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Rooting traits of peanut genotypes differing in drought tolerance under drought stress

H. Ding[a], Z. Zhang[a,*], T. Kang[b], L. Dai[a], D. Ci[a], F. Qin[a], W. Song[a]

[a]*Shandong Peanut Research Institute, Qingdao 266100, China.*
[b]*Taian Academy of Agricultural Sciences, Taian 271000, China.*
*Corresponding author. E-mail: qinhdao@126.com

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Abstract

The effects of two water regimes (well-watered condition or drought stress) on root length, root surface area and root volume were tested on two peanut genotypes (the drought-resistant variety HuaYu 22 (HY22) and the drought-sensitive variety HuaYu 23 (HY23)), measured 101 days after sowing. The roots were sampled from the upper (0–40 cm) and deeper (40–100 cm) soil layers. Root diameter was measured to the nearest 0.5 mm in describing its distribution. Total dry weight and pod yield were measured at harvest. The drought tolerance index of pod yield and the harvest index in HY22 were higher than those in HY23. The total root length density (RLD), total root surface area and volume were significantly higher for HY22 than HY23. The RLD in the deeper soil layer was lower for HY23 than HY22. Under drought stress, the percent RLD in the deeper layers increased in both genotypes. Compared to well-watered condition, the total root surface area and root volume in the upper soil layer were lower under drought stress and root traits in deeper soil layers were higher. Drought stress had no impact on very fine roots (diameter < 0.5 mm) of HY22 in the deeper soil layer but lowered their share in HY23 markedly. The RLD and root surface area in the deeper soil layer were related to the pod yield of peanut. This finding could be useful in growing peanut under drought conditions.

Keywords: Drought stress; Root diameter classes; Pod yield; *Arachis hypogaea*; Drought tolerance index (DTI).

Introduction

Peanut (*Arachis hypogaea* L.) is a major economic crop widely cultivated in arid areas. Drought is one of the important factors limiting crop production in rain-fed areas (Ludlow and Muchow, 1990). Low and unpredictable rainfall causes severe reduction in yield, deterioration in seed quality and aflatoxin contamination of peanut (Nageswara Rao et al., 2002). Prolonged drought stress leads to fewer and smaller leaves and shorter main axis and cotyledonary branches due to water deficit (Chung et al., 1997) and intermodal length is reduced more drastically than the number of nodes (Reddy et al., 2003). Early-season drought increased SPAD chlorophyll meter reading and transpiration efficiency but decreased specific leaf area (Puangbut et al., 2009). The effects of drought stress on aboveground parts of peanut have been well documented (Nageswara Rao et al., 1990; Awal and Ikeda, 2002; Jongrungklang et al., 2008). However, information on the responses of roots to water deficit is limited.

Roots are an important determinant of peanut productivity under water stress. Meisner and Karnok (1992) reported that peanut roots grew rate more slowly under drought stress, which also increased the root:shoot ratio and roots grew faster after re-watering (Awal and Ikeda, 2002). Root density in the peanut variety 'Florunner' did not differ significantly between drought stress and watered adequately (Robertson et al., 1980). Root length density (RLD), root dry weight ratio and root surface area for peanut and rice in deeper soil layers increased under drought stress (Songsri et al., 2008; Kato and Okami, 2010; Jongrungklanga et al., 2011), whereas the vertical distribution of roots in soybean was not influenced by drought stress (Benjamin and Nielsen, 2006). Root traits such as RLD, root distribution and root surface area have been identified as being critical to drought resistance (Matsui and Singh, 2003). Roots in the deeper layer continued to grow even after vegetative growth had stopped because of drought stress and RLD distribution increased in this layer (Allen et al., 1976). Larger root systems in peanut could obtain relatively high yield under drought stress, whereas RLD in the deeper soil layers may contribute more to pod yield and harvest index (Songsri et al., 2008; Jongrungklang et al., 2012). Peanut has high root characteristics that help maintain yield under terminal drought (Junjittakarn et al., 2014). Jongrungklang et al. (2014) measured root traits using an auger method in peanut plants under drought stress during the pre-flowering stage and suggested that root surface area in the deeper soil layer contributed to pod yield. Five peanut plants were studied using the monolith method and the results showed that RLD could be a useful selection criterion for yield under terminal drought conditions (Koolachart et al., 2013).

