Biomass and Bioenergy 81 (2015) 369–377

Contents lists available at ScienceDirect

Biomass and Bioenergy

journal homepage: http://www.elsevier.com/locate/biombioe

Research paper

Root responses of Jerusalem artichoke genotypes to different water regimes

R. Ruttanaprasert [a], S. Jogloy [a, b, *], N. Vorasoot [a], T. Kesmala [a], R.S. Kanwar [c], C.C. Holbrook [d], A. Patanothai [a]

[a] Department of Plant Science and Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Muang, Khon Kaen, Thailand
[b] Peanut and Jerusalem Artichoke Improvement for Functional Food Research Group, Khon Kaen University, Muang, Khon Kaen, Thailand
[c] Department of Agricultural & Biosystems Engineering, Iowa State University, Ames, IA, USA
[d] USDA-ARS, Coastal Plain Experiment Station, P.O. Box 748, Tifton, 31793, GA, USA

ARTICLE INFO

Article history:
Received 10 November 2014
Received in revised form
19 July 2015
Accepted 20 July 2015
Available online 31 July 2015

Keywords:
Drought
Available soil water
Helianthus tuberosus L.
Crop adaptation
Drought tolerance
Bioenergy

ABSTRACT

The objective of this study was to determine effects of drought on selected root growth parameters and develop relationships between root parameters and tuber yield for selected Jerusalem artichoke (JA) genotypes. Three water regimes (Field capacity, 50% available soil water (AW) and 25% AW) and five JA varieties (JA 60, JA 125, JA 5, JA 89 and HEL 65) were planted with factorial treatments in a randomized complete block design with four replications. Data on root dry weight (RDW) and root: shoot ratios (RSR) were measured manually. Root diameter (RD), root length (RL), root surface area (RSA) and root volume (RV) were collected at harvest. Drought tolerance indices (DTI) were calculated for all root parameters. Drought reduced all root parameters and DTI but increased RSR in JA 60, JA 125, JA 5, and HEL 65. JA 125 had high values for all root traits and DTI of these traits under drought stress. JA 60 had high DTI of RDW, RD and RSR under mild and severe water stress. JA 5 had high DTI of RDW, RD, RL, RSR and RV under drought conditions. JA 89 and HEL 65 performed well for RDW, RD, RL and low DTI of all root characteristics. DTI for root parameters were positively correlated with tuber dry weight under mild and severe water stress. The JA 5, JA 60 and JA 125 varieties showed high DTI for some root traits, indicating that better root parameters contributed to higher tuber yield under drought stress.

1. Introduction

Jerusalem artichoke (*Helianthus tuberosus* L.) is a tuber crop containing inulin that can be used as raw material in many industries. Inulin can be used as soluble dietary fiber or sugar replacement for diabetes disease in the medicine industry, as a stabilizer in the pharmaceutical industry [1] and as raw material for biofuels [2,3]. Jerusalem artichoke is a new crop that has the potential to be grown in temperate and tropical regions of the world.

Global warming may cause more severe and frequent droughts due to either decreased precipitation and/or increased evaporation [4]. Drought reduces productivity of agricultural crops including Jerusalem artichoke [5–10]. Yield loss of 20% under mild water stress has been reported [5,6] and yield loss higher than 90% has been reported under severe drought stress [11]. Although drought problems can be alleviated by irrigation, management of irrigation systems is sometimes difficult in those geographical areas of the world where water resource are not either readily available or too expensive to maintain. The development and utilization of drought tolerant varieties would be ideal in these drought prone areas of the world.

The selection of Jerusalem artichoke for drought tolerance has primary been based on biomass production and tuber dry weight under drought stress conditions. In tropical regions of the world, JA 5 was reported as a drought tolerant variety with high tuber yield under drought stress conditions [11]. The progress in breeding for drought tolerance varieties has been slow because yield and related traits vary greatly, depending on ecological environmental conditions. A better understanding of some physiological mechanisms of drought resistance varieties should accelerate the progress in breeding for high tuber productivity under drought stress.

Drought tolerance may be enhanced by exploiting drought

* Corresponding author. Department of Plant Science and Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Muang, Khon Kaen 40002, Thailand. Tel./fax: +66 43 364 637.
E-mail address: sjogloy@gmail.com (S. Jogloy).

http://dx.doi.org/10.1016/j.biombioe.2015.07.027
0961-9534/

avoidance mechanisms such as the ability of roots to extract water from the soil. Root dry weight, root length, root: shoot ratio [12], deep root and root length density [13–16] have been identified as drought-adaptive traits and they could be used as selection criteria for drought resistance traits. However, root characteristics of Jerusalem artichoke in responses to drought have not been clearly investigated. Therefore, the objective of this study was to determine the effects of drought on selected root growth parameters of Jerusalem artichoke and develop relationships between root growth parameters (characters) and tuber yield for selected drought resistance varieties of Jerusalem artichoke genotypes. The new scientific information from this research on the ability of root traits of selected Jerusalem artichoke genotypes contributing to high tuber yield under water stress are likely to reveal the avoidance mechanism and could result in the development of improved breeding strategies for drought tolerance in Jerusalem artichoke.

2. Materials and methods

2.1. Experimental design and treatments

Pot experiments were conducted at the Field Crop Research Station of Khon Kaen University located in Khon Kaen province, Thailand (16°28′ N, 102°48′ E, 200 m above mean sea level). The experimental treatments were arranged in a 3 × 5 factorial experiment in randomized complete block design with four replications for each treatment and experiments were conducted for two years during May to September 2012 and May to September 2013. Factor A consisted of three water regimes including field capacity (FC), 50% available soil water (50% AW) and 25% available soil water (25% AW) and factor B included five Jerusalem artichoke varieties with different drought tolerance levels based on tuber yield under drought stress. The experimental unit consisted of 5 pots requiring a total of 300 pots for each experiment. The varieties JA 60 and JA 125 had low tuber yield, JA 5 had intermediate tuber yield and JA 89 and HEL 65 had high tuber dry weight under drought stress conditions [11].

2.2. Preparation of plants and pot materials

Tubers with uniform size were cut into small pieces with 2–3 buds per piece. The tuber pieces were then pre-sprouted in charred rice husk with mixed trichoderma in the ratio of 3:1 by volume under ambient conditions for 4–7 days to control *Sclerotium rolfsii*. The sprouted tuber pieces were then transferred to germinating plug trays with mixed medium containing soil, charred rice husk and trichoderma (3:2:2) for 7 days to complete sprouting. Healthy and uniform seedlings were then transplanted to plastic pot containers (1 plant pot^{-1}).

The plastic containers with 35 cm in diameters and 25 cm in height were then filled with 20 kg of dry soil which was separated into two layers to create uniform bulk density. The first soil fraction of 10 kg of dry soil was filled in the bottom of the container at 10 cm below the soil surface, and the second soil fraction of remaining 10 kg was filled to 5 cm below the top of the pot. The water tubes were installed at the middle of these soil fractions. One seedling was transplanted into each container. Wood vinegar obtained from slow pyrolysis of wood was sprayed on Jerusalem artichoke plants two times per week at the dilution of 5 cm^3 wood vinegar in a liter of water to control insects in the pots. Weeds were controlled manually after transplanting and fertilizer grade 15-15-15 was applied to each pot at the rate of 2 g per pot or 265 kg ha^{-1} at 15 days after transplanting (DAT).

