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Nutrient uptakes and their contributions to yield in peanut genotypes with different levels of terminal drought resistance

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Abstract: Different peanut yields under terminal drought might be due to the different nutrient uptakes among peanut genotypes. Nutrient uptake was presumed to be a drought-resistant trait and might involve drought tolerance mechanisms. The aims of this study, therefore, were to characterize the effect of terminal drought on peanut nutrient uptake and to investigate the genotypic variability of nutrient uptake and its interactions with terminal drought. Field experiments were conducted at the Field Crop Research Station of Khon Kaen University, Khon Kaen, Thailand, from October 2010 to January 2011 and October 2011 to January 2012. Six peanut genotypes were tested under well-watered and terminal drought conditions. Data were recorded for N, P, K, Ca, and Mg uptake and biomass (BM) and pod yield (PY); the ratio of nutrient uptake under stress condition was calculated. Terminal drought significantly reduced nutrient uptake in both years, and peanut genotypes differed considerably with respect to nutrient uptakes under well-watered and terminal drought conditions. ICGV 98324 and ICGV 98348 were the best genotypes for nutrient uptake under terminal drought. Tainan 9 and Tifton 8 had low nutrient uptake under both conditions. ICGV 98308 and Tifton 8 had medium uptake and Tainan 9 had the lowest. Significant correlations between nutrient uptakes and BM and PY were mostly observed under well-watered and drought conditions. Based on nutrient uptake, ICGV 98324 and ICGV 98348 were identified as drought-tolerant lines. These genotypes could maintain high nutrient uptakes across water regimes; consequently, these traits can also be used as efficient tools for selecting peanut genotypes with terminal drought tolerance.

Key words: Arachis hypogaea L., water stress, genotype, drought tolerance, mineral nutrients, relationship

1. Introduction

Peanut (*Arachis hypogaea* L.) is an important cash crop legume and a rich source of oil (40%–50%) and protein (20%–40%). Since it is mainly grown as a rainfed crop, drought is the most limiting factor, resulting in low yields in many parts of the world (Reddy et al., 2003; Songsri et al., 2008). Frequent failure of rains late in the season has resulted in decreased yield and poor quality peanuts (Kambiranda et al., 2012). Drought during the pod-filling phase of peanut is common and causes the greatest reduction in peanut pod yield (Nageswara Rao et al., 1985; Ravindra et al., 1990). In recent research, Girdthai et al. (2010) reported that terminal drought or end of season drought reduced pod yield (PY) by up to 35% and biomass (BM) by 21%.

In previous studies, yield was used as a drought resistance trait, but it was characterized by low heritability and high genotype × environment interaction (Wright et al., 1996; Richards et al., 2001; Pimratch et al., 2008). Wallace et al. (1993) suggested that indirect selection for yield is most effective when applied to traits that already integrate most of the genetic and environmental effects that lead to yield. More rapid progress may be achieved by using physiological and morphological traits (Nigam et al., 2005). Several physiological and morphological traits that have been associated with drought stress adaptation have been observed and used so far. Physiological traits such as SPAD chlorophyll meter reading, specific leaf area (Wright and Nageswara Rao, 1994; Arunyanark et al., 2009), biological N_2-fixation (Pimtrach et al., 2008; Htoon et al., 2009), and root length density (RLD) (Songsri et al., 2008; Jongrungklang et al., 2011) have been used as surrogate traits and they could increase plant potential in a breeding scheme. Nonetheless, there is still a need to explore other mechanisms or traits to investigate the underlying mechanisms of drought tolerance in peanut.

The growth of peanut plants depends on the supply of nutrients. Most of the plant's nutrients, besides carbon,

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hydrogen, and oxygen, originate from the soil (Marschner, 1986). Drought is deleterious for plant growth, yield, and mineral uptake (Suther and Patel, 1992) and cultivars differ in their responses to environmental stress at different growth stages (Garg, 2003; Gunes et al., 2006). Under water-stressed conditions, there is a reduction in total nutrient uptake, followed by a reduction in mineral nutrient concentrations in crop plants, due to the decreased soil moisture (Baligar et al., 2001; Gunes et al., 2006). Fageria et al. (2002) indicated that drought stress may involve the uptake of mineral elements in plant tissues by affecting root growth, nutrient mobility in soil, and nutrient uptake. Similarly, Kulkarni et al. (1988) observed that N, P, and K uptake in peanut were reduced by drought stress. In a study carried out by Kolay (2008), water stress at flowering, pegging, pod formation, and pod development stages of peanut cultivar CG-2 reduced pod yields, and it also affected N, P, K, Ca, Mg, and S uptake.