Currently, information on peanut rooting traits under drought stress is limited to experiments on RLD distribution using the root auger method. The response of root surface area, root volume and root diameter to long periods of drought stress is lacking and further investigations are necessary. Thus, the objectives of this study were to investigate the root morphology responses to drought stress for RLD, and root surface area and root volume in different root diameter categories; and to determine the relationship between the response of rooting traits and yield. The information would advance our understanding of the responses of peanut cultivars to drought stress and aid in peanut production under these conditions.

Materials and Methods

Experimental details

The experiments were conducted in 2011 and in 2012 (May–September in both years) at Shandong Peanut Research Institute, Qingdao, China (36°48′47″ N, 120°30′17″ E). Peanut plants were grown in PVC columns (40 cm in diameter and 100 cm tall) in a tank with the large moving water-proof shed. The experiment was laid out in a randomized complete block design with three replications. The treatments comprised two sets of treatments. The first set was water regime, which consisted of plants either well-watered (WW), with the water level maintained at 85% field capacity, or subjected to drought stress (DS), with water level at 65% field capacity (Jongrungklang et al., 2008). The other set was the genotype, which consisted of two peanut genotypes: HuaYu 22 (HY22), which is resistant to drought; and HuaYu 23 (HY23), which is sensitive to drought (Zhang et al., 2012).

Each PVC column was filled with 100 kg of sandy soil. The nutrient status of the soil is shown in Table 1. A basal dose of fertilizers was given before sowing by mixing the fertilizers with the top layer (0–20 cm) of the soil column. The fertilizer dose consisted of 90 kg ha^{-1} N as urea, 119.2 kg ha^{-1} P as calcium superphosphate and 135.9 kg ha^{-1} K as potassium sulfate. At the time of sowing, soil water content was at field capacity and was then maintained at 85% of field capacity until seedling emergence, after which the water content of soil was allowed to decrease. Ten days after sowing (DAS), the plants were thinned to maintain two individual plants to a column in 2011 and three plants to a column in 2012.

Table 1. Soil basic properties in the experimental site in 2011 (season 1) and 2012 (season 2).

Year	Organic matter ($g \cdot kg^{-1}$)	Total nitrogen ($g \cdot kg^{-1}$)	Available P ($mg \cdot kg^{-1}$)	Available K ($mg \cdot kg^{-1}$)	pH
2011	16.7	1.8	49.6	93.6	7.6
2012	15.8	1.5	43.5	95.1	7.5

Soil moisture

Soil moisture in each column was measured at 5-day intervals with time-domain reflectometry (TRIME-tube system, IMKO GmbH, Ettlingen, Germany). The soil volumetric moisture content was recorded in each 20-cm soil layer. Soil volumetric water content was 16.9% at field capacity. Water was added to each column based on the crop water requirement and surface evaporation, calculated by the methods described by Doorenbos and Pruitt (1992) and Singh and Russell (1981).

Root sampling

Root samples were collected 101 DAS, when the root system is at its peak, as shown by Meisner and Karnok (1992), who found that the peanut plant's root system was the most extensive during 100–110 DAS. The plants were clipped at the soil surface and the shoots were removed before sampling the roots. As suggested by Songsri et al. (2008), the 0–40 cm soil layer was defined as the upper layer and the 40–100 cm layer as the deeper layer. Accordingly, the soil columns were divided into 0–40 cm and 40–100 cm segments and the roots were separated from the substrate by sieving and then washing under running water. The samples were placed in self-sealing polythene bags and stored in a refrigerator. The following day, the roots were measured using a scanner and WinRHIZO Pro ver. 2004a (Regent Instruments Inc., Ville de Québec, Quebec, Canada). The following root traits were recorded: root length, root surface area, root volume and root diameter. RLD was calculated as the ratio between root length (cm) and soil volume (cm^3) and percent RLD (%RLD) was calculated as the share of each of the two soil layers in RLD. A 0.5-mm interval was used to categorize root diameter: very fine (< 0.5 mm), fine (0.5–1.0 mm), or thick (> 1.0 mm). The proportions of each of the three categories were recorded for each parameter.

