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ROOT DISTRIBUTION PATTERN AND THEIR CONTRIBUTION IN PHOTOSYNTHESIS AND BIOMASS IN JERUSALEM ARTICHOKEUNDER DROUGHT CONDITIONS

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Abstract

Root length density and rooting depth have been established as drought resistant traits and these could be used as selection criteria for drought resistant genotype in many plant species. However, information on deep rooting and the root distribution pattern of Jerusalem artichoke under drought conditions is not well documented in the literature. The objective of this study was to investigate the root distribution pattern in Jerusalem artichoke genotypes under irrigated and drought conditions. This experiment was conducted within a greenhouse using rhizoboxes. Three Jerusalem artichoke genotypes were tested under two water regimes (irrigated and drought). A 2 × 3 factorial experiment was arranged in a randomized complete block design with three replications over two years. Data were recorded for root traits, photosynthesis and biomass at 30 days after imposing drought. The drought decreased root length, root surface area and root dry weight, while increased the root: shoot ratio, root distribution in the deeper soil and the percentage of root length at deeper in the soil, when compared to the irrigated conditions JA-5 and JA-60 showed high root length in the lower soil profile under drought conditions, indicating these genotypes could be identified as drought resistant genotype. The highest positive correlation was found between root length at deeper soil layer with relative water content (RWC), net photosynthetic rate (P_n) and biomass. It is expected that selection of Jerusalem artichoke with high root length coupled with maintaining high RWC and their promotion to P_n could improve the biomass and tuber yield under drought conditions.

Keywords: Root length, RWC, P_n, Drought, *Helianthus tuberosus* L.

Introduction

Large areas of Jerusalem artichoke (*Helianthus tuberosus* L.) production is under rainfed conditions in the semi-arid tropics of Thailand, where drought poses a major threat to tuber production (Ruttanaprasert *et al.*, 2016a). Yield reductions ranging from 20-90% are dependent on drought severity (Ruttanaprasert *et al.*, 2014, 2016a). Irrigation help in reducing the severity of drought, water access is often very limited. Thus, breeding for drought resistance has become an important strategy in mitigating this problem, and, similar to many crops, root characteristics are one of the key attributes to focus on (Kashiwagi *et al.*, 2006; Songsri *et al.*, 2009; Kano-Nakata *et al.*, 2011; Leitner *et al.*, 2014).Selection of Jerusalem artichoke genotypes with ability of root traits to acquire water during drought period might help breeders in identifying Jerusalem artichoke genotypes with drought tolerance.

The implementation of drought avoidance mechanisms such as increasing water uptake from deeper soil layer by an increased depth and density of roots, drought resistance may be enhanced. Root length, root dry weight and root: shoot ratio (Nahar & Gretzmacher, 2011), rooting depth, root length density and root distribution (Songsri *et al.*, 2008; Jongrungklang *et al.*, 2011; Leitner *et al.*, 2014; Obidiegwu *et al.*, 2015) have been identified in other crops as drought resistant traits, and these should be a useful selection criteria for drought resistance traits in Jerusalem artichoke.

Information on root distribution patterns of Jerusalem artichoke under both irrigated and drought conditions are very limited. In a small pot study, reported by Ruttanaprasert *et al.*, (2015), drought significantly increased root to shoot ratio while root length, root surface area, root diameter and root dry weight decreased with drastic drought conditions. Because of the small pot size, deep rooting and root distribution patterns in deeper soil layers were not documented.

A better understanding of the genetic variability within Jerusalem artichoke to increase root length and maintain high photosynthesis might be a promising strategy to improve tuber yield under drought conditions. The objectives of this study were to (1) investigate the root distribution pattern and deep rooting in Jerusalem artichoke genotypes under irrigated and drought conditions, (2) evaluate the root traits associated with photosynthesis and biomass in Jerusalem artichoke genotypes under drought conditions.

Materials and Methods

Plant material and experiment conditions: To better control conditions, this experiment was conducted within a greenhouse using rhizoboxes. The three Jerusalem artichoke genotypes used, JA-5, JA-60 and HEL-65 were chosen because of their previously reported differences in drought tolerance indexes, and tuber yield reduction (Rattanaprasert *et al.*, 2014, 2015). JA-5 is drought resistant genotype with high drought tolerance index (DTI) for root traits and high reduction in tuber yield under drought conditions. JA-60 was identified as drought resistant genotype with high DTI for root traits coupled with low reduction in tuber yield under water stress. HEL-65 is susceptible genotype with low DTI for root trait combined with high reduction in tuber yield under drought conditions. These lines were tested under two water regimes (irrigated (maintained at field capacity, FC) and drought (no water applied between 16 to 46 days after transplanting). The experiment was designed 2 × 3 factorial in a randomized complete block design with three replications repeated over two years.