Girdthai et al. (2010) revealed the differences among peanut genotypes for total BM and PY under terminal drought over the course of 2 years. They observed that Tifton 8 had the highest total BM and PY under well-watered and terminal drought conditions (Vorasoot et al., 2003; Girdthai et al., 2010). Girdthai et al. (2010) also described the response of each peanut genotype with a drought tolerance index (DTI), which was calculated as the ratio of stressed to nonstressed conditions. ICGV 98324 had a high DTI for total BM in both years, whereas ICGV 98348 also had a high DTI for PY across both years. ICGV 98308 had low DTI for PY. Tainan 9 performed poorly for these traits under terminal drought and had the highest reduction in total BM. Such genotypic variability of peanut in yield is important in peanut breeding programs. Samarah et al. (2004) stated that nutrient uptake in soybean under drought stress might have an important role in drought tolerance mechanisms. Therefore, yield difference under terminal drought may be due to the different nutrient uptake of peanut under limited soil moisture. Despite our increased understanding of stress physiology, so far there is no information on the nutrient uptake in peanut plants during terminal drought. Information is also lacking on the response of peanut genotypes to nutrient uptakes under terminal drought and whether the stability of nutrient uptake contributes to drought resistance and yield in peanut. Gunes et al. (2006) reported that chickpea cultivars exhibiting smaller reductions in nutrient uptake and efficiency should be presumed to be drought-resistant, and nutrient uptake efficiency involves drought tolerance mechanisms. Genotypic variability in the nutrient uptake of peanut genotypes is crucially important for selection and this mechanism can be used as a potential selection criterion for drought tolerance in peanut. This information should improve understanding of how peanut genotypes could achieve high yield under terminal drought and could have important implications on breeding for drought resistance in peanut. Therefore, the aims of the current study were to characterize the effect of terminal drought on nutrient uptakes and to investigate the genotypic variability and the genotypes' interaction with terminal drought with regard to nutrient uptake.

2. Materials and methods

2.1. Experimental design and plant materials

The field experiments were conducted at the Field Crop Research Station of Khon Kaen University, Thailand, from October 2010 to January 2011 and from October 2011 to January 2012. Soil type at the field site has been classified as Yasothon soil series (sand, Oxic Paleustults) (Table 1). The experimental design was a split plot in a randomized complete block design with 4 replicates. Plot size was 5 × 5 m with 50 cm of spacing between rows and 20 cm between plants. Main plot treatments were well watered and terminal drought conditions lasted from the R7 growth stage (Boote, 1982) to harvest. For the well-watered treatment, water was applied regularly from seed sowing until harvest. Similarly, terminal drought treatment subplots received regular water treatment before the R7 growth stage, but afterwards, irrigation was withheld in order to initiate the drought conditions, which were maintained from R7 until harvest. Drought conditions were defined as one-third of the available water (1/3 AW) of soil moisture, or terminal drought (Girdthai et al., 2010).

Table 1. Physical and chemical properties of the soil at the depth of 0–30 cm in the experimental fields of 2010/2011 and 2011/2012.

Properties	2010/2011	2011/2012
Texture class	Sand	Sand
Sand [2.0–0.05 (%)]	85.08	83.98
Silt [0.05–0.002 (%)]	7.30	8.32
Clay [<0.002 (%)]	7.62	7.70
pH (1:1 H_20)	6.08	6.18
EC (1:5 H_20) (dS/m)	0.03	0.05
CEC (cmol kg^{-1})	5.22	5.93
OM (%)	0.44	0.41
Total N (mg kg^{-1})	185.00	203.00
Available P (mg kg^{-1})	23.95	40.74
Exchangeable K (mg kg^{-1})	33.09	38.34
Exchangeable Ca (mg kg^{-1})	418.33	446.67

Subplot treatments consisted of 6 peanut genotypes: ICGV 98308, ICGV 98324, ICGV 98348, Tainan 9, Tifton 8, and a nonnodulating line, which was used as a control variety for N_2-fixation. ICGV lines were from ICRISAT and they were identified as drought-resistant lines with different DTIs (Girdthai et al., 2010).

2.2. Crop cultivation

Land preparation was done by plowing the field 3 times and incorporating lime ($CaCO_3$) at a rate of 625 kg ha^{-1}. Both P and K fertilizer were incorporated into the top soil at the rate of 24.7 kg P ha^{-1} and 31.1 kg K ha^{-1} shortly prior to planting. Three to 4 seeds were sown per hill by hand. After germination, they were thinned to 1 plant per hill. In order to increase the *Rhizobium* population in the soil, *Rhizobium* inoculation was done by applying a water-diluted commercial peat-based inoculum of *Bradyrhizobium* (mixture of strains THA 201 and THA 205; Department of Agriculture, Ministry of Agriculture and Cooperatives, Bangkok, Thailand) after planting at the rate of 13 g kg seed^{-1} in each plot. Gypsum ($CaSO_4$) at the rate of 312 kg ha^{-1} was applied at 40 days after emergence. Normal practices were performed to control weeds, diseases, and insects (Koolachart et al., 2013).

2.3. Irrigation

A subsurface drip irrigation system was installed with a spacing of 50 cm midway between peanut plant rows to supply water. Drip lines with a distance of 20 cm between emitters were installed 10 cm below the soil surface and fitted with a pressure valve and water meter to make sure that the water supply was efficient and uniform across each plot. Subvalves were set up for each water-stressed genotype, i.e. at each subplot, to individually monitor the water supply to respective genotypes in order to get the predetermined water-stressed level. For the well-watered treatment, water was applied daily from planting to harvest, but the growth stages of plants were checked regularly in water-stressed plots in order to determine the right time at which terminal drought treatment should be given. In general, the drought treatment was initiated at 15–20 days before the R7 growth stage. The times of treatment initiation were different within genotypes according to growth stages of peanut genotypes, the data from preliminary trials, and the simulated data of Girdthai et al. (2010). At the terminal drought plots, irrigation was withheld and soil moisture was allowed to decrease gradually to meet the drought condition at the R7 growth stage of each genotype. From then on, drought conditions were maintained until harvest. Rainout shelters were used to protect the water-stressed plots from unseasonal rain at 90–93 days after planting in 2011–2012.