Biomass, pod yield and harvest index

For each column, biomass, pod yield and harvest index were obtained from plants after the harvest. Fresh shoots were oven-dried at 80 °C until constant weight and their weight was recorded as the dry weight. Pods were air-dried to approximately 8% moisture for determining the pod dry weight. The total dry weight of the shoot, roots and pods per plant was taken as the total biomass. The harvest index was taken as the ratio of pod yield to biomass.

Drought tolerance index

Drought tolerance index (DTI) was computed for pod yield, RLD, root surface area and root volume by comparing the means of the respective parameters under the DS treatment to the corresponding means from the WW treatment, as suggested by Nautiyal et al. (2002), with DTI > 1 indicative of increased tolerance to drought and DTI < 1 indicative of decreased tolerance to drought:

DTI = Data of DS treatment / Data of WW treatment

Statistical analysis

Analysis of variance was performed for each character in each year with a two-way ANOVA at a significance level of 0.05 using SPSS ver. 17.0. The water treatment and genotype as the independent variables. The relationships between the DTI for rooting traits and DTI for pod yield were determined based on correlation.

Results

The response of pod yield, biomass and harvest index to drought stress

Water stress significantly reduced pod yield in both years and the magnitude of reduction varied with the genotype (Table 2). Compared to WW, the pod yield of the drought-resistant HY22 under DS decreased by 8.9% and 21.1% in the two years, respectively; whereas pod yield for drought-sensitive HY23 was markedly lower than under WW, by 41.9% in 2011 and 34.0% in 2012. Total biomass of both genotypes was significantly lower under DS in 2012 but only in HY23 in 2011. Under DS, the harvest index in HY22 was markedly higher in 2012 and that in HY23 was significantly lower in 2011. The overall DTI of HY22 in both years was higher than that of HY23, confirming the greater drought resistance of HY22. In 2011, water treatment had a significant effect on pod yield, biomass and HI and the interaction between water and genotype was significant for these measures.

Table 2. Pod Yield, biomass, harvest index (HI) and drought tolerance index (DTI) for pod yield, biomass and HI of two peanut genotypes grown under different water regimes in 2011 (season 1) and 2012 (season 2).

Genotype	Water regime	Pod Yield (g·plant^{-1})		Biomass (g·plant^{-1})		HI	
		2011	2012	2011	2012	2011	2012
HY22	WW	12.03^{a}	13.67^{a}	20.81^{a}	27.19^{a}	0.58^{a}	0.50^{b}
	WS	10.96^{b}	10.78^{b}	19.35^{a}	18.97^{b}	0.57^{a}	0.57^{a}
	DTI	0.91	0.79	0.93	0.70	0.98	1.14
HY23	WW	15.00^{a}	14.28^{a}	25.62^{a}	26.80^{a}	0.59^{a}	0.53^{a}
	WS	8.71^{b}	9.42^{b}	19.65^{b}	17.31^{b}	0.44^{b}	0.54^{a}
	DTI	0.59	0.67	0.79	0.64	0.69	1.01
Analysis of variance(P value)							
Water (W)		P＜0.001	0.001	P＜0.001	P＜0.001	0.010	0.004
Genotype (G)		0.572	0.605	0.003	0.437	0.040	0.722
W×G		0.003	0.199	0.007	0.627	0.022	0.019

Different letters in the same column show significance at P<0.05 level.
DTI, drought tolerance index (WS/WW; more than 1=increased, less than 1=decreased).

RLD under drought stress

The total RLD (RLDtot) and RLD in the upper and deeper soil layers were lower for HY23 than HY22 (Table 3). RLDtot and RLD in the upper soil layer in HY22 under DS were significantly lower than those under WW in 2011, whereas RLD in the deeper layer did not differ significantly between the two water regimes. Both RLDtot and RLD in the upper soil layer in HY23 under DS were significantly lower than those under WW in both years and the DTI of RLDtot and RLD in both the layers in HY23 was lower than that in HY22 in 2012. Except for RLD in the deeper soil layer in 2012, the effect of water treatment was significant on RLDtot and RLD in both layers. The genotype effect was significant on RLDtot and RLD in the upper soil layer. The interaction effect was significant on RLDtot. The %RLD in the deeper soil layer, an important index of the plant's capacity to absorb water, was higher under DS than under WW (Figure 1), by 19.45% in 2011 and 17.32% in 2012 in HY22; in HY23, the corresponding increase was much lower, being 3.66% and 9.25%. The genotype effect was significant for %RLD in the deeper soil layer in both years, but water and genotype interaction was significant only in 2011.