2.3. Water management

Water was applied to each pot as per each water treatment and based on crop water requirements (ETcrop) [17] plus to meet the daily surface evaporation (S.E.) needs of pots [18]. Crop water requirements for each pot were calculated as per the requirements of experimental treatments and using the methods described by Ref. [17]:

$$\mathrm{ETcrop} = \mathrm{kc} \times \mathrm{ETo},$$

where ETcrop is the crop water requirement (mm day^{-1}), ETo is evapotranspiration of reference crop and kc is the coefficient of the crop at different growth stages. The crop coefficient (kc) of the Jerusalem artichoke was not found in literature, therefore, kc of sunflower was used [8,10].

Surface evaporation (S.E.) was calculated as [18]:

$$\mathrm{S.E.} = \beta(E_o/t),$$

where S.E. is the soil evaporation (mm), β is the light transmission coefficient measured depending on crop cover, E_o is the evaporation from class A pan (mm day^{-1}), t is the days from the last irrigation.

To maintain a uniform water supply in the whole pot, the irrigation was divided into two fractions. Water was supplied to the soil fractions through the plastic tubes previously installed to the containers. At pre-transplanting, water was supplied to all pots and moisture level was maintained at FC (20.5% of soil moisture content) until 10 DAT for uniform establishment of the plants. Water treatments (20.5% of soil moisture content in FC, 13.9% of soil moisture content in 50% AW and 10.6% of soil moisture content in 25% AW) were imposed to the crop after 14 DAT and maintained uniformly with no more than 1% fluctuation until harvest.

The irrigation supplied to each pot was equal to the sum of water used by the crop and to meet the daily soil surface evaporation needs. The soil water status was also monitored by gravimetric method for soil moisture collection at 7-days interval. The added water irrigation was applied to each pot once a week for maintaining the level of soil moisture treatment.

2.4. Data collection

2.4.1. Meteorology conditions

Weather data for two years were recorded daily from transplanting until crop harvest by a weather station located 100 m away from the experimental field. Maximum temperatures, minimum temperature, daily pan evaporation and daily relative humidity were recorded at this experiment station (Fig. 1).

2.4.2. Soil data

The data on soil texture and chemical properties were collected using ten randomly selected points in the field from where the whole soil was collected and mixed to create two sets of soil samples. The first set was analyzed for field capacity and permanent wilting percentage of soil for irrigation management. The second set was analyzed for the soil texture and the soil chemical properties including total N and available P, pH, organic matter, exchangeable K and Ca and cation exchange capacity.

Soil moisture contents were recorded by gravimetric method at 30, 60 and 90 DAT at the depth of 0–20 cm (Fig. 2).

2.4.3. Plant data

Relative water content (RWC) in each experimental unit was measured at 30, 60 and 90 DAT to estimate plant water status. The

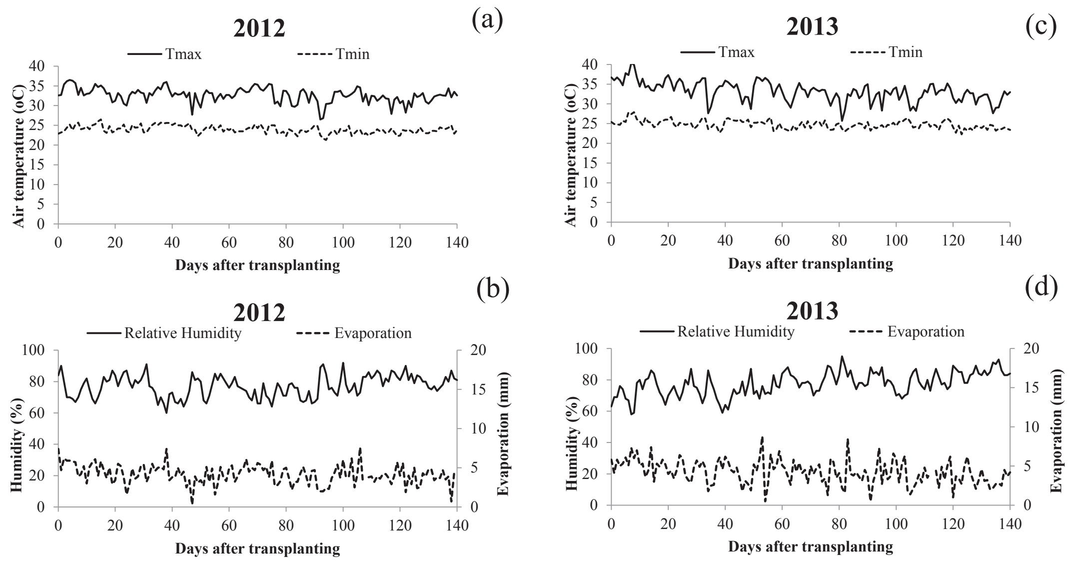

Fig. 1. Maximum temperatures (Tmax), minimum air temperatures (Tmin) (°C), evaporation (mm) and relative humidity (%) in 2012 (a), (b) and 2013 (c), (d).

second leaves from the top of the main stem the five plants in each experimental unit were bored by a disc borer with 1 cm^2 in leaf area. Saturated weight was determined by putting the leaf samples in water for 8 h, blot drying the outer surface, and then measuring leaf weight. The leaf samples were then oven-dried at 80 °C for at least 72 h or until the leaf weights were constant. RWC was calculated as follows [19]:

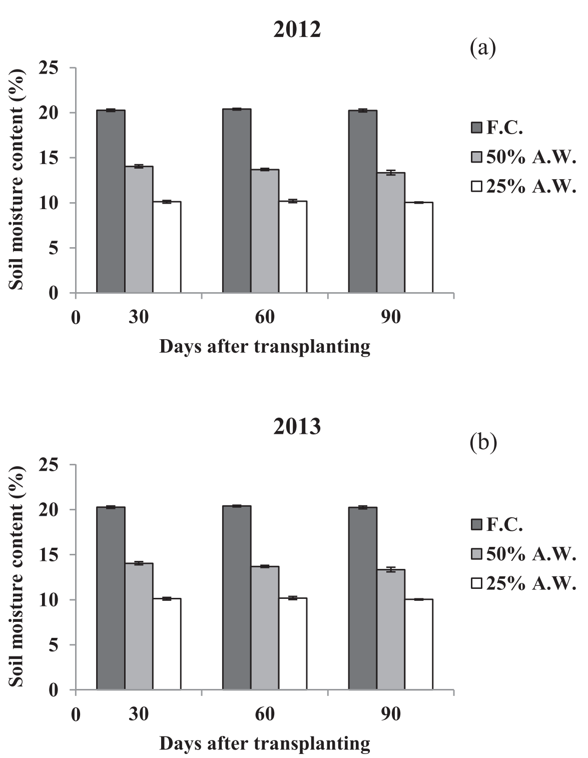

Fig. 2. Soil moisture content (%) under three water regimes (FC = field capacity, 50% AW = 50% of soil available water and 25% AW = 25% of soil available water) at 30 days after transplanting (DAT), 60 DAT and 90 DAT of five Jerusalem artichoke genotypes during 2012 (a) and 2013 (b).