In order to maintain the specific water regimes, the amount of water that was applied was based on crop water requirements using the methodology of Doorenbos and Pruitt (1992) along with water loss from surface evaporation as calculated by Singh and Russell (1981).

2.4. Weather parameters

Relative humidity (%), water evaporation (mm), rainfall (mm), maximum and minimum air temperature (°C), and solar radiation (MJ m^{-2} day^{-1}) were recorded daily from sowing until harvest by a weather station located 100 m away from the experimental field. Weather data are presented in Figure 1.

2.5. Soil properties, moisture content, and plant water status

The physical and chemical properties of the soil in all treatments and replications were determined before planting. Before planting, soil samples were taken from 5 points per main plot at the depths of 0–5, 5–15, and 15–30 cm. After mixing and bulking, the representative soil samples were analyzed to determine their physical and chemical properties. Data are presented in Table 1. In addition, water-holding capacity, field capacity, and permanent wilting point were also determined with a pressure plate method. Data are presented in Table 2.

Soil moisture was monitored gravimetrically at depths of 0–5, 10–15, 25–30, 40–45, and 55–60 cm at planting, the day irrigation was withdrawn, the R7 growth stage, and harvest. Jongrungklang et al. (2012) reported that soil depths of 0–30 and 0–60 cm contained 50%–66% and 74%–95% of peanut RLD, respectively. Soil moisture was averaged for soil depths of 0–30 and 0–60 cm. Data are presented in Table 2. Relative water content (RWC) was used to evaluate plant water status and it was measured following Kramer (1980): at the day irrigation was withdrawn, at the R7 growth stage, and at harvest. RWC was measured in 1 leaflet of the second fully expanded leaf from the top of the main stem of 5 plants for each plot at 1000–1200 hours (Clavel et al., 2006; Girdthai et al., 2010). These leaflets were put into a vial with a rubber stopper and the vial was sealed with Parafilm. The vials were immediately placed inside an ice box to prevent moisture loss. After measuring the field weights, the leaflets were soaked in distilled water for 8 h and turgid weights were determined again. These leaflets were then oven-dried at 80 °C for 48 h or until the dry weight became constant. Finally, RWC was determined as follows:

$$\text{RWC } (\%) = [(\text{FW} - \text{DW}) / (\text{TW} - \text{DW})] \times 100,$$

where FW is sample field weight, TW is sample turgid weight (saturated weight), and

DW is sample dry weight. Data are presented in Figure 2.

2.6. Biomass and pod yield

Upon reaching full maturity (R8), plants in an area of 8 m^2 in each plot (excluding the border) were harvested and leaf, stem, and pods were separated. These plant parts were oven-dried at 80 °C for 48 h or until the dry weight