Table 3. Total root length density (RLDtot), root length density in upper soil layer (0-40 cm) and deeper soil layer (40-100 cm) of two peanut genotypes grown under different water regimes in 2011 (season 1) and 2012 (season 2).

Genotype	Water regime	RLDtot (cm cm^{-3})		RLD (0-40 cm) (cm cm^{-3})		RLD (40-100 cm) (cm cm^{-3})	
		2011	2012	2011	2012	2011	2012
HY22	WW	0.14^{a}	0.13^{a}	0.24^{a}	0.20^{a}	0.07^{a}	0.08^{a}
	WS	0.11^{b}	0.12^{a}	0.17^{b}	0.18^{b}	0.07^{a}	0.09^{a}
	DTI	0.78	1.00	0.71	0.90	1.00	1.12
HY23	WW	0.11^{a}	0.12^{a}	0.18^{a}	0.16^{a}	0.07^{a}	0.09^{a}
	WS	0.09^{b}	0.09^{b}	0.14^{b}	0.11^{b}	0.06^{b}	0.07^{a}
	DTI	0.82	0.75	0.78	0.69	0.86	0.78
Analysis of variance (P value)							
Water (W)		P＜0.001	0.033	P＜0.001	0.021	0.001	0.568
Genotype (G)		P＜0.001	0.012	P＜0.001	0.004	0.157	0.963
W×G		0.071	0.074	0.007	0.321	0.269	0.057

Different letters in the same column show significance at P<0.05 level.
DTI, drought tolerance index (WS/WW; more than 1=increased, less than 1=decreased).

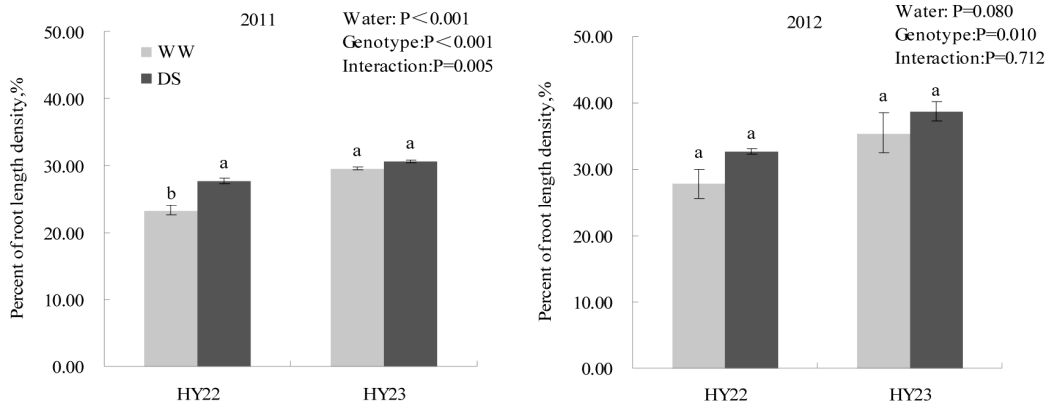

Figure 1. Percent of root length density (%RLD) in deeper soil layer (40–100 cm) in two peanut genotypes grown under well-watered (WW) and drought stress (DS) in 2011 (season 1) and 2012 (season 2). Error bars represent ±SED.

Root surface area under drought stress

The total root surface area and root surface area in the upper layer in both the genotypes were lower under DS than under WW (Table 4). The very fine and fine categories accounted for the highest shares, which represented the longest parts of the root system. Total root surface area in both genotypes in both years contributed by very fine roots was less under DS than in WW and that contributed by the other two classes was lower in 2012. The variation in root surface area in the upper layer was similar to that in the total root surface area. In 2011, root surface area in the deeper layer in HY22 in all the categories (very fine, fine, or thick) was greater under DS than that in WW. In 2012, root surface area in HY22 contributed by the very fine roots was higher under DS than under WW, whereas in HY23, very fine roots accounted for a smaller proportion of root surface area under DS than in WW. Also, the DTI of root surface area in the case of very fine roots in HY23 was lower than that in HY22. The effects of water and genotype were significant on total surface area and surface area in the upper soil layer in the very fine and fine categories. The water and genotype interaction had a significant effect on root surface area in the deeper soil layer except for the thick category in 2011.