Seedlings of each genotype were transplanted into the rhizoboxes at the V4 stage (fourth leaf-sprouted (Puangbut *et al.*, 2015). Fertilizer (15-15-15) was applied 15 days after transplanting (DAT) at a rate of 1.56 g per rhizobox.

Seedlings were transplanted into the center of rhizoboxes. Each rhizobox was 10 cm in thickness, 50 cm in width and 120 cm in height. Additional details on preparation of rhizobox experiment is available in Thangthong *et al.*, (2016); similar studies using similar boxes have been used for peanut (Thangthong *et al.*, 2016), rice (Kano-Nakata *et al.*, 2011) and cassava (Izumi &Iijima, 2002). Soil texture was sandy loam (sand 75.0%, silt 17.1% and clay 7.9%) in both years.

Before transplanting, each rhizobox was watered to FC to a depth of 35 cm for crop establishment. One day after transplanting, the water was applied at FC to a depth of 35-95 cm. The well-watered treatment was maintained at FC throughout the crop growth cycle, watering at 1-day intervals. The drought treatment was maintained at FC, watering at 1 day intervals until 15 days after transplanting (DAT). At 16 DAT, soil moisture was allowed to decline until 46 DAT (30 days after imposing drought).

Soil moisture contents at FC and permanent wilting point (PWP) were determined at 14.1% and 4.7%, respectively, using the pressure plate method. The amount of water applied was based on crop water requirements along with water loss from surface evaporation and using the methods described by Puangbut *et al.*, (2017).

Soil moisture content: Soil moisture content was measured by gravimetric method using micro auger method at 30 days after imposing drought at 10, 25, 45, 65, and 85 cm of soil depths. Soil moisture content for each rhizobox was calculated as;

$$\text{Soil moisture content} = \left[\frac{\text{wetweight} - \text{dryweight}}{\text{dryweight}}\right] x100$$

Relative water content (RWC): RWC was measured at 7 and 30 days after imposing drought. The third fully-expanded leaf from the top of the main stem was sampled for each plot between 10:00 h to 12:00 h. After recording the fresh weight, turgid weight was measured after placing the leaf sample in water for 8 h. Leaf dry weight was measured after oven-drying at 80ºC for 48 h. RWC was computed as published by Puangbut *et al.*, (2017).

Leaf gas exchange: Leaf gas exchange was measured at 30 days after imposing drought. The newly expanded leaves was sampled for measuring photosynthesis by using a LI-6400XT portable photosynthesis measuring system (LI-6400, LiCor, Inc., Lincoln, NE, USA) with a 6400-02B LED source providing a PPFD of 1,500 μmol m^{-2} s^{-1} and temperature was set at 25ºC.CO_2 concentration was set at 400 μmol m^{-2} s^{-1} and relative humidity at 70%. Net photosynthetic rate (P_n) was obtained from three plants per treatment.

Shoot dry weight: At 30 days after imposing drought, six plants per treatment were cut at the soil surface and separated into leaf and stem. The leaf and stem samples were oven-dried at 80ºC for 48 h or until the weight was constant and weighted.

Root characteristics: Root traits were measured at 30 days after imposing drought. Each rhizobox was carefully washed with tap water to remove the soil form the root samples. The root arrangement in the soil was fixed by needles. The needles on the black sheet were removed. After this process, two procedures were used to determine root traits, (i) taking photographs and (ii) root scanning. The photographs were taken by Canon EOS6D (Canon Ltd, Tokyo, Japan). The photographs showed root distribution patterns of the whole root system on a black sheet with a scale bar. Roots were separated into square sections taken from the left, center and right columns, each divided into 11 soil layers at 10 cm intervals from the top to the bottom of the box (Fig. 1).

Root surface and root length were analyzed with WinRHIZO program (WinRHIZO Pro(s) V.2004a by Regent Instruments inc.). Root surface and root length from 0-10, 10-20, 20-30 cm layers were combined as a single 0-30cmlayer or upper soil layer, while the root traits for the deeper layers were combined to form a single 30-110cm layer or lower soil layer. The root samples were oven-dried at 80ºC for 48 h and until constant weights and dry weight was recorded.

Statistical analysis: Analysis of variance was performed for individual years and error variances were tested for homogeneity by Bartlett's test (Hoshmand, 2006). Combined analyses of variance were done for those characters whose error variances for the two years were homogeneous. Due to significance of water regime × genotype interaction (Table 2), data for each water regime were analyzed separately according to a randomized complete block (RCB) design and a least significant difference (LSD) test was used to compare means. Calculation procedures were done using the STATISTIX 8 software program. Simple correlation was computed to determine the relationship between root length at lower and upper soil layers with relative water content, photosynthetic rate and biomass under drought treatments.

Results and Discussion

Soil moisture data and relative water content: Figure 2 provides the results of soil moisture monitoring (gravimetric method) at 15, 25, 45, 65 and 85 cm from the soil surface at 46 days after transplanting (30days after imposing drought). Soil moisture content between the irrigated and drought treatment showed clear distinctions at all soil depths for each genotype.