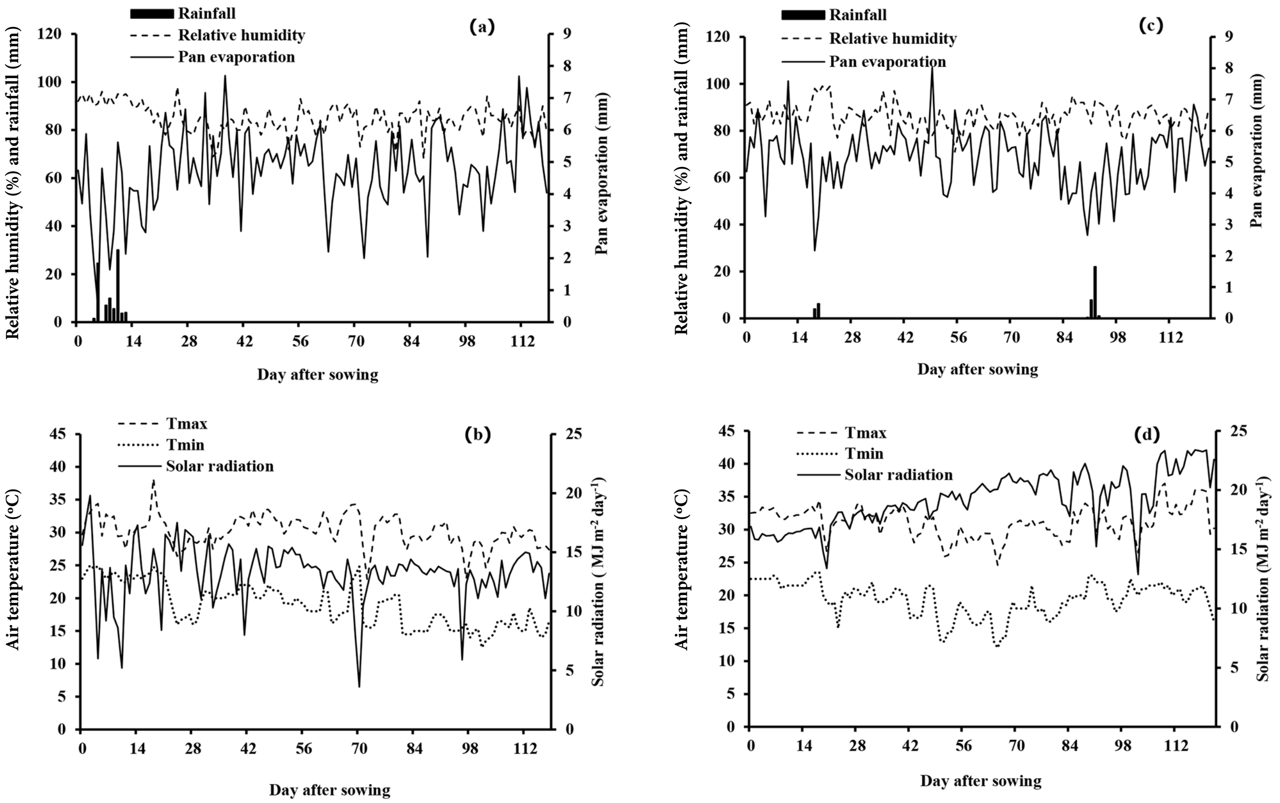

Figure 1. Rainfall, relative humidity (RH), evaporation (E_0), maximum (Tmax) and minimum (Tmin) temperatures, and solar radiation from October to January 2010/2011 (a, b) and 2011/2012 (c, d) at the meteorological station of Khon Kaen University, Thailand.

Table 2. Soil moisture percentage (%) at sowing, the last day of irrigation, the R7 growth stage, and harvest at 0–30 cm and 0–60 cm under well-watered and terminal drought conditions in 2010/2011 and 2011/2012.

Year	Treatments	Soil depth (cm)	Soil moisture percentage (%)			
			Sowing	Last day of irrigation	R7 stage	Harvest
2010/2011	Well-watered	0–30	10.51	9.91	9.74	10.25
	Terminal drought	0–30	10.24	9.87	6.16	6.21
	Well-watered	0–60	10.13	8.77	8.64	9.61
	Terminal drought	0–60	10.26	8.47	5.91	6.43
2011/2012	Well-watered	0–30	10.88	10.84	10.99	10.92
	Terminal drought	0–30	10.52	10.54	6.11	6.09
	Well-watered	0–60	10.81	10.63	10.83	10.76
	Terminal drought	0–60	10.42	10.42	6.12	6.44

2010/11; FC = 10.14%, PWP = 4.47, 1/3 AW = 6.33 using pressure plate method.
2011/12; FC = 10.18%, PWP = 4.50, 1/3 AW = 6.37 using pressure plate method.
FC: Field capacity, PWP: permanent wilting point, AW: available water.

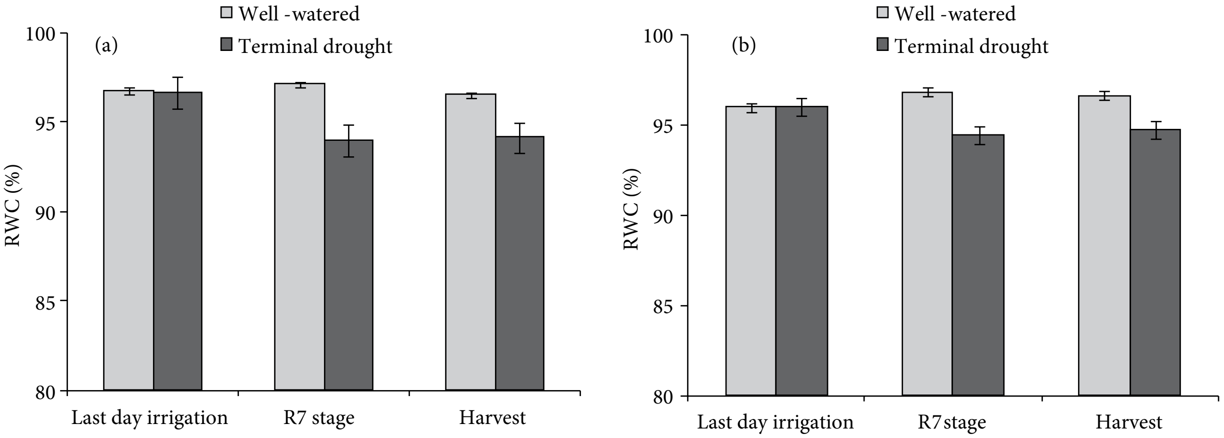

Figure 2. Relative water content (RWC) at the last day of irrigation, the R7 growth stage, and the harvest stage of 6 peanut genotypes grown under well-watered and terminal drought conditions in 2010/2011 (a) and 2011/2012 (b).

became constant and their dry weights were recorded. The pods were removed from the plants, air-dried to obtain approximately 8% moisture content, and hand-shelled. BM production was calculated as the sum of the dry weight of shoots and pods.