Root volume under drought stress

Total root volume and root volumes in both the soil layers under DS were lower than those under WW in both the genotypes in 2012; in 2011, this was so only in HY23. The thicker roots contributed the most to total root volume and root volume in the upper layer, whereas the finer roots did so for the deeper layer. Total root volume and root volume in the upper layer in all the categories were lower under DS except in the case of thick roots in 2011, the differences being greater in HY22 than in HY23. The share of very fine roots of HY22 in the total root volume in the deeper layer under DS was not significantly different from that under WW (Table 5), whereas their share in HY23 was markedly lower under DS, by 32.6% in 2011 and 22.6% in 2012. In HY22, the DTI of total root volume and root volumes in the upper layer in all the diameter-classes and in the deeper layer, for very fine roots, was larger than that in HY23. The effects of water and genotype were significant on root volume in the very fine category in total and both soil layers. The water and genotype interaction had a significant effect on root volume in the deeper soil layer in all categories in 2011 only.

Table 4. Total root surface area, root surface area in upper soil layer (0-40 cm) and deeper soil layer (40-100 cm) of two peanut genotypes grown under different water regimes in year 2011 (season 1) and 2012 (season 2).

Year	Genotype	Water regime	Total Root surface area (cm^2 $plant^{-1}$)			Root surface area (0-40cm, cm^2 $plant^{-1}$)			Root surface area (40-100cm, cm^2 $plant^{-1}$)		
			Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)	Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)	Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)
2011	HY22	WW	388.88^{a}	117.72^{a}	54.02^{a}	266.00^{a}	78.86^{a}	41.46^{a}	122.87^{a}	38.85^{a}	12.56^{b}
		WS	318.51^{b}	123.48^{a}	61.88^{a}	192.52^{b}	79.65^{a}	44.87^{a}	125.99^{a}	43.83^{a}	17.02^{a}
		DTI	0.82	1.05	1.15	0.72	1.01	1.08	1.03	1.13	1.36
	HY23	WW	318.29^{a}	127.64^{a}	65.27^{a}	196.87^{a}	75.71^{a}	46.74^{a}	121.42^{a}	51.93^{a}	18.54^{a}
		WS	209.01^{b}	81.83^{b}	66.05^{a}	127.93^{b}	46.12^{b}	50.64^{a}	81.09^{b}	35.71^{b}	15.40^{b}
		DTI	0.66	0.64	1.01	0.65	0.61	1.08	0.67	0.69	0.83
Analysis of variance (P value)											
Water (W)			P<0.001	0.003	0.387	P<0.001	0.014	0.345	P<0.001	0.017	0.600
Genotype (G)			P<0.001	0.010	0.141	0.001	0.004	0.169	P<0.001	0.222	0.110
W×G			0.213	0.001	0.474	0.861	0.011	0.948	P<0.001	P<0.001	0.014
2012	HY22	WW	368.38^{a}	126.06^{a}	93.11^{a}	226.82^{a}	75.07^{a}	63.99^{a}	141.56^{a}	50.99^{a}	29.11^{a}
		WS	338.04^{a}	94.31^{b}	67.13^{b}	189.83^{a}	56.84^{b}	50.38^{b}	148.21^{a}	37.48^{b}	16.75^{b}
		DTI	0.92	0.75	0.72	0.84	0.76	0.79	1.05	0.74	0.58
	HY23	WW	326.11^{a}	103.99^{a}	82.96^{a}	169.42^{a}	57.99^{a}	63.62^{a}	156.69^{a}	46.00^{a}	19.34^{a}
		WS	251.43^{b}	80.13^{b}	53.81^{b}	127.93^{b}	39.01^{b}	39.65^{b}	123.50^{a}	41.12^{a}	14.17^{b}
		DTI	0.77	0.77	0.65	0.76	0.67	0.62	0.79	0.89	0.73
Analysis of variance (P value)											
Water (W)			0.019	P<0.001	0.001	0.027	P<0.001	0.001	0.231	0.009	0.006
Genotype (G)			0.007	0.002	0.072	0.003	P<0.001	0.170	0.652	0.810	0.030
W×G			0.250	0.336	0.786	0.880	0.883	0.197	0.087	0.146	0.165

Different letters in the same column show significance at P<0.05 level.
DTI, drought tolerance index (WS/WW; more than 1=increased, less than 1=decreased).