$$\mathrm{RWC} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Saturated weight} - \text{Dry weight}} \times 100$$

The mature plants, which were determined by stem browning of 50%, were cut at the soil surface at harvest. The below ground parts of plants were then separated and washed with tap water to remove soil particles and then separated into tubers and roots. Ten percentage of mass fraction were then taken from the total root mass for further root characteristics including root diameter (mm), root surface (cm^2 $plant^{-1}$), root length (cm $plant^{-1}$) and root volume (cm^3 $plant^{-1}$). Data on root characterization were analyzed using the WINRHIZO Pro2004a software. Roots (plus ten percentage mass fraction of roots) and tubers were then oven-dried at 80 °C for at least 72 h or until the weights were found to be constant. Tuber dry weight (g $plant^{-1}$) and root dry weight (plus ten percentage mass fraction of roots) (g) were recorded.

DTI was calculated for root characteristics (root surface, root length and root volume) using the relationship as follows:

$$\mathrm{DTI} = \frac{\text{Root characteristics under drought stress conditions}}{\text{Root characteristics under non} - \text{drought stress conditions}}$$

2.5. Statistical analysis

Individual analysis of variance was conducted for each root growth parameter or characteristics for each year according to randomize complete block design (RCBD) [20] and all calculations were done using STATISTIX8 software. Variances for all root growth parameters/characters were tested for homogeneity. Least significant difference (LSD) was used to compare means when the differences of main effects were significant ($p \leq 0.05$). Correlation coefficients between DTI of root traits and tuber dry weight were calculated to determine their relationship between the parameters.

3. Results

3.1. Weather conditions

Maximum temperature (Tmax) and minimum temperature

(Tmin) in 2012 ranged between 26.5 and 36.5 °C and between 21.3 and 26.5 °C, respectively (Fig. 1a), Tmax and Tmin in 2013 ranged between 25.7–40.4 °C and 22.3–27.9 °C, respectively (Fig. 1c).Daily pan evaporation ranged from 0.3 to 7.6 mm per day in 2012 and from 0.5 to 8.8 mm per day in 2013 (Fig. 1b and d). The relative humidity values were 60%–92.0% and 58%–95% in the first and second years, respectively (Fig. 1b and d).

3.2. Soil type, soil moisture contents, and plant water status

The soil used for this experiment was loamy sand in both years and characterized as having proportions of sand ranged from 80 to 81%, silt ranged from 15 to 18% and clay ranged from 2 to 4% (Table 1). The soils had 0.59%–0.64% of organic matter, 0.02%–0.03% of total nitrogen contents, 11.21–15.14 mg kg^{-1} of phosphorus and 69–70 mg kg^{-1} of potassium.

Soil moisture contents for FC, 50% AW and 25% AW at 30, 60 and 90 DAT in 2012 and 2013 are presented in Fig. 2. The differences among water regimes were significant during the experiment periods for both years. The FC (19.5–21.1%) was the highest followed by 50% AW (12.3–14.6%) and 25% AW (9.6–10.8%), respectively. These results indicated that soil moisture content was adequately controlled and well managed during the entire duration of the experiment.

Water regimes were also significantly different for relative water content (RWC) at 30, 60 and 90 DAT in both years (Fig. 3). The differences among water regimes in RWC were rather narrow compared to soil water contents, ranging between 88.5 and 91.7% under well-watered condition, 81.1–87.7% under mild water stress and 70.3–84.8% under severe water stress conditions in 2012. These results were also similar in 2013 and RWC values ranged between 80.2 and 88.7% under well-watered condition, 78.5–82.1% under mild water stress and 75.8–77.6%under severe water stress conditions.

3.3. Combined analysis of variance for water use and root traits (root growth parameters)

Combined analysis of variance indicated that differences between years (Y), among water regimes (W) and among varieties (V) were significant for water use (Table 2). There were also significant interactions between year and water regime (Y × W), between year and variety (Y × V), between water and variety (W × V) and secondary levels interactions (Y × W × V) for water use. The interactions between the year and water regime, between year and variety and the secondary interaction contributed a small percent of sum of squares, therefore data on water use for two years were combined and presented together. A larger percent of sum of squares was contributed by water regime x variety, therefore, data on water use for each year and each water regime were analyzed and presented separately.

Combined analysis of variance showed that differences among water regimes (W) and among varieties (V) were significant for all root traits (characters) (Table 2). However, the difference between years (Y) was significant for most root characters except for root dry weight, root surface area and total root volume.

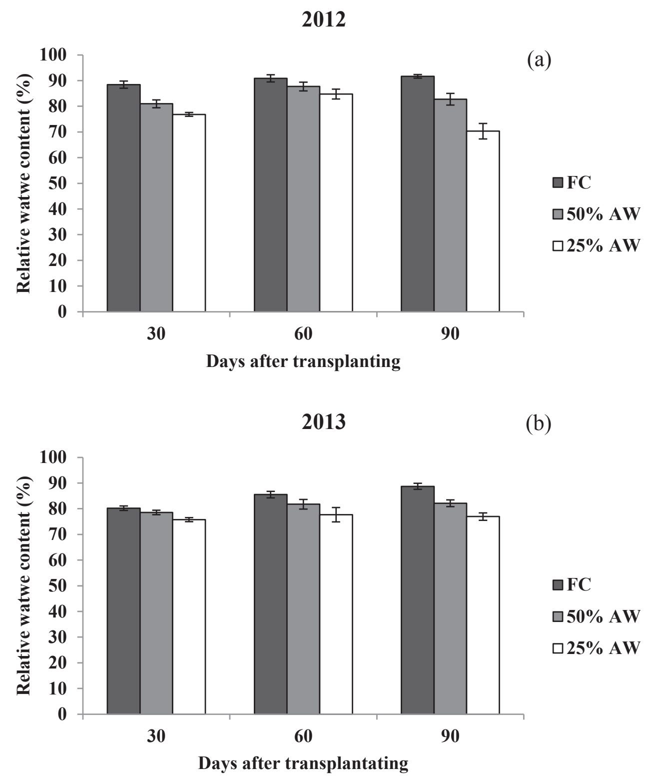

Fig. 3. Leaf relative water content (RWC) under three water regimes (FC = field capacity, 50% AW = 50% of soil available water and 25% AW = 25% of soil available water) at 30 days after transplanting (DAT), 60 DAT and 90 DAT of five Jerusalem artichoke genotypes during 2012 (3a) and 2013 (3b).