2.7. Plant nutrient analysis

After recording the dry weight of BM and PY, the dried leaves, stems, shells, and seeds were ground using a hammer mill. In this case, dry leaf and stem samples were proportionally taken according to the leaf and stem dry weight ratio. Individual nutrients were then analyzed for each shoot, shell, and seed. Nitrogen content was measured using the automated indophenol method (Schuman et al., 1973; Pimratch et al., 2008) and was read on a flow injection analyzer (model 5012, Tecator Inc., Hoganas, Sweden).

Total phosphorous was determined by spectrophotometer and total potassium was measured by flame photometer (Kaewpradit et al., 2009). Total Ca and Mg were determined by atomic absorption spectroscopy (Al-Karaki and Al-Raddad, 1997). Finally, nutrient uptake (g plant^{-1}) was calculated individually by multiplying dry weight and nutrient concentration.

Ratio of nutrient uptake under stress conditions (RNS) was calculated as follows:

$$\text{RNS} = \frac{\text{nutrient uptake in terminal drought}}{\text{nutrient uptake in well-watered condition}}.$$

2.8. Data analysis

The data were subjected to analysis of variance according to a split-plot design (Gomez and Gomez, 1984) and all calculations were performed using MSTAT-C (Bricker, 1989). Combined analyses of variance were done for those characters where error variances for the 2 years were homogeneous. Due to the significance of year × genotype interaction for uptake of N and K and water regime × genotype interaction (Table 3), data from each year and each water regime were analyzed and presented separately according to a randomized complete block design, and Duncan's multiple range test was used to compare means (Gomez and Gomez, 1984) (Tables 4 and 5). Correlation coefficients between nutrient uptake and BM and PY were calculated separately for each genotype in each water regime for each replication to assess their relationship (Table 6).

3. Results

3.1. Meteorological conditions, soil properties, and plant water stress

The 2 experiments were conducted from October 2010 to February 2011 and from October 2011 to February 2012. There was no rainfall during the drought-stress period in 2010/2011, whereas total rainfall during the drought-stress period in 2011/2012 was 30.2 mm. Since rainout shelters were used to protect the drought-stressed main plots from rain, there was no interference from rain in 2011/2012. Mean air temperatures ranged from 18.92 to 30.25 °C and 19.38 to 31.15 °C during 2010/2011 and 2011/2012, respectively (Figure 1).

Soil properties analyzed in 2010/2011 and 2011/2012 are described in Table 1. Physical properties were not much different between the 2 years. Soil pH values (1:1 H_2O) in 2010/2011 and 2011/2012 were 6.08 and 6.18, respectively. Total N in 2011/2012 (203.00 mg kg^{-1}) was higher than in 2010/2011 (185.00 mg kg^{-1}). Similarly, higher available P (mg kg^{-1}), exchangeable K, and exchangeable Ca were observed in 2011/2012 (Table 1). Soil moisture percentages at the soil depths of 30 cm and 60 cm at sowing, last day of irrigation, R7 growth stage, and harvest under well-watered and terminal drought conditions are presented in Table 2.

Table 3. Mean square from the combined analyses of variance for N, P, K, Ca, and Mg uptake of 6 peanut genotypes grown under well-watered and terminal drought conditions at harvest stage in dry seasons of 2010/2011 and 2011/2012.

Source of variance	df	Mean square				
		N	P	K	Ca	Mg
Year (Y)	1	174,331*	1912*	47,945*	18,532*	7530*
Reps within Y (Y × R)	6	58,693.2	739	2160	2248	301
Water regimes (W)	1	6,049,642**	190,991**	463,371**	330,909**	43,337**
Y × W	1	109,561	19	2633	27,387	1308
Error Y × R × W	6	52,689.9	924	13,225	29,858	2049
Genotypes (G)	5	2,615,037**	117,521**	260,945**	217,189**	43,345**
Y × G	5	178,826*	1318	51,296*	31,740	2402
W × G	5	1,119,136**	10,606**	170,274**	118,733**	17,324**
Y × W × G	5	31,499.6	557	6878	28,025	879
Error Y × R × W × G	60	64,898.4	808	18,057	23,410	1534

*, ** = Significant at $P < 0.05$ and $P < 0.01$, respectively.
df = Degrees of freedom.

Table 4. The effect of terminal drought stress on N, P, and K uptake and RNS of 6 peanut genotypes under well-watered and terminal drought conditions in 2010/2011 and 2011/2012, respectively.