Table 5. Total root volume, root volume in upper soil layer (0-40 cm) and deeper soil layer (40-100 cm) of two peanut genotypes grown under different water regimes in year 2011 (season 1) and 2012 (season 2).

Year	Genotype	Water regime	Total Root volume (cm^3 $plant^{-1}$)			Root volume (0-40cm, cm^3 $plant^{-1}$)			Root volume (40-100cm, cm^3 $plant^{-1}$)		
			Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)	Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)	Very fine roots (0.0<D≤0.5mm)	Fine roots (0.5<D≤1.0mm)	thick root (D>1.0mm)
2011	HY22	WW	3.02^{a}	2.24^{a}	2.99^{a}	2.07^{a}	1.53^{a}	2.34^{a}	0.95^{a}	0.72^{b}	0.65^{b}
		WS	2.43^{b}	2.46^{a}	3.70^{a}	1.51^{b}	1.38^{a}	2.82^{a}	0.92^{a}	1.08^{a}	0.89^{a}
		DTI	0.80	1.10	1.24	0.73	0.90	1.21	0.97	1.50	1.37
	HY23	WW	2.59^{a}	2.53^{a}	3.43^{a}	1.61^{a}	1.51^{a}	2.58^{a}	0.98^{a}	1.02^{a}	0.85^{a}
		WS	1.61^{b}	1.71^{b}	3.55^{a}	0.96^{b}	1.03^{b}	2.79^{a}	0.65^{b}	0.68^{b}	0.75^{a}
		DTI	0.62	0.68	1.03	0.60	0.68	1.08	0.66	0.67	0.88
Analysis of variance (P value)											
Water (W)			P<0.001	0.036	0.212	P<0.001	0.005	0.206	P<0.001	0.858	0.280
Genotype (G)			P<0.001	0.091	0.658	0.001	0.062	0.680	0.001	0.382	0.596
W×G			0.116	0.002	0.359	0.671	0.085	0.616	P<0.001	P<0.001	0.025
2012	HY22	WW	2.82^{a}	2.23^{a}	4.72^{a}	1.66^{a}	1.34^{a}	3.60^{a}	1.16^{a}	0.89^{a}	1.12^{a}
		WS	2.46^{a}	1.67^{b}	3.44^{b}	1.39^{b}	1.03^{b}	2.82^{b}	1.06^{a}	0.65^{b}	0.62^{b}
		DTI	0.87	0.75	0.73	0.84	0.77	0.78	0.91	0.73	0.55
	HY23	WW	2.31^{a}	1.86^{a}	4.03^{a}	1.16^{a}	1.05^{a}	3.37^{a}	1.15^{a}	0.81^{a}	0.66^{a}
		WS	1.84^{b}	1.39^{b}	2.66^{b}	0.95^{a}	0.69^{b}	2.18^{b}	0.90^{b}	0.70^{a}	0.48^{a}
		DTI	0.80	0.75	0.66	0.82	0.66	0.65	0.78	0.86	0.73
Analysis of variance (P value)											
Water (W)			0.016	P<0.001	0.001	0.052	P<0.001	0.001	0.049	0.007	0.009
Genotype (G)			0.003	0.001	0.028	0.002	P<0.001	0.049	0.267	0.763	0.017
W×G			0.706	0.492	0.874	0.796	0.529	0.299	0.321	0.193	0.140

Different letters in the same column show significance at P<0.05 level.
DTI, drought tolerance index (WS/WW; more than 1=increased, less than 1=decreased).