Relative water content (RWC) at 7 days after imposing drought (DAD) was similar between irrigated and drought conditions, likely due to short time duration of stress, yet by 30 DAD, RWC of drought conditions was clearly lower than the irrigated conditions (Table 1). Drought reduced RWC in all Jerusalem artichoke genotypes and the similar results have also been reported by Ruttanaprasert *et al.,* (2016b). The highest RWC was found in the genotype JA-5 under both well-watered and water deficit conditions, while genotypes HEL-65 had the lowest. When comparing RWC in the irrigated treatment to the drought treatment, JA-5 had a relatively low reduction (21.6%) and HEL-65 a high reduction (35.0%). The ability of genotype to maintain a high RWC under drought conditions could be due to many traits including a large root system, a deeper rooting pattern, longer roots and a high root to shoot ratio. The genotype with high root to shoot ratio have been shown to maintain high tuber dry weight under drought conditions (Ruttanaprasert *et al.,* 2015). However, the relationships between RWC and root traits are not well understood in Jerusalem artichoke.

Genotypic variation and genotype × environments interactions for all traits: For root length (RL), root surface (RS), root dry weight (RDW) and root: shoot ratio (R: S ratio) the means differences were non-significant between years (Y) (Table 2). Differences between water regimes (W) for root length, root surface, root dry weight and root: shoot ratio were significant ($p \leq 0.01$). Significant differences in Jerusalem artichoke genotypes (G) for all root traits were found. Water regime × genotype interaction was significant ($p \leq 0.05$) for RL and R: S ratio. Genotype × year (G × Y) and genotype × year × water regime interactions (G × Y × W) were non-significant for all root traits. These trait stabilities and relationships could improve the potential for their use in Jerusalem artichoke breeding programs for drought resistance.

Root distribution pattern of Jerusalem artichoke: The root distribution patterns were the same between R and L columns, and therefore combined as a lateral root from the totals for each layer (data not shown).

Figure 3 shows the root distribution patterns of whole Jerusalem artichoke root on black sheet with scale bar under irrigated (Fig. 3a-3c) and drought conditions (Fig. 3d-3f). Drought reduced overall root growth in all genotypes, when compared to the irrigated treatment.

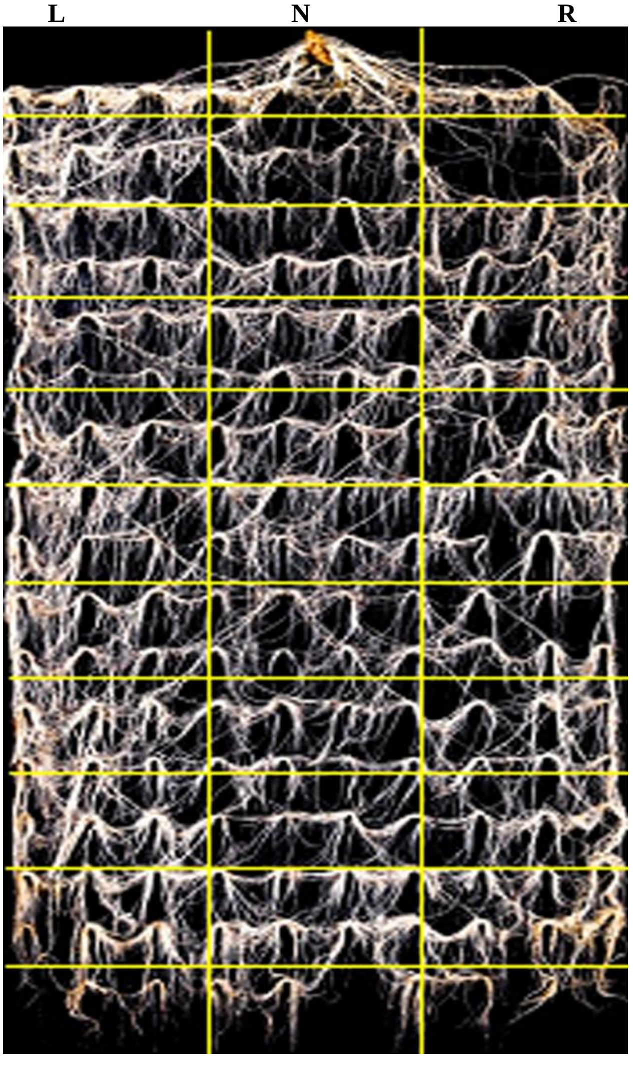

Fig. 1. Digitized image of Jerusalem artichoke root system growth in rhizobox at 30 days after drought imposing and size of grid unit is 10 cm ×10 cm was observed area. L; left column, N; center column, R; right column.