Genotype	N g plant^{-1}			P g plant^{-1}			K g plant^{-1}		
	Well-watered	Drought	N-RNS	Well-watered	Drought	P-RNS	Well-watered	Drought	K-RNS
2010/2011									
ICGV 98308	3.70a	2.34ab	0.63c	0.35b	0.21bc	0.61b	1.30a	0.83b	0.64b
ICGV 98324	2.77b	2.61a	0.94a	0.27c	0.22b	0.83a	1.17ab	0.84ab	0.71b
ICGV 98348	2.46b	2.62a	1.06a	0.27c	0.22b	0.82a	1.01c	0.98a	0.97a
Tainan 9	2.60b	1.53c	0.59c	0.27c	0.15d	0.58b	1.05bc	0.59c	0.56b
Tifton 8	2.65b	2.01b	0.76b	0.27c	0.19cd	0.69ab	0.86d	0.73bc	0.85ab
Nonnodulating	1.75c	1.41c	0.81b	0.44a	0.32a	0.73ab	1.19ab	0.82b	0.69b
Mean	2.66	2.09	0.80	0.31	0.22	0.71	1.10	0.80	0.74
2011/2012									
ICGV 98308	2.36a	1.34b	0.57c	0.25b	0.14b	0.54b	1.94a	0.77bc	0.40c
ICGV 98324	1.96ab	1.64a	0.84b	0.19c	0.14b	0.73b	1.42b	1.01a	0.71b
ICGV 98348	1.38cd	1.77a	1.28a	0.13d	0.14b	1.06a	0.97c	0.93a	0.96a
Tainan 9	1.77bc	0.91c	0.52c	0.18cd	0.10c	0.53b	1.30b	0.62d	0.48c
Tifton 8	1.74bc	1.25b	0.72bc	0.17cd	0.09c	0.56b	1.31b	0.70cd	0.54bc
Nonnodulating	1.18d	0.87c	0.74bc	0.42a	0.21a	0.50b	1.46b	0.90ab	0.62b
Mean	1.73	1.30	0.78	0.22	0.14	0.65	1.40	0.82	0.62

Different letters adjacent to data in the same column show significance at $P < 0.05$ by Duncan's multiple range test.

Table 5. The effect of terminal drought stress on Ca and Mg uptake and RNS of 6 peanut genotypes under well-watered and terminal drought conditions in 2010/2011 and 2011/2012, respectively.

Genotype	Ca g plant^{-1}			Mg g plant^{-1}		
	Well-watered	Drought	Ca-RNS	Well-watered	Drought	Mg-RNS
2010/2011						
ICGV 98308	1.82a	1.10b	0.60c	0.57a	0.38ab	0.66b
ICGV 98324	1.81a	1.34a	0.74b	0.47b	0.43a	0.92a
ICGV 98348	1.38c	1.37a	0.99a	0.37c	0.33bc	0.90a
Tainan 9	1.53bc	1.00b	0.65c	0.39c	0.26d	0.68b
Tifton 8	1.80a	1.40a	0.78ab	0.46b	0.31	0.66b
Nonnodulating	1.76ab	1.46a	0.83ab	0.51ab	0.41a	0.81ab
Mean	1.68	1.28	0.77	0.46	0.35	0.77
2011/2012						
ICGV 98308	1.56a	0.70c	0.45d	0.41a	0.21b	0.52b
ICGV 98324	1.27b	0.89ab	0.70c	0.33b	0.27a	0.81b
ICGV 98348	0.76c	1.01a	1.33a	0.21c	0.23ab	1.08a
Tainan 9	1.12b	0.70c	0.62cd	0.27bc	0.17c	0.62b
Tifton 8	1.24b	1.05a	0.85b	0.28b	0.17c	0.59b
Nonnodulating	1.25b	0.83bc	0.66cd	0.33b	0.23ab	0.71b
Mean	1.20	0.86	0.77	0.31	0.21	0.72

Different letters adjacent to data in the same column show significance at $P < 0.05$ by Duncan's multiple range test.

Table 6. Correlation coefficients between N, P, K, Ca, and Mg uptake and BM and PY under well-watered and terminal drought conditions.

Yield	Nutrient uptake, mg plant^{-1}				
	N	P	K	Ca	Mg
Well-watered					
BM mg plant^{-1}	0.61**	0.52**	0.95**	0.94**	0.95**
PY mg plant^{-1}	0.67**	0.35*	0.75**	0.70**	0.68**
Terminal drought					
BM mg plant^{-1}	0.50**	0.70**	0.90**	0.70**	0.92**
PY mg plant^{-1}	0.86**	0.26	0.84**	0.46*	0.59**

*, ** = Significant at $P < 0.05$ and $P < 0.01$, respectively.

In well-watered treatments, the soil moisture contents measured at 30 cm on the day of sowing (10.51%), last day of irrigation (9.91%), R7 (9.74%), and harvest (10.25%) were more consistent than soil moisture content at 60 cm in 2010/2011. In general, the soil moisture contents at 30 cm and 60 cm measured in 2011/2012 were closer to the desired soil moisture content in both well-watered and terminal drought conditions (1/3 AW) compared to those measured in 2010/2011.

The effect of drought on peanut could also be seen from the values of RWC of peanut leaves under different water treatments at R7 and harvest (Figure 2). RWC was significantly lower in the stressed treatment than the well-watered treatment in both years, indicating that RWC was decreased by drought treatment. The highest RWC was observed at R7 under well-watered treatments in both years, followed by RWC under well-watered treatments on the last day of irrigation and harvest. Plants under terminal drought stress also showed water deficit symptoms since a few days after withholding water and then showed severe wilting during the treatment period, whereas well-watered plants were normal. Leaf senescence and abscission were not observed in any genotype during the terminal drought treatment**.**

3.2. Effects of water stress on uptakes of N, P, K, Ca, and Mg

Combined analysis of variance based on the 2-year data showed significant effects of year on N, P, K, Ca, and Mg uptake ($P < 0.05$) (Table 3). The effects of water regimes and genotypes were also significant ($P < 0.01$) for uptakes of all nutrients. Similarly, water regime × genotype interactions were also significant for the uptake of N, P, K, Ca, and Mg ($P < 0.01$), but they were relatively lower than the effects of water regimes or genotypes. Year × genotype interaction was also significant for the uptake of N and P. The data are separately presented for each year and each water stress based on genotype × year and genotype × water interactions.