The interactions between year and variety (Y × V) were significant for root: shoot ratio, root length, root surface area and root volume. The interactions between water and variety (W × V) were significant for most root characters except for root diameter. The secondary level interactions (Y × W × V) were also found to be significantly different for root shoot ratio, root length and root volume. Due to the significance difference between the year x variety as well as water regime x variety and the secondary interaction for root shoot ratio, root length, root surface area and root volume, data on root traits for each year and for each water regime were analyzed and presented separately.

3.4. Water use

The water use was highest under field capacity conditions, lower under mild water stress and lowest under severe drought stress (Table 3.). The range in values of water use under well water was 60.06–65.07 L pot^{-1}. Under mild water stress, the amount of water use ranged from 30.00 to 32.10 L pot^{-1}. Under severe water stress, the amount of water use ranged from 17.00 to 19.00 L pot^{-1}. In three water conditions, differences among Jerusalem artichoke genotypes were significant for water use. JA 125 showed the highest

Table 1
Soil texture and chemical properties for pot experiments in 2012 and 2013.

Years	Soil texture			Soil type	Soil chemical properties							
	Sand	Silt	Clay		pH	EC (dSm^{-1})	CEC (cmolkg^{-1})	OM (%)	Total N (%)	Available P (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})
2012	80%	18%	2%	Loamy sand	6.4	0.02	17.84	0.59	0.03	11.2	69	1005
2013	81%	15%	4%	Loamy sand	6.1	0.02	7.76	0.64	0.02	15.1	70	823

Table 2
Mean squares for water use (L pot^{-1}), root dry weight (g plant^{-1}), root: shoot ratio, root length (cm plant^{-1}), root surface (cm^2 plant^{-1}), root volume (cm^3 plant^{-1}) and root diameter (mm) of five Jerusalem artichoke genotypes grown under three water regimes (FC = field capacity, 50% AW = 50% of soil available water and 25% AW = 25% of soil available water) in 2012 and 2013.

Source of variance	df	Water use (L pot^{-1})	Root dry weight (g plant^{-1})	Root: shoot ratio	Root length (km plant^{-1})	Root surface (cm^2 plant^{-1})	Root volume (cm^3 plant^{-1})	Root diameter (mm)
Year (Y)	1	0.13 (0.00)**	1.51 (0.11) ns	0.108 (5.92)*	0.0906 (0.60)*	30,49,641 (0.15) ns	6 (0.00) ns	0.0171 (16.17)**
Rep within year	6	0.00 (0.00)	0.61 (0.27)	0.008 (2.63)	0.0079 (0.32)	12,18,461 (0.37)	74 (0.29)	0.0009 (4.92)
Water (W)	2	22,080.80 (99.51)**	461.03 (68.58)**	0.231 (25.28) **	5.1220 (68.49)**	63,28,00,000 (63.68)**	49,764 (65.33)**	0.0043 (8.08)**
Y × W	4	0.03 (0.00)**	0.31 (0.05) ns	0.001 (0.15) ns	0.3889 (0.03) ns	158,083 (0.02) ns	19 (0.02) ns	0.0013 (2.41) ns
Variety (V)	2	40.65 (0.37)**	44.99 (13.38)**	0.018 (3.92)*	0.0023 (10.40)**	740,10,000 (14.89)**	5531 (14.52)**	0.0055 (20.83)**
Y × V	4	0.01 (0.00)**	0.96 (0.29) ns	0.014 (3.17)*	0.0736 (1.97)**	45,87,265 (0.92)*	313 (0.82)**	0.0002 (0.68) ns
W × V	8	6.58 (0.12)**	19.79 (11.78)**	0.060 (26.38) **	0.1839 (9.84)**	329,00,000 (13.24)**	2779 (14.59)**	0.0006 (4.47) ns
Y × W × V	8	0.00 (0.00)**	0.73 (0.44) ns	0.015 (6.66)*	0.0326 (1.74)**	25,53,567 (1.03) ns	158 (0.83)*	0.0004 (3.28) ns
Error	84	0.00 (0.00)	0.82 (5.11)	0.006 (25.89)	0.0116 (6.54)	13,53,413 (5.71)	65 (3.57)	0.0005 (39.15)
Total	119							

Numbers in the parentheses are percent (%) of sum squares to total sum of squares.
ns, *,** Non significant, significant and highly significant at P ≤ 0.05 and ≤ 0.01 probability levels, respectively.

Table 3
Water use (L pot^{-1}), Root dry weight (g plant^{-1}), drought tolerance index (DTI) of root dry weight, root diameter (mm) and DTI of root diameter of five Jerusalem artichoke genotypes grown under different water regimes at harvest in 2012 and 2013.

Genotypes	Water use (L pot^{-1})			Root dry weight (g plant^{-1})					Root diameter (mm)				
	FC	50% AW	25% AW	FC	50% AW	25% AW	DTI (50% AW)	DTI (25% AW)	FC	50% AW	25% AW	DTI (50% AW)	DTI (25% AW)
JA 60	63.06b	32.10b	17.00d	6.70d	3.29b	1.74	0.50b	0.27b	0.3448b	0.3246b	0.3145	0.95	0.91
JA 125	65.05a	33.00a	19.00a	8.32c	5.21a	2.15	0.63a	0.26b	0.3454b	0.3570a	0.34	1.04	0.99
JA 5	60.06c	30.00c	17.00d	4.95e	2.68b	1.69	0.55ab	0.35a	0.3221c	0.3248b	0.3184	1.01	0.99
JA 89	65.07a	32.05b	18.00c	12.86a	4.80a	1.95	0.38c	0.16c	0.3650a	0.3558a	0.327	0.98	0.9
HEL 65	65.06a	32.06b	18.01b	10.05b	4.82a	1.98	0.48bc	0.20bc	0.3651a	0.3615a	0.3452	0.99	0.94
Means	63.66	31.84	17.8	8.58	4.16	1.9	0.51	0.25	0.3485	0.3447	0.329	0.99	0.95

Means in the same column with the same letter(s) are not significantly different by LSD at P ≤ 0.05.
DTI for genotype was calculated by the ratio of stressed (50% soil available water (AW) or 25% AW)/non-stressed (field capacity; FC) conditions.

water use across the three water levels.

3.5. Root characters and drought tolerance index (DTI)

The results of this study showed that drought stress reduced root dry weight and root diameter (Table 3). Means of root dry weight were found to be equal to 8.58, 4.16 and 1.90 g plant^{-1} under well-watered, mild water stress and severe drought stress, respectively. Further, the drought tolerance index (DTI) for root dry weight was reduced by drought stress. Under mild water stress, DTI for root dry weight was 0.51 and it was lower under severe drought stress (0.25).

Means of root diameter were 0.35, 0.34 and 0.33 mm under well-watered, mild water stress and severe water stress, respectively. DTI for root diameter was also reduced by drought stress. DTI values were 0.99 and 0.95 under mild water stress and under severe water stress, respectively.