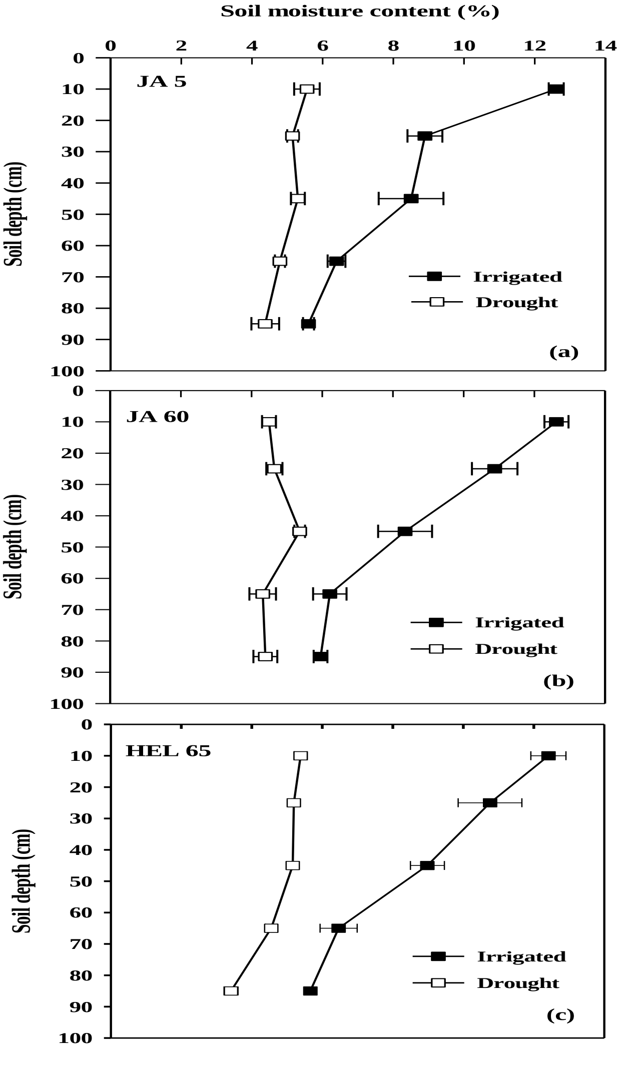

Fig. 2. Soil moisture content of irrigated and drought conditions at 10, 25, 45, 65 and 85 cm of soil depth in three Jerusalem artichoke genotypes.

Table 1. Relative water content (RWC) of three Jerusalem artichoke genotypes under irrigated and drought conditions at 7 and 30 days after imposing drought (DAD).

Genotypes	Relative water content (%)					
	7 DAD			30 DAD		
	Irrigated	Drought	LSD	Irrigated	Drought	LSD
JA 5	87.2 a	86.7 a	ns	85.2 a	66.8 a	**
JA 60	86.8 a	85.0 a	ns	82.6 b	56.3 b	**
HEL 65	85.2 a	84.2 b	ns	82.0 b	53.3 b	**
Mean	86.4	85.3		83.3	58.8	

ns,** Non significant and significant at $p \leq 0.01$

Means in the same column with the same letters are not significantly different by LSD ($p \leq 0.05$)

Table 2. Mean squares from combined analysis of variance for root length (RL), root surface (RS), root dry weight (RDW) and root: shoot ratio observed in year 1 and year 2.

SOV	DF	RL	RS	RDW	R:S ratio
Year (Y)	1	2839ns	0.01ns	6.34ns	0.006ns
Reps. within Y	4	21975	0.08	0.93	0.003
Water regimes (W)	1	469339**	0.44**	11.70**	0.018**
Genotype (G)	2	70868**	0.03**	1.16*	0.008**
W × G	2	21619*	0.008ns	0.01ns	0.001*
G × Y	1	1970ns	0.004ns	0.23ns	0.000ns
G × Y × W	2	6869ns	0.007ns	0.15ns	0.000ns
Pooled Error	20	4690	0.004	0.25	0.000

ns, * ,** Non significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively

Root length and root surface of three Jerusalem artichoke genotypes were divided into two soil layers as the upper soil layer (0-30 cm) and the lower soil layer (30-110 cm) (Figs. 4 and 5). In the upper soil layer, the percentage of total lateral root length and total nodal root length under irrigated were higher than under drought conditions. However, drought resulted in an average increased the percentage of total lateral root length and total nodal root lenght in the lower soil profile by 9.7% and 7.0%, respectively.

The percentage of total lateral root length and total nodal root length in the lower soil layer was increased with drought conditions when compared to irrigated conditions in all genotypes (Fig.4). In JA-5 under irrigated conditions, the percentage of total lateral root length in the lower soil layer was 72.4%, while the percentage of total lateral root length in the lower soil layer was77.6% under drought conditions (Fig. 4a). In JA-60 under irrigated conditions, the percentage of total lateral root length in the lower soil layer was 67.7%, while the percentage of total lateral root length in the lower soil layer was 73.6% under drought conditions (Fig. 4b). In HEL-65 under irrigated conditions, the percentage of total lateral root length in the lower soil layer was 61.7%, whereas the percentage of total lateral root length in the lower soil layer was 70.5% under drought conditions (Fig. 4c). Total nodal root lengths in the irrigated and drought treatments behaved similarly to lateral root patterns in all genotypes (Fig. 4d-4f).