Nutrient uptake and RNS of N, P, K, Ca, and Mg of the 6 peanut genotypes are presented in Tables 4 and 5. In general, the results clearly show that terminal drought stress reduced the uptake of N, P, K, Ca, and Mg in both years. Moreover, peanut genotypes differed considerably with respect to N, P, K, Ca, and Mg uptake under well-watered and terminal drought conditions. ICGV 98308 had the highest uptake of N, K, Ca, and Mg under well-watered conditions in both years. However, under terminal drought conditions, nutrient uptakes of this genotype were reduced. ICGV 98308 was not the best genotype for uptake of P under both water regimes in both years (Tables 4 and 5).

Tainan 9 had low uptake of N, P, K, Ca, and Mg under both well-watered and terminal drought conditions in both 2010/2011 and 2011/2012. Although Tifton 8 had low uptake of N, P, K, and Mg under both conditions, it showed the highest uptake of Ca, even under terminal drought, in the first year. Tifton 8 showed similar results for N, P, K, and Mg uptake in the second year, but the uptake of Ca was still the highest under drought conditions in that year (Tables 4 and 5).

The nonnodulating line was the best genotype for the uptake of P, K, Ca, and Mg under well-watered conditions. It was also the best for the uptake of P, Ca, and Mg, but not K, under terminal drought conditions in 2010/2011 (Tables 4 and 5). The nonnodulating line only had the highest uptake of P in 2011/2012; moreover, the uptakes of K and Mg were relatively high under drought conditions in this year. The nonnodulating line, which did not fix atmospheric N, had poor soil N uptake. It was the lowest not only under well-watered but also under terminal drought conditions in both years.

The drought-resistant genotype ICGV 98324 had the highest uptake of Ca and it also had high K uptake under well-watered conditions in the first year, whereas its uptake of other nutrients (such as N, P, and Mg) was relatively low. In 2011/2012, ICGV 98324 only had high N uptake under well-watered treatments. In this study, like other genotypes, nutrient uptake in ICGV 98324 was decreased by terminal drought. Under this stressed condition, ICGV 98324 performed well for all nutrient uptakes, even though it was not the best genotype under well-watered conditions. Such strong performances were observed for the uptake of N, P, K, Ca, and Mg in both years. Similar performances were observed in ICGV 98348, which showed high uptakes of N, P, K, Ca, and Mg under drought compared to nutrient uptakes of other genotypes in both years.

3.3. Effects of water stress on RNS

The calculated RNS of all genotypes except ICGV 98348 were lower in 2011/2012. In 2010/2011, ICGV 98348 had high P, K, Ca, and Mg RNS; values were 0.82, 0.97, 0.99, and 0.90, respectively (Tables 4 and 5). This genotype had better N uptake under terminal drought with N-RNS of 1.06. In the second year, ICGV 98348 had the highest calculated K-RNS (0.96). It also had better N, P, Ca, and Mg uptake under terminal drought and its calculated N, P, Ca, and Mg RNS values were 1.28, 1.06, 1.33, and 1.08 respectively. N-RNS of ICGV 98324 was comparatively high: 0.94 and 0.84 in 2010/2011 and 2011/2012, respectively. ICGV 98324 also had consistently high P, K, Ca, and Mg RNS values in both years. In the first year, N, Ca, and Mg RNS values for the nonnodulating line were relatively high, but they decreased in the second year. However, the nonnodulating genotype had medium P and K RNS values in 2010/2011 and 2011/2012; they varied between 0.50 and 0.73. The calculated K and Ca RNS in Tifton 8 were high in 2010/2011 (0.85 and 0.78, respectively), but only Ca RNS was still high (0.85) in 2011/2012. Tifton 8 had medium N, P, and Mg RNS values in both years, as did ICGV 98308 for all nutrient RNS values in both years. In term of RNS, Tainan 9 was the genotype with the lowest values in both years.

3.4. Correlations between uptakes of N, P, K, Ca, and Mg and BM and PY

Close associations between nutrient uptakes and BM and PY were found across both years (Table 6). Positive correlations between N, P, K, Ca, and Mg uptakes and BM were observed under well-watered and drought conditions across both years ($P < 0.01$). Similarly, there were significant correlations between N, K, Ca, and Mg uptake and PY under both treatments. P uptake was correlated with PY under well-watered conditions ($r = 0.35$, $P < 0.05$), but there was no significant correlation between P uptake and PY under terminal drought. However, the correlation coefficients between N, K, Ca, and Mg uptake and BM were higher in well-watered treatments than under terminal drought conditions. Higher coefficients of correlation were observed between N and K uptake and PY under water stress, while correlation coefficients between Ca and Mg uptake and PY were lower under water stress.

4. Discussion

The different abilities in plants for adaptation to drought are due to the differential mechanisms of drought resistance with different genetic makeup. Information on the additional morphological and physiological characteristics involved in adaptation to water stress and selection of improved peanut genotypes would be a great contribution to peanut production under drought condition.