Severe drought stress (25% AW) increased root: shoot ratio (Table 4). Overall means for root: shoot ratios in 2012 were 0.36, 0.33 and 0.47 under well watered, mild water stress and severe water stress, respectively. In 2013, means for root: shoot ratios were 0.30, 0.26 and 0.42 under well watered, mild water stress and severe water stress, respectively. Mean DTI for root: shoot ratios (1.39 in 2012 and 1.52 in 2013) under severe water stress were higher than under mild water stress (1.00 in 2012 and 0.92 in 2013).

Drought reduced root lengths of all Jerusalem artichoke varieties. Mean roots lengths in 2012 were 0.91, 0.43 and 0.21 km plant^{-1} under well watered, mild water stress and severe water stress, respectively and mean root lengths in 2013 were 0.96, 0.50 and 0.25 km plant^{-1} under well watered, mild water stress and severe water stress, respectively. Mean DTI for root length under mild drought stress were 0.51 in 2012 and 0.53 in 2013 and under severe drought stress were 0.25 in 2012 and 0.28 in 2013.

Roots surface areas were reduced by drought stress in both years. Mean roots surface areas in 2012 were 9988, 4830 and 2037 cm^2 plant^{-1} under well watered, mild drought stress and severe drought stress, respectively. In 2013, mean roots surfaces were 10,162, 5234 and 2415 cm^2 plant^{-1} under well watered, mild drought stress and severe drought stress, respectively. Mean DTI for root surface were 0.54 (in 2012) and 0.52 (in 2013) under mild water stress and 0.24 (in 2012) and 0.25 (in 2013) under severe drought stress.

Drought stress reduced root volumes in both years. Mean root volumes in 2012 were 89, 44 and 18 cm^3 plant^{-1} under well watered, mild drought stress and severe drought stress, respectively. Mean root volumes in 2012 were 88, 44 and 19 cm^3 plant^{-1} under well watered, mild drought stress and severe drought stress, respectively. Mean DTI for root volumes were 0.56 (in 2012) and 0.51 (in 2013) under mild water stress and 0.26 (in 2012) and 0.24 (in 2013) under severe drought stress.

3.6. Variability of root characteristics

Under well watered condition, differences among Jerusalem artichoke genotypes were significant for root dry weight and root diameter (Table 3). Jerusalem artichoke genotypes could be classified into the group with high root dry weight and the group with low root dry weight. JA 89 and HEL 65 exhibited the highest root

Table 4
Root: shoot ratio, drought tolerance index (DTI) of root: shoot ratio, root length (cm $plant^{-1}$), DTI of root length, root surface (cm^2 $plant^{-1}$), DTI of root surface, root volume (cm^3 $plant^{-1}$) and DTI of root volume of five Jerusalem artichoke genotypes grown under different water regimes (FC; field capacity, 50% AW; 50% soil available water and 25% AW; 25% soil available water) at harvest in 2012 and 2013.

Varieties	2012			DTI (50% AW)	DTI (25% AW)	2013			DTI (50% AW)	DTI (25% AW)
	FC	50% AW	25% AW			FC	50% AW	25% AW		
Root: shoot ratio										
JA 60	0.33b	0.33	0.56a	1.01	1.69	0.29bc	0.32	0.51ab	1.10	1.75
JA 125	0.24b	0.39	0.43bc	1.62	1.77	0.22c	0.28	0.58a	1.30	2.66
JA 5	0.30b	0.29	0.53ab	0.97	1.75	0.29bc	0.23	0.36bc	0.78	1.24
JA 89	0.48a	0.26	0.34c	0.55	0.70	0.40a	0.26	0.23c	0.65	0.57
HEL 65	0.46a	0.39	0.48ab	0.84	1.04	0.31b	0.23	0.43ab	0.74	1.40
Means	0.36	0.33	0.47	1.00	1.39	0.30	0.26	0.42	0.92	1.52
Root length (km $plant^{-1}$)										
JA 60	0.71cd	0.37	0.21	0.52	0.30	1.09ab	0.50ab	0.23b	0.46	0.22
JA 125	0.78c	0.46	0.22	0.59	0.28	0.91b	0.67a	0.38a	0.74	0.42
JA 5	0.55d	0.35	0.17	0.64	0.31	0.55c	0.26c	0.20b	0.47	0.37
JA 89	1.39a	0.45	0.21	0.33	0.15	1.28a	0.61ab	0.22b	0.48	0.17
HEL 65	1.13b	0.52	0.22	0.46	0.20	0.96b	0.47b	0.24b	0.49	0.25
Means	0.91	0.43	0.21	0.51	0.25	0.96	0.50	0.25	0.53	0.28
Root surface (cm^2 $plant^{-1}$)										
JA 60	8227c	3846b	2082ab	0.47	0.25	10,025b	5016b	2368b	0.50	0.24
JA 125	8445c	5464a	2623a	0.65	0.31	9142b	7000a	3810a	0.77	0.42
JA 5	3971d	3153b	1539b	0.79	0.39	5855c	2488c	1552b	0.42	0.27
JA 89	15,804a	5682a	1918ab	0.36	0.12	14,476a	6552ab	2122b	0.45	0.15
HEL 65	13,492b	6007a	2022ab	0.45	0.15	11,314b	5115b	2224b	0.45	0.20
Means	9988	4830	2037	0.54	0.24	10,162	5234	2415	0.52	0.25
Root volume (cm^3 $plant^{-1}$)										
JA 60	75c	36a	17	0.48	0.23	83b	37cd	20b	0.45	0.24
JA 125	81c	50a	24	0.62	0.30	84b	53ab	33a	0.63	0.39
JA 5	32d	28b	16	0.87	0.50	48c	26d	17b	0.53	0.35
JA 89	142a	53a	16	0.37	0.12	126a	59a	12b	0.47	0.10
HEL 65	116b	55a	18	0.47	0.15	96b	45bc	15b	0.46	0.15
Means	89	44	18	0.56	0.26	88	44	19	0.51	0.24

Means in the same column with the same letter(s) are not significantly different by LSD at $P \leq 0.05$.
DTI for genotype was calculated by the ratio of stressed (50% available water (AW) or 25% AW)/non-stressed (field capacity; FC) conditions.

dry weight and root diameter. In contrast, JA 5, JA 60 and JA 125 showed the lowest root dry weight and root diameter.

Under mild water stress, JA 125 performed well as it had high root dry weight and DTI for root dry weight, whereas JA 5 and JA 60 had low root dry weight and high DTI of root dry weight. In contrast, JA 89 and HEL 65 were categorized into the group with high root dry weight and low DTI for root dry weight.

JA 125, JA 89 and HEL 65 had high root diameter and high DTI for root diameter, whereas JA 60 and JA 5 had low root diameter and high DTI of root diameter. However, the differences among five Jerusalem artichoke genotypes for root dry weight and root diameter under severe water stress were not significant.