At shallow soil layer, the percentage of total lateral root surface and total nodal root surface areas under drought were lower than under irrigated conditions (Fig. 5).However, drought increased the percentage of total lateral root surface and total nodal root surface areas in the lower soil layer by an average of 9.0% and 10.3% when compared with irrigated treatment (Fig. 5).

Over all genotypes, the percentage of total root length and total root surface increased in the lower soil profile under drought when compared to the irrigated treatment. This reallocation of root growth is likely due to changes in the soil moisture availability at the different depths, and is a drought avoidance mechanism in Jerusalem artichoke. Root traits such as root length, root surface and root volume have been established as a constituting factor of drought avoidance in Jerusalem artichoke (Ruttanaprasert *et al.,* 2015), and in other crops such as peanut (Songsri *et al.*, 2008). Deeper rooting and root distribution are important traits for uptake of water and minerals from deep soil layer, especially when plants are under water deficit.

Root response to water stress of Jerusalem artichoke: Drought decreased root length, root surface area and root dry weight, but increased root: shoot ratio in all the genotypes (Tables 3 and 4).

Significant genotypic differences were observed for total root length and total root surface under drought conditions (Table 3). The highest in total root length and total root surface was detectd in JA-60 and JA-5. In addition, JA-60 also had high DTI for total root length and total root surface (0.78 and 0.63, respectively). Under drought, JA-60 was highest for root dry weight, root: shoot ratio (2.95 g plant^{-1} and 0.21, respectively) and had the highest DTI (Table 4). Ruttanaprasert *et al.*, (2015) reported that genotypes JA-60 and JA-5 were found with high drought tolerant index for root traits under severe drought.