Responses of root traits and yield

The DTI is as an indicator of drought stress and the response of characteristics of peanut genotypes is shown in Tables 2–5. The correlation coefficients were calculated for each year between DTI for root traits at the deeper soil layer (40–100 cm) and DTI for pod yield. The DTI for RLD and root surface area in the deeper soil layer were significantly positively correlated with DTI for pod yield in both years (Figure 2). The correlation of DTI for root volume with DTI for pod yield was also significant in 2011, but not in 2012. So, the responses of RLD and root surface area in the deeper soil layer for peanut were related to the responses of pod yield; and RLD and root surface area could be used as indicators for selecting peanut genotypes for cultivation in areas experiencing long durations of drought stress.

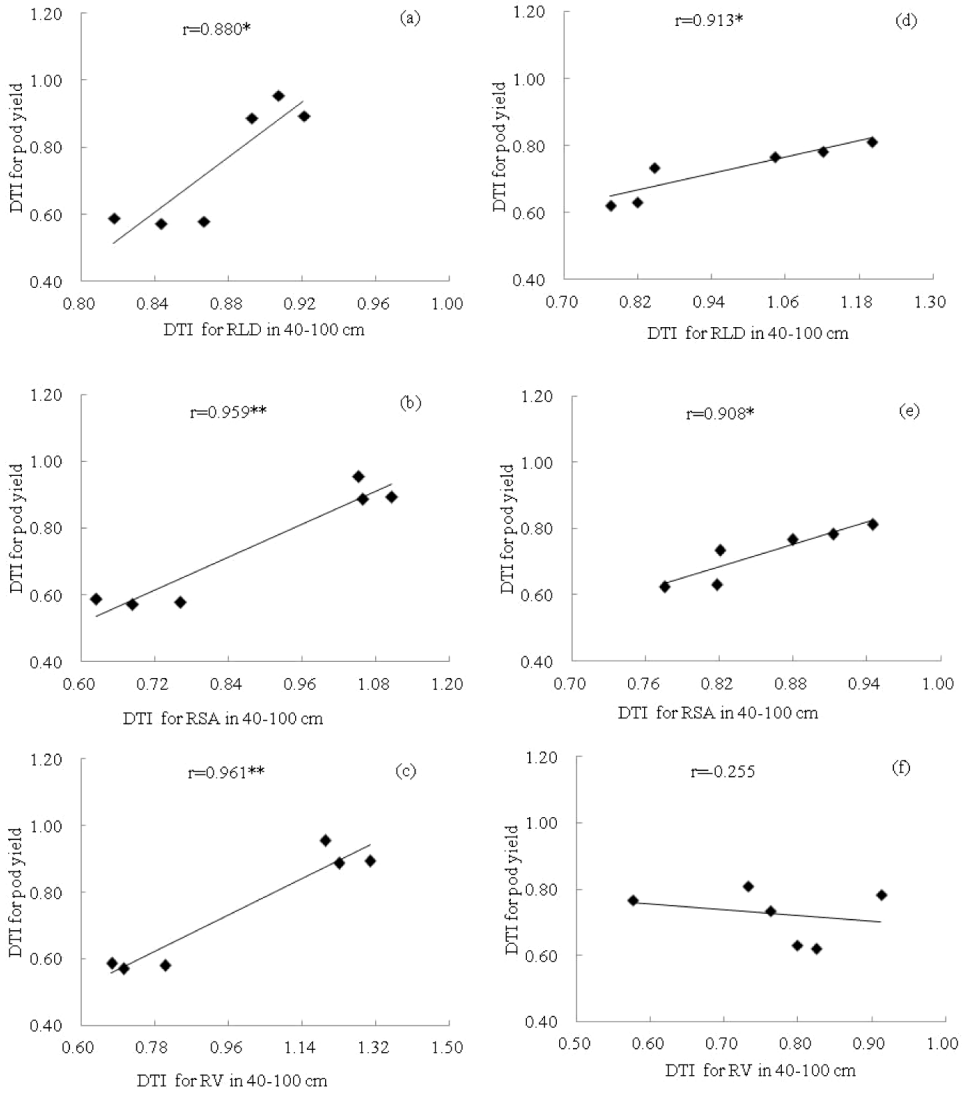

Figure 2. DTI for RLD (a), RSA (b), RV (c) in 40 to 100 cm soil layer related to DTI for pod yield in 2011 (season 1) and RLD (d), RSA (e), RV (f) in 2012 (season 2). RLD, root length density; RSA, root surface area; RV, root volume. DTI, drought tolerance index (WS/WW; more than 1=increased, less than 1=decreased).