Jerusalem artichoke genotypes responded differently for root: shoot ratio, root length, root surface and root volume under well watered conditions in both years (Table 4). JA 89 and HEL 65 had high root: shoot ratio, root length, root surface area and root volume under well watered conditions in both years. JA 125 and JA 5 had low root: shoot ratio, root length, root surface and root volume under well watered conditions in both years. JA 60 had high, root length, root surface and root volume under well watered conditions in 2013 only.

Severe water stress increased root: shoot ratio in JA 60, JA 125 JA 5 and HEL 65 in both years, whereas JA 89 did not respond to drought for root: shoot ratio. JA 60 performed well for root: shoot ratio under mild and severe water stress conditions in both years. JA 125 also performed well under mild and severe water stresses as it had highest DTI of root: shoot ratio in both years, whereas JA 89 performed poorly as it had low DTI for root: shoot ratio in both years.

JA 125 performed well for root length under mild and severe water stress in both years as it had high root length and DTI of root length in both years. JA 125 and JA 5 had high DTI of root length under mild and severe water stress in both years but JA 89 and HEL 65 had rather low DTI of root length under mild and severe water stress in both years. JA 125 had high root surface and DTI for root surface under mild and severe water stresses in both years, whereas JA 89 and HEL 65 had high root surface but they had low DTI of root surface under mild and severe water stress in both years. JA 125 and JA 5 showed consistently high DTI for root volume under mild and severe water stress. JA 125 had also high root volume under mild and severe water stress in both years.

JA 125 had high root dry weight, root diameter, root: shoot ratio, root length, root surface, root volume across years, and values of DTI for these traits under mild and severe water stress were also high. JA 60 was identified as the genotype with high DTI of root dry weight, root diameter and root: shoot ratio under mild and severe water stress. JA 5 was identified as the genotype with high DTI of root dry weight, root diameter, root length, root surface and root volume under mild and severe water stress. JA 89 and HEL 65 performed well for root dry weigh, root diameter, root length and low DTI of all root characteristics. JA 125, JA 60 and JA 5 consistently performed well under drought stress by maintaining the ability to absorb water by having high DTI of some root traits.

3.7. Relationship between tuber dry weight and root characteristics

Tuber dry weight was positively correlated with DTI for root dry weight under severe water stress ($r = 0.95$, $P \leq 0.05$) and mild water stress ($r = 0.80$, $P > 0.05$) (Fig. 4).

The correlation coefficient between tuber dry weight and DTI for root: shoot ratio was significant under mild water stress ($r = 0.63$, $P \leq 0.05$) but not significant under severe water stress ($r = 0.41$,

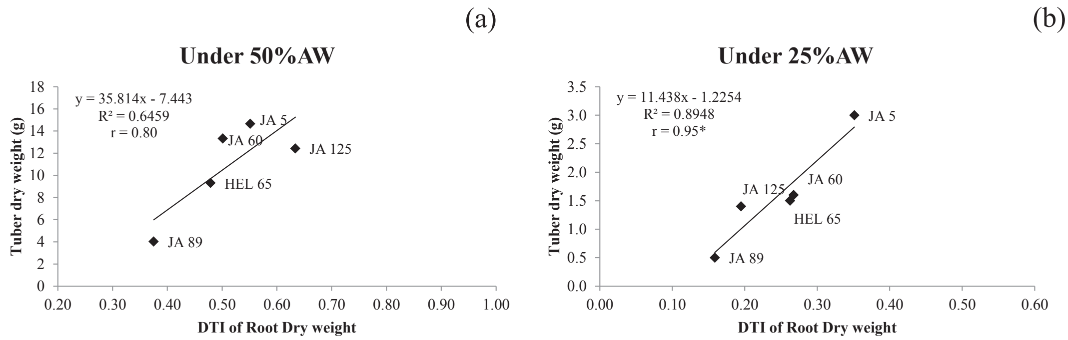

Fig. 4. -Relationship between tuber dry weight (g) and drought tolerance index (DTI) of root dry weight under 50% AW (50% soil available water) (a) and under 25% AW (b) of five Jerusalem artichoke genotypes in 2012 and 2013.

$P > 0.05$) (Fig. 5a and b).Positive correlations coefficients were observed between tuber dry weight with DTI for root length, DTI for root surface and DTI for root volume. Correlation coefficient (0.72, $P \leq 0.01$) between tuber dry weight and DTI for root length was significant under severe water stress, but the correlation was not significant under mild water stress (0.51, $P > 0.05$) (Fig. 5c and d).The correlation coefficients between tuber dry weight and DTI for root surface was positive and significant under severe water stress (0.72, $P \leq 0.01$) (Fig. 5e and f).The correlation coefficients between tuber dry weight and DTI for root volume were not significant under mild water stress ($r = 0.59$, $P > 0.05$) and under severe water stress ($r = 0.61$, $P > 0.05$) (Fig. 5g and h).

4. Discussion

How Jerusalem artichoke could maintain high tuber yield under drought stress has not been clearly understood. A better understanding on the mechanisms underlying high tuber yield under drought stress could lead to the success in breeding of Jerusalem artichoke for drought resistance. The information on the physiological traits related to drought avoidance mechanism that can maintain high water uptake and high tuber yield under drought has not been clearly investigated for Jerusalem artichoke. A better understanding on the root response of Jerusalem artichoke under drought stress should be useful for improving high tuber dry weight under water limited conditions. Drought resistance in crop may be enhanced by improving the extraction of water from the soil. Our study demonstrated that Jerusalem artichoke genotypes responded to drought to maintain high tuber dry weight under mild and severe soil moisture conditions. The results of this study also demonstrated the significant correlations between root traits and tuber weight under mild and severe drought conditions, indicating that roots are important in maintaining tuber yield in Jerusalem artichoke under drought conditions.

The interactions between year and variety for root: shoot ratio, root length, root surface area and root volume, though significant, were very small compared to main effects (water regime and variety). Low interactions indicated that the varieties performed rather consistently across years. The interactions between year and water regime were not significant for all of the root traits. This indicated that the effect of water regime was rather consistent across years. Low interaction level favors selection of better genotypes under both, non-stress or drought stress conditions. Greater variations in root dry weight, root: shoot ratio, root length, root surface, root volume and root diameter were found among varieties. These results clearly indicated that it is possible to select Jerusalem artichoke genotypes for better performance for these traits under differing levels of soil moisture.

The interaction between water regime and variety was significant for root dry weight, root: shoot ratio, root length, root surface and root volume. This revealed that those root traits were expressed under partially mild and severe water stress. Therefore, the selection for high root: shoot ratio of Jerusalem artichoke under severe water stress could be recommended. Likewise, differences for root length, root surface and root volume traits were expressed under mild water stress.

Drought increased root: shoot ratio but it reduced root dry weight, root diameter, root length, root surface area and root volume. Severe water stress resulted in greater reductions of those traits compared to mild water stress. These observations are in agreement with some previous studies. In sunflower, drought stress reduced root volume, total root length [21,22] and root diameter [21]. Del- Rosario and Fajardo [23] found that root dry weight of peanut was reduced by drought but root: shoot ratio was increased. Nevertheless, the response for root dry weight to drought conditions occurred in some genotype which had low leaf water potential. In some drought tolerance varieties of tomato, drought (withholding water) increased root dry weight, root: shoot ratio and root length [12]. Songsri et al. [16] found that root length density in deeper subsoil level was increased in response to drought.