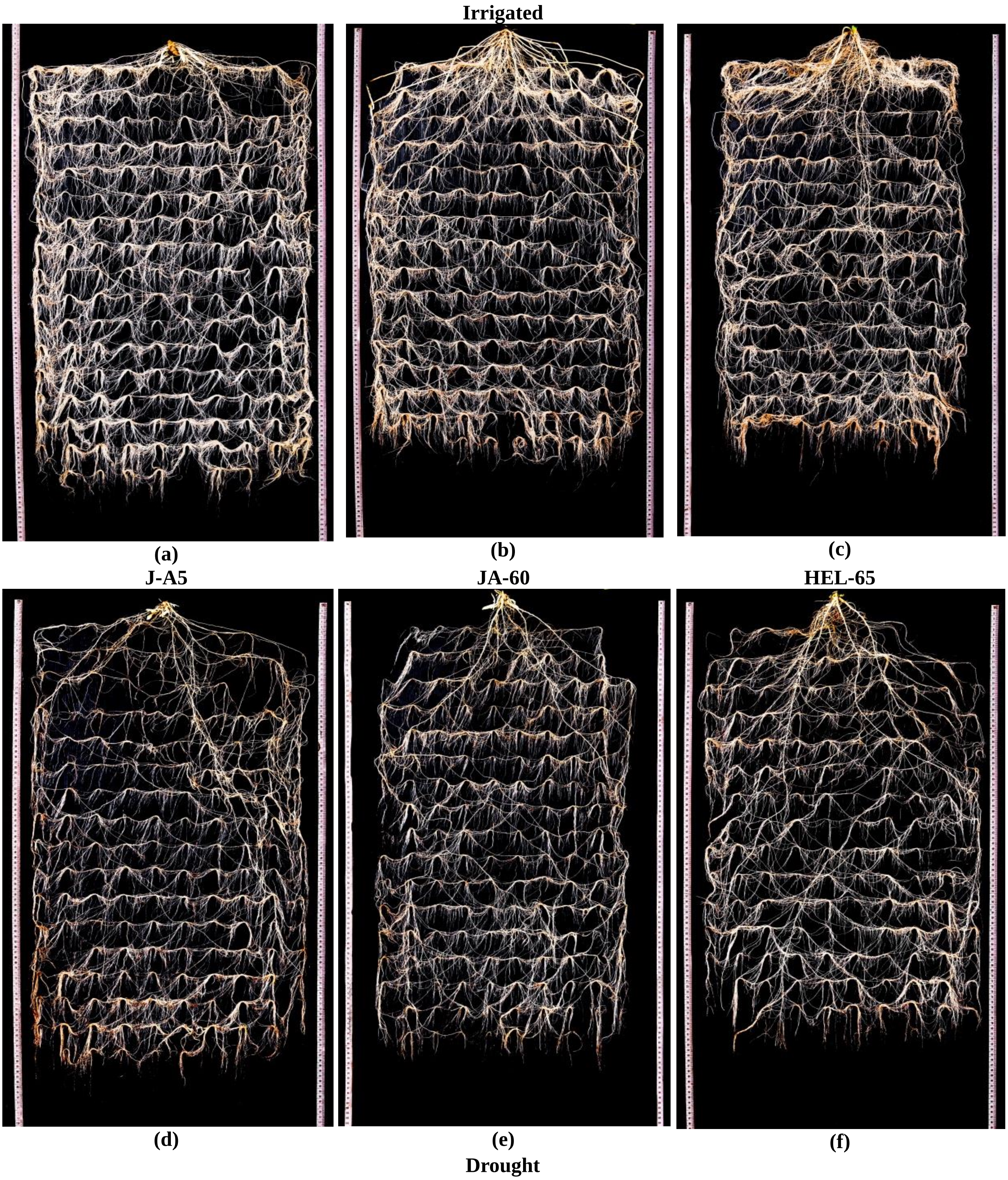

Fig. 3. Root growth of three Jerusalem artichoke genotypes under irrigated (a, b, c) and drought (d, e, f) conditions.

In several plants, deep rooting, root length density and root distribution have been identified as drought adaptation traits which are useful as selection criteria in breeding programs (Watt *et al.,* 2008; Jongrungklang *et al.*, 2012; Leitner *et al.*, 2014; Obidiegwu *et al.*, 2015; Ruttanaprasert*et al.*, 2015). Thus, JA-5 and JA-60 are two Jerusalem artichoke genotypes which should be useful to breeders desiring to improve performance under drought stress.

The relationship between total root length (RL)with RWC, P_n and biomass: DemonstratedPuangbut *et al.,* (2017). They reported that RWC, Pn and biomass were decreased by drought conditions. RWC, $P_n$and biomass was used to determine the relationship with root length under drought conditions in this study.

There was no significant correlation between RL with RWC, P_n and biomass at the upper layer (0-30 cm) under drought conditions (Table 5). Thepositive correlation was found between RL with RWC ($r = 0.79$; $p \leq 0.01$), P_n (r =

0.74; p≤0.01) and biomass (r = 0.64; p≤0.05) at lower soil layer (30-110 cm).

Root length in the deeper soil is an important trait for maintaining RWC under drought conditions. Enhanced root length in the lower soil layers enables plants to better extract available soil moisture from the soil profile (Songsri *et al.*, 2008; Jongrungklang *et al.*, 2013). Selection of genotypes with high root lengthin lower soil layers will likely improve RWC and enhance photosynthetic capacity and plant growth during a drought.

Several reports revealed that root length density and root surface at deep soil layer were important traits related to biomass and yield under drought stress in many crops (Kashiwagi *et al.*, 2006; Comas *et al.*, 2013; Jongrungklang *et al.*, 2014; Zhang *et al.*, 2017). In addition, Ruttanaprasert *et al.*, (2015, 2016a) reported that drought tolerant index for root length was associated with tuber dry weight in Jerusalem artichoke under severe drought. However, information for the relationship between biomass and root length at lower soil layer was not investigated in previous research. This study revealed that root length at lower layer was an important trait contributing to photosynthetic rate (P_n) and biomass under drought conditions. Likewise, Lavinsky *et al.*, (2016) in the study of maize noted that P_n was strongly correlated with root traits under drought conditions therefore, selection of Jerusalem artichoke genotypes for high root length at lower soil depths could result in improving P_n and make a contribution to biomass during drought conditions.

Previous researches on many crops have demonstrated that deep rooting is an important trait to increase water extraction from the deeper soil and improve the plant's ability to continue growth during drought (Watt *et al.*, 2008; Hund *et al.*, 2009; Henry *et al.*, 2011; Obidiegwu *et al.*, 2015, Zhang *et al.*, 2017). The ability of plants to better explore the soil profile for available water will profoundly increase plant productivity under drought (Comas *et al.*, 2013).

Table 3. Total root length and root surface of three Jerusalem artichoke genotypes grown in rhizobox under irrigated and drought conditions.

Genotypes	Total root length (m plant^{-1})			Total root surface (m^2 plant^{-1})		
	Irrigated	Drought	DTI	Irrigated	Drought	DTI
JA 5	858.3 a	537.2 a	0.63	0.69 a	0.41 a	0.60
JA 60	690.6 b	540.4 a	0.78	0.56 a	0.40 a	0.72
HEL 65	651.6 b	401.5 b	0.60	0.53 a	0.29 b	0.55
Mean	733.5	501.4	0.67	0.59	0.37	0.62

Means in the same column with the same letters are not significantly different by LSD (p≤0.05)
DTI for a genotype was calculated by the ratio of drought / irrigated conditions

Table 4. Root dry weight and root: shoot ratio of three Jerusalem artichoke genotypes grown in rhizobox under irrigated and drought conditions.

