe stress damaged the PSII reaction center and decreased the electron transfer efficiency, which is in agreement with earlier results [7], [29]. Variation among genotypes in response of PS II activity to drought has been found in a number of crop species, including maize [6] and groundnut [53], which could be exploited as trait for selection to drought tolerance.

CONCLUSION

The present study indicates that all the investigated parameters were affected during water stress. The reduction in leaf dry weight was due to decreased leaf extension as well as decreased P_N including a decline in Ψ_L and chlorophyll content. The g_s and E changed in parallel with P_N , indicating that P_N was greatly affected by g_s . Reduced P_N as a response to the decrease in the Ψ_L was modulated by stomatal and non-stomatal components, an effort largely determined by the severity of stress. Genetic variability in groundnut cultivars was associated with maintenance of plant water status. The drought tolerance of cv. K-134 could be ascertained from the present study, based on relatively lesser decrease in P_N and g_s coupled with better C_i and WUE. This study can provide a theoretical basis and reference for the selection of groundnut cultivars to breed and cultivate against drought stress.

Conflicts of interest

The authors declare no conflict of interest.

Authors' contributions

KVM: Performed the research, collected data, analyzed the data, writing -original draft preparation CS: Designed and supervised the study, writing- reviewing and editing. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

Ψ_L : Leaf water potential

cv.: Cultivar
LDW: Leaf dry weight
P_N: Net photosynthetic rate or net CO₂ assimilation rate
g_s: Stomatal conductance
E: Transpiration rate

Ci: Intercellular CO₂ concentration
WUE: Water use efficiency
PSII: Photosystem II activity (DCPIP reduction)
Chl: Total chlorophyll content
Rubisco: *Ribulose-1,5-bisphosphate carboxylase/oxygenase*

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