Discussion

Yield and rooting traits under drought

Drought is a major cause of lower yields in peanut and lowered them in the present experiment, although the magnitude of reduction varied with the genotype (Table 2). These results are consistent with earlier reports of reduced yields from peanut subjected to drought stress (Boontang et al., 2010; Girdthai et al., 2010; Junjittakarn et al., 2014) and of the variation in such reduction among peanut genotypes (Matthews et al., 1988).

Drought resistance may be enhanced by improving the ability of a crop to extract water from soil (Lilley and Fukai, 1994). Root growth in peanut is influenced by soil water. Root length density and root distribution are drought-adaptive traits. Soil water contents affect peanut root depth and distribution (Pandey et al., 1984), although other researchers found that RLD and root-dry-weight density did not differ significantly between two peanut genotypes subjected to various water regimes (Ketring and Reid, 1993; Robertson et al., 1980). In the present experiment, RLDtot and RLD in the upper layer under DS were significantly lower than those under WW in 2011, whereas RLD in the deeper layer showed no significant difference between the two water regimes (Table 3). The change in RLD and in %RLD in the deeper layer in a genotype may indicate a potential mechanism of avoiding drought. In an earlier study, when water level was two-thirds of the available water, the drought-avoiding genotype ICGV 98300 increased its RLD by 50% and its %RLD by 40% in the deeper layer compared to their corresponding values at field capacity, whereas Tainan 9, which not adapted to drought, showed no such differences between the two levels of available water (Songsri et al., 2008). In the present study, under DS, the magnitude of increase in RLD and %RLD in the deeper layer in the drought-resistant HY22 was greater than that in the drought-sensitive HY23, corroborating the previous observation.

Roots morphology can change to adapt to changes in the external environment (Valladares et al., 2007; Kano et al., 2011). In wheat, both total root length and root surface area decreased significantly under water-deficit conditions (Han et al., 2015). Our study showed that the total root surface area and root volume were decreased remarkably under drought stress compared to well-watered condition. However, before this study, little information was available on the effect of DS on root traits as seen in roots of different diameters. Fine roots are particularly important under DS because they expand the area of contact between the root system and soil to obtain more nutrients and water. Under DS, the root surface area contributed by fine roots increased in HY22 but decreased in HY23 (Table 4). The thicker roots contributed the most to total root volume and root volume in the upper layer, whereas the finer roots did so for the deeper layer (Table 5).

Correlations between DTI for pod yield and DTI for root traits

Jongrungklang et al. (2011) reported that root dry weight and higher RLD in deeper layers were associated with yield improvement under pre-flowering drought stress. The %RLD in the lower layer is an important trait that affects pod yield under mid-season drought conditions (Jongrungklang et al., 2012). DTI was used to determine the degree of resistance of the genotypes to drought, although the correlations between DTI for peanut root traits and DTI for pod yield were limited. In peanut, the relationship

between DTI for RLD in the 40–100 cm soil layer and DTI for pod yield was significant in response to long-period drought stress (Songsri et al., 2008). Jongrungklang et al. (2014) showed that the correlation between DTI for root surface area in the deeper soil layer (30–90 cm) and DTI for pod yield was positive and significant during pre-flowering drought stress. In this study, the DTI for RLD and root surface area in the deeper soil layer was significantly positively correlated with DTI for pod yield, which showed that RLD and root surface area in the deeper layer contributed greatly to pod yield.

Conclusions

Drought stress reduced peanut yield, more so in the drought-sensitive genotype HY23 than in the drought-resistant genotype HY22. Under DS, in the deeper soil layer, DTI of RLDtot and RLD was lower in HY23 than in HY22 and the increase range of %RLD in the deeper soil layer of HY22 was larger. Root surface area contributed by fine roots in HY22 increased under DS, whereas their contribution to root surface area and root volume decreased in HY23. The relationship among the DTI for RLD and root surface area in the deeper soil layer and DTI for pod yield were positive and significant. The RLD and root surface area in the deeper layer contributed greatly to pod yield under long-period drought stress.

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