Genotypes	Root dry weight (g plant^{-1})			Root: shoot ratio		
	irrigated	drought	DTI	irrigated	drought	DTI
JA 5	3.34 a	2.54 b	0.76	0.14 b	0.16 b	1.14
JA 60	3.32 a	2.95 a	0.88	0.18 a	0.21 a	1.16
HEL 65	3.00 ab	2.43 b	0.81	0.17 a	0.19 ab	1.12
Mean	3.22	2.64	0.82	0.16	0.19	1.22

Means in the same column with the same letters are not significantly different by LSD (p≤0.05)
DTI for a genotype was calculated by the ratio of drought / irrigated conditions

Table 5. Simple correlation coefficient (r) between relative water content, net photosynthetic rate, biomass and root length in upper soil layer (0-30 cm) and lower soil layer (30-110 cm) under drought conditions (n = 9).

Traits	Root length $_{\text{upper soil layer}}$	Root length $_{\text{lower soil layer}}$
Relative water content	0.47ns	0.79**
Net photosynthetic rate	0.32ns	0.74**
Biomass	0.38 ns	0.64*

ns, * and ** non-significant, significant at p≤0.05 and significant at p≤0.01, respectively

Conclusions

Drought significantly reduced the root length, root surface, root dry weight, however, the root: shoot ratio was increased. Significant differences among genotypes were found for root traits under drought with JA-5 and JA-60 showed, high root length at the deeper soil and this trait could be identified as drought avoidance mechanism. Present study further revealed that enhanced root length in deep soil layer is important trait to maintaining RWC, P_n and biomass under drought conditions, and a useful trait to be used in futrre breeding program of Jerusalem artichoke to target the drought.

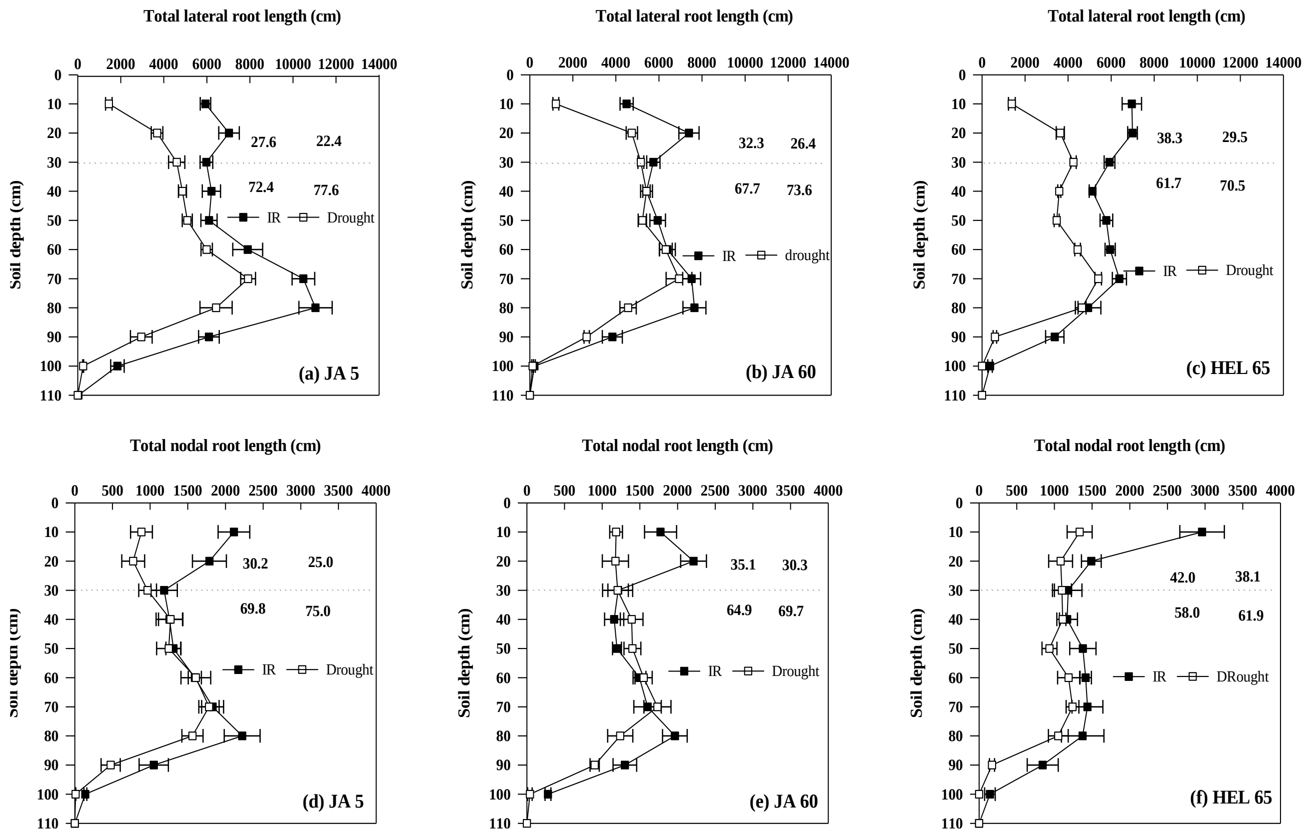

Fig. 4. Total lateral root length (a, b, c) and total nodal root length (d, e, f) of three Jerusalem artichoke genotypes under irrigated (IR) and drought conditions. Numeric values above and below the dotted line indicate percentage of total root length in 0–30 and 30–110 cm soil layers. First column was irrigated (IR) and second column was drought conditions.