In this study, Jerusalem artichoke varieties responded differently for root traits under both mild water stress and severe water stress. Increase in root traits was related to tuber dry weight, indicating that roots contributed to high tuber yield under drought. The relationships between DTI of root trait and tuber yield in Jerusalem artichoke have not been reported previously. In peanut, Songsri et al. [16] found that the ability to maintain the percentage of root length density (DTI) was related to pod yield, DTI for pod yield and DTI for harvest index. The ability of peanut to maintain a viable root system during water stress may contribute to the crop's drought resistance [24].

Jerusalem artichoke genotypes were classified into the group with high DTI values for root dry weight, root diameter, root: shoot ratio, root length, root surface area and root volume and the group with low DTI values for these traits. These Jerusalem artichoke genotypes were previously identified as drought tolerant varieties based on tuber yield, but their responses to drought based on root traits was not investigated. JA 125, JA 5 and JA 60 showed the highest DTI values for root parameters, and JA 89 and HEL 65 showed the lowest DTI values for root parameters.

JA 89 had the highest root dry weight but it had the lowest DTI values for root traits under mild water stress and severe water stress. In this genotype, the contribution of dry matter was partitioned to vegetative growth rather than harvestable organ. The sink competition between the harvestable part and the root sink should

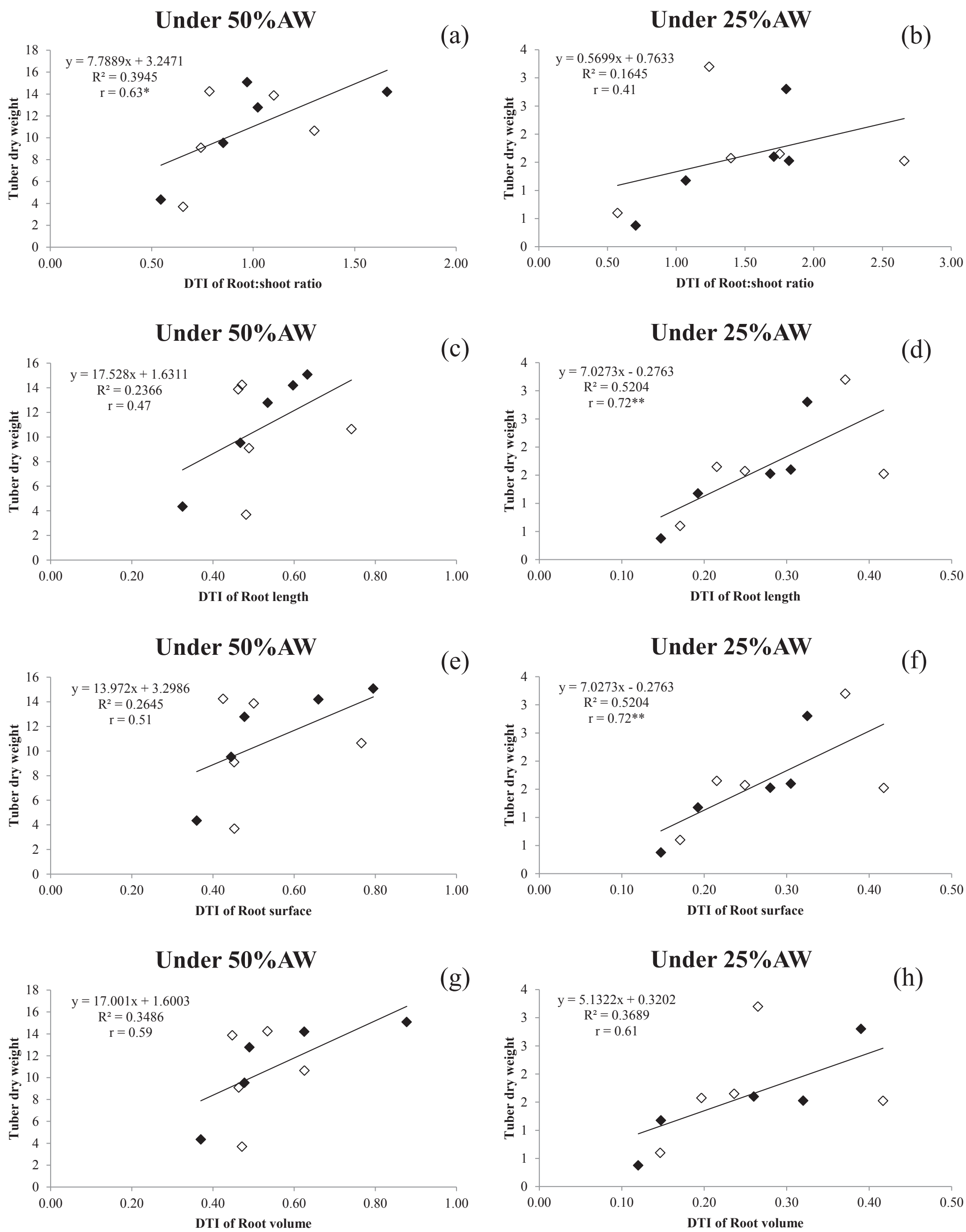

Fig. 5. Relationship between tuber dry weight (g) and drought tolerance index (DTI) of root: shoot ratio under 50% AW (50% soil available water) (a) and under 25% AW (b), between tuber dry weight (g) and DTI for root length under 50% AW (c) and under 25% AW (d), between tuber dry weight (g) and DTI for root surface under 50% AW (e) and under 25% AW (f), between tuber dry weight (g) and DTI of root volume under 50% AW (g) and under 25% AW (h) of five Jerusalem artichoke genotypes in 2012 and 2013.

be considered when devising breeding strategies to improve drought resistance [25]. JA 125, JA 5 and JA 60 were classified as a group with high tuber dry weight under mild water stress, and JA 5 was identified as the drought tolerant genotypes under severe drought stress because it had the highest tuber dry weight under severe water stress. Some varieties had low means for root parameters but they had high DTI values for these parameters. The results indicated that Jerusalem artichoke varieties changed root growth patterns in response to drought to mine more water from drying soils, and, therefore, these varieties could maintain high tuber yield under drought.

5. Conclusion

Drought stress reduced root dry weight, root diameter, root length, root surface area, root volume, and DTI for these root characteristics in all Jerusalem artichoke varieties. Drought stress increased root: shoot ratio of JA 60 and JA 125 varieties. Tuber dry weight was positively correlated with DTI for root dry weight, root diameter, root: shoot ratio, root length, root surface and root volume under mild water stress and severe water stress. Variations in responses to drought for root traits were observed among Jerusalem artichoke genotypes. Based on DTI for root traits, JA 5, JA 60 and

JA 125 were identified as the varieties with drought avoidance mechanism because these varieties could stabilize tuber yield and have the capability to absorb water under drought conditions. This mechanism might help Jerusalem artichoke to obtain higher tuber yields under drought conditions. Breeding for maintaining yield under water-limited conditions by the adaptation of root parameters may facilitate the development of improved Jerusalem artichoke varieties in specific water limited-environments.