Terminal drought generally reduced pod weight, seed weight, and harvest index (Nautiyal et al., 1999; Reddy et al., 2003) and resulted in yield reduction and low seed quality. Koolachart et al. (2013) showed that terminal drought caused 38%–42% yield reduction. ICGV 98324 and ICGV 98348 showed the highest PY under stress conditions. We found that N, P, K, Ca, and Mg uptake were reduced by terminal drought. This observation was in agreement with the findings of Kolay (2008), who reported that N, P, K, Ca, Mg, and S uptakes in peanut cultivar CG-2 were affected by water stress from the reproductive stage to the pod development stage. Kulkarni et al. (1988) reported that N, P, and K uptake in peanut was reduced by moisture stress. It is still necessary to identify information gaps in the research and suggest future needs. According to Xia (1997), N, P, and K uptake decreased significantly under water stress in faba bean. In a study carried out with chickpea, 11 screened cultivars varied greatly with respect to nutrient uptake in both optimal and drought conditions (Gunes et al., 2006). They also reported that drought treatments significantly reduced nutrient uptakes and efficiencies of the cultivars and that the decrease in nutrient uptakes was more serious in late drought stress treatment than in early drought stress treatment. In general, soil water availability affects plant nutrient uptake by influencing the supply of nutrients to roots through changes in diffusion and mass flow, through reduced root growth, and by modifying root uptake capacity (Barber, 1985; Kuchenbuch et al., 1986). Decreasing water availability under drought generally results in reduced total nutrient uptake and frequently in reduced concentrations of mineral nutrients in crop plants (Baligar et al., 2001).

Evidence presented in this study indicates that there was a substantial genotypic variation in nutrient uptakes among the 6 peanut genotypes. This result was in accordance with the findings of Garg (2003), who reported that plant species and genotypes within species varied in their responses to mineral uptake under water stress. In fact, genetic variation is needed for a trait to be successfully used as a surrogate for drought resistance. Better understanding of genotypic control of nutrient uptake mechanisms is required to maintain production under drought conditions (Gunes et al., 2006). In our study, ICGV 98348 exhibited high and consistent uptakes of nutrients and the highest RNS values. This drought-tolerant genotype performed better under terminal drought conditions for N, P, Ca, and Mg uptake in 2011/2012, though K uptake under terminal drought conditions was the same as under well-watered conditions. Similarly, ICGV 98324 also exhibited high nutrient uptake and RNS in both years. These 2 genotypes are able to take up nutrients even better under terminal drought conditions and are supposed to be drought-tolerant (Tables 4 and 5). According to Girdthai et al. (2010) and Koolachart et al. (2013), peanut genotypes ICGV 98324 and ICGV 98348 are categorized as drought-tolerant genotypes based on high yield under stress conditions and low reduction of total BM and PY. Tifton 8 might be drought-tolerant in those categories, but in this study, it was only average for nutrient uptake and RNS. As suggested by Samarah et al. (2004), peanut genotypes exhibiting smaller reductions in nutrient uptakes should be presumed to be drought-resistant, and RNS may involve drought tolerance mechanisms. Therefore, it can be hypothesized that peanut genotypes that can manage high nutrient uptakes under drought conditions could be presumed to be drought-resistant. Similarly, a genotype that has a high level of RNS would have a high drought resistance level; subsequently, this genotype would be highly productive under terminal drought conditions.

The present study supports earlier findings that there is a high correlation between nutrient uptakes under long periods of drought and BM and PY (Junjittakarn et al., 2013). The correlation coefficients between nutrient uptake and BM became lower under terminal drought conditions. The correlation coefficients between N and K uptakes and PY increased with decreasing correlation coefficients between N, K, and BM under terminal drought. N and K might reduce their contribution to BM and they might contribute more to PY under terminal drought conditions. P uptake did not contribute to PY under terminal drought conditions; however, its correlation to BM was higher under terminal drought conditions, indicating that under terminal drought conditions, P uptake contributed more to BM compared to PY. Uptakes of other nutrients were consistently correlated with PY across both conditions (Junjittakarn et al., 2013). Under terminal drought conditions, the correlation coefficients between Ca and Mg and BM as well as their correlations to PY decreased. N, P, K, Ca, and Mg uptake contributed significantly to BM under both conditions. Therefore, when peanut genotypes were subjected to terminal drought conditions, nutrient uptakes decreased and some of them contributed more to PY rather than to BM.

Terminal drought reduced nutrient uptake, but the responses of peanut genotypes to nutrient uptakes under terminal drought varied based on their drought resistance levels. The genotypes ICGV 98324 and ICGV 98348, which are characterized as drought-resistant lines from ICRISAT, were the best genotypes for nutrient uptake and RNS. Drought-tolerant peanut genotypes could maintain high nutrient uptakes across water regimes and sometimes they would perform better for these traits under terminal drought conditions. Consequently, nutrient uptake and RNS can also be used as efficient tools for the selection of peanut genotypes with terminal drought tolerance. Moreover, our findings showed that nutrient uptake seems to be the new surrogate trait for drought tolerance. It may possibly have a part in drought tolerance based on its high and consistent correlations with BM and PY.

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