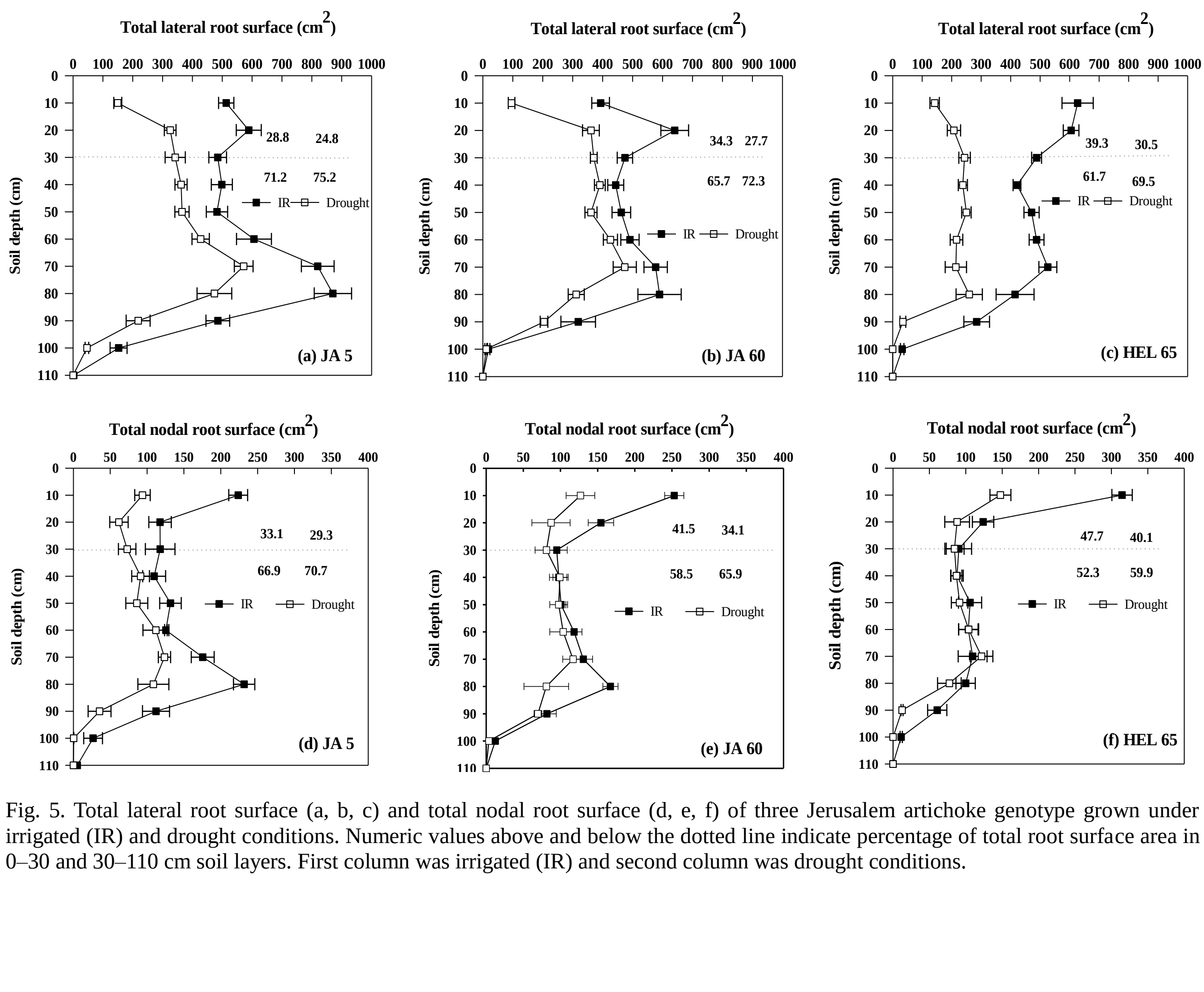

Fig. 5. Total lateral root surface (a, b, c) and total nodal root surface (d, e, f) of three Jerusalem artichoke genotype grown under irrigated (IR) and drought conditions. Numeric values above and below the dotted line indicate percentage of total root surface area in 0–30 and 30–110 cm soil layers. First column was irrigated (IR) and second column was drought conditions.

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