Acknowledgments

The Royal Golden Jubilee Ph.D. Program (jointly funded by Khon Kaen University and the Thailand Research Fund) (grant no. PHD/0026/2551), the Thailand Research Fund, provided financial supports to this research through the Senior Research Scholar Project of Professor Dr. Sanun Jogloy and the project was partially supported by the Plant Breeding Research Center for Sustainable Agriculture, Khon Kaen University. The Higher Education Promotion and National Research University Project of Thailand of the Office of Higher Education Commission were also acknowledged for funding support through the Food and Functional Food Research Cluster of Khon Kaen University. Finally, we would like to thank the Thailand Research Fund (TRF) Khon Kaen University (KKU) and Faculty of Agriculture KKU for providing financial support for training on manuscript preparation.

References

[1] T. Barclay, M. Ginic-Markovic, P. Coope, N. Petrovsky, Inulin—a versatile polysaccharide with multiple pharmaceutical and food chemical uses, J. Excip. Food Chem. 1 (3) (2010) 27–50.
[2] T. Zhang, Z. Chi, C.H. Zhao, Z.M. Chi, F. Gong, Bioethanol production from hydrolysates of inulin and the tuber meal of Jerusalem artichoke by *Saccharomyces sp.* W0, Bioresour. Technol. 101 (21) (2010) 8166–8170.
[3] F. Yang, Q. Liu, X. Bai, Y. Du, Conversion of biomass into 5–hydroxymethylfurfural using solid acid catalyst, Bioresour. Technol. 102 (3) (2011) 3424–3429.
[4] A. Dai, Increasing drought under global warming in observations and models, Nat. Clim. Ch. 3 (2013) 52–58.
[5] J.R. Conde, J.L. Tenorio, B. Rodriguez-Maribona, L. Ayerbe, Tuber yield of Jerusalem artichoke (*Helianthus tuberosus* L.) in relation to water stress, Biomass Bioenerg. 1 (3) (1991) 137–142.
[6] N. Losavio, N. lamascese, A.V. Vonella, Water requirements and nitrogen fertilization in Jerusalem artichoke (*Helianthus tuberosus* L.) grown under Mediterranean conditions, Acta Hortic. 449 (1997) 205–209.
[7] S. Schittenhelm, Agronomic performance of root chicory, Jerusalem artichoke and sugar beet in stress and non-stress environment, Crop Sci. 39 (1999) 1815–1823.
[8] A. Monti, M.T. Amaducci, G. Venturi, Growth response, leaf gas exchange and fructans accumulation of Jerusalem artichoke (*Helianthus tuberosus* L.) as affected by different water regimes, Eur. J. Agron. 23 (2005) 136–145.
[9] Z.X. Liu, J.H.J. Spiertz, S. Jing, X. Shuai, H.X. Guang, Growth and yield performance of Jerusalem artichoke clones in a semiarid region of China, Agron. J. 104 (6) (2012) 1538–1546.
[10] R. Ruttanaprasert, B. Poramate, S. Jogloy, N. Vorasoot, T. Kesmala, R.S. Kanwar, et al., Genotypic variability for tuber yield, biomass and drought tolerance in Jerusalem artichoke germplasm, Turk J Agric For 38 (2014) 570–580.
[11] R. Ruttanaprasert, S. Jogloy, N. Vorasoot, T. Kesmala, R.S. Kanwar, C.C. Holbrook, et al., Effects of water stress on total biomass, tuber yield and harvest index in Jerusalem artichoke, Agr. Water Manage. (2015) (Submitted).
[12] K. Nahar, R. Gretzmacher, Response of shoot and root development of seven tomato cultivars in hydrophonic system under water stress academic, Acad. J. Plant Sci. 4 (2) (2011) 57–63.
[13] M.M. Ludlow, R.C. Muchow, A critical evaluation of traits for improving crop yields in water—limited environments, Adv. Agron. 43 (1990) 107–153.
[14] T. Matsui, B.B. Singh, Root characteristics in cowpea related to drought tolerance at the seedling stage, Exp. Agric. 39 (2003) 29–38.
[15] L. Taiz, E. Zeiger, Stress physiology, in: L. Taiz, E. Zeiger (Eds.), Plant Physiology, fourth ed., Sinauer Associates Inc, Sunderland, Massachusetts, 2006, pp. 671–681.
[16] P. Songsri, S. Jogloy, N. Vorasoot, C. Akkasaeng, A. Patanothai, C.C. Holbrook, Root distribution of drought-resistant peanut genotypes in response to drought, J. Agron. Crop Sci. 194 (2008) 92–103.
[17] J. Doorenbos, W.O. Pruitt, Guideline for Predicting Crop Water Requirements, FAO Irrigation and Drainage Paper No. 24, FAO, Rome, 1992, pp. p.1–p65.
[18] S. Singh, M.B. Russell, Water use by maize/pigeonpeas intercrop on a deep vertisol, in: Y.L. Nene, V. Kumble (Eds.), International Workshop on Pigeonpeas Volume 1. Proceeding of The International Workshop on Pigeonpeas Volume 1; 1980 Dec 15–19, ICRISAT Center Patancheru, India, AP, 1980, pp. 271–282.
[19] P.J. Kramer, Drought, stress and the origin of adaptation, in: N.C. Turner, P.J. Kramer (Eds.), Adaptation of Plant to Water and High Temperature Stress, John Wiley & Sons, New York, 1980, pp. 7–20.
[20] K.A. Gomez, A.A. Gomez, Statistical Procedures for Agricultural Research, second ed., John Wiley & Sons, New York, 1984.
[21] M. Perbea, E. Petcu, The effect of soil water content on sunflower seedlings, Rom. Agric. Res. (2000) 43–47.
[22] M.I. Hossain, A. Khatun, M.S.A. Talukder, M.M.R. Dewan, M.S. Uddin, Effect of drought on physiology and yield contributing characters of sunflower, Bangladesh J. Agric. Res. 35 (2010) 113–124.
[23] D.A. Del-Rosario, F.F. Fajardo, Morphophysiological responses of ten peanut (*Arachis hypogaea* L.) varieties to drought stress, Philipp. Agric 71 (1988) 447–459.
[24] T.Y. Reddy, V.R. Reddy, V. Anbumozhi, Physiological responses of groundnut (*Arachis hypogaea* L.) to drought stress and its amelioration: a critical review, Plant Growth Regul. 41 (2003) 75–88.
[25] R. Ruttanaprasert, S. Jogloy, N. Vorasoot, T. Kesmala, R.S. Kanwar, et al., Photoperiod and growing degree days effect on dry matter partitioning in Jerusalem artichoke, Int. J. Plant Prod. 7 (3) (2013) 393–416.