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Genetic diversity of water use efficiency in Jerusalem artichoke (*Helianthus tuberosus* L.) germplasm

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Abstract

Genetic diversity in crop germplasm is an important resource for crop improvement, but information on genetic diversity is rare for Jerusalem artichoke, especially for traits related to water use efficiency. The objectives of this study were to investigate genetic variations for water use and water use efficiency in Jerusalem artichoke accessions and to identify superior genotypes for these characters under different water regimes. Forty Jerusalem artichoke accessions were arranged in a strip plot design with four replications for two years. Three strip plots represented three water regimes (W1 = 100%, W2 = 75% and W3 = 45% of crop water requirement). Data were recorded for tuber dry weight, biomass, relative water content, water use and water use efficiency. The effects of water regimes and Jerusalem artichoke accessions were significant for all characters. Genotypes contributed the largest portions for water use efficiency for biomass and tubers. These results documented genetic diversity for water use efficiency in Jerusalem artichoke. The genotypes with high water use efficiency for biomass were HEL 231, HEL 65 and JA102×JA89(8). HEL 65 had high water use efficiency for tubers. These genotypes should be useful in future breeding programs for higher water use efficiency.

Keywords: Diversity, Drought resistance, Sun-choke, Transpiration efficiency, Water stress.
Abbreviations: WU- Water use; WUEb- Water use efficiency for biomass; WUEt- Water use efficiency for tuber.

Introduction

Jerusalem artichoke (*Helianthus tuberosus* L.) is an underutilized crop that originated in the temperate regions of North America. It has been known as "potato for the poor" and was consumed as vegetable by native Americans and the early settlers (Cosgrove et al., 1991). Jerusalem artichoke stores inulin in stems and tubers, which can be used as raw material for supplementing various value-added and health food products (Kay and Nottingham, 2008; Roberfroid, 2000). More recently, interest in Jerusalem artichoke research has increased substantially as indicated by the number of research articles in the freely-accessed sources. This is because it can be grown in a wide range of environments (Pimsean et al., 2010), while other inulin producing crops such as root chicory (*Chicorium intybus* var. *sativum*) and globe artichoke (*Cynara cardunculus* var. *scolymus*) have a rather limited production range in the temperate regions or high altitude areas (Burke, 2005; Robert et al., 2007). Jerusalem artichoke has been grown in many parts of the world and production conditions range from rainfed to fully irrigated and the crop can be grown in all seasons in a wide range of climates, although the productivity varies greatly across regions (Baldini et al., 2006; Rodrigues et al., 2007). Drought is a recurring problem for crops including Jerusalem artichoke grown in most growing conditions. When only 50% of the water requirement was available, tuber yield of Jerusalem artichoke was reduced by 20% (Conde et al., 1991) and 22.8% (Losavio et al., 1997). Among inulin containing and sugar containing crops, Jerusalem artichoke is more susceptible to water stress than sugar beet and root chicory (Schittenhelm, 1999). The previous studies indicated that the crop requires adequate soil moisture for optimum yield. The questions arising from the previous studies are "1) what is the optimal amount of water to be applied to Jerusalem artichoke with supplemental irrigation or full irrigation under rainfed conditions, and 2) is there variation in water use efficiency among Jerusalem artichoke accessions under different water gradients?" These questions are important for water management of the crop and further improvement of water use efficiency by the crop. Jerusalem artichoke varieties with high water use efficiency should be more productive under water limited conditions. The trait can be used as a selection criterion for drought resistance (Teare et al., 1982). The use of water use efficiency, which is relatively simple to assess, as an indicator trait for the more complex and difficult to access trait of drought resistance would be effective and efficient. Variation in water use efficiency among genotypes has been reported in other crops such as peanut (*Arachis hypogaea* L.) (Jongrungklang et al., 2008; Puangbut et al., 2009), Isabgol (*Plantago ovata*) and French phyllium (*Plantago psyllium*) (Rahimi et al., 2011) and Cotton (*Gossypium herbaceum* L.) (Tennakoon and Milroy, 2002). Previous investigations on water use and water use efficiency

Table 1. Mean squares for water use (WU), water use efficiency for biomass (WUEb) and water use efficiency of tubers (WUEt) of 40 Jerusalem artichoke genotypes grown under three water regimes (W1,W2 and W3) in the dry seasons 2010/11 and 2011/12.

Source of variation	DF	Mean square		
		WU	WUEb	WUEt
Year (Y)	1	33^{ns} (0.0)	2.36056** (20.0)	0.63644** (10.4)
Reps within Year	6	19648 (5.8)	0.02775 (1.4)	0.02216 (2.2)
Water regimes (W)	2	894720** (88.4)	0.06598** (1.1)	0.04403** (1.4)
Y×W	2	2683^{ns} (0.3)	0.00148^{ns} (0.0)	0.00468^{ns} (0.2)
Error (a)	12	2914 (1.7)	0.00419 (0.4)	0.00157 (0.3)
Genotypes (G)	39	792** (1.5)	0.14837** (49.0)	0.06839** (43.7)
Y ×G	39	152** (1.5)	0.03142** (10.4)	0.02557** (16.4)
Error (b)	234	73 (0.8)	0.00191 (3.8)	0.00145 (5.6)
W×G	78	59** (0.2)	0.00633** (4.2)	0.00533** (6.8)
Y×W ×G	78	39^{ns} (0.2)	0.00616** (4.1)	0.00449** (5.7)
Error (c)	468	32 (0.7)	0.00140 (5.6)	0.00095 (7.3)
CV (%) (a)		36.36	21.51	17.63
CV (%) (b)		5.77	14.52	16.95
CV (%) (c)		3.83	12.44	13.71

ns, *, ** = non-significant and significant at $P < 0.05$ and $P < 0.01$ probability levels, respectively.
Values in parenthesis are percentages of sum squares. W1= 100%ET, W2= 75%ET and W3=45%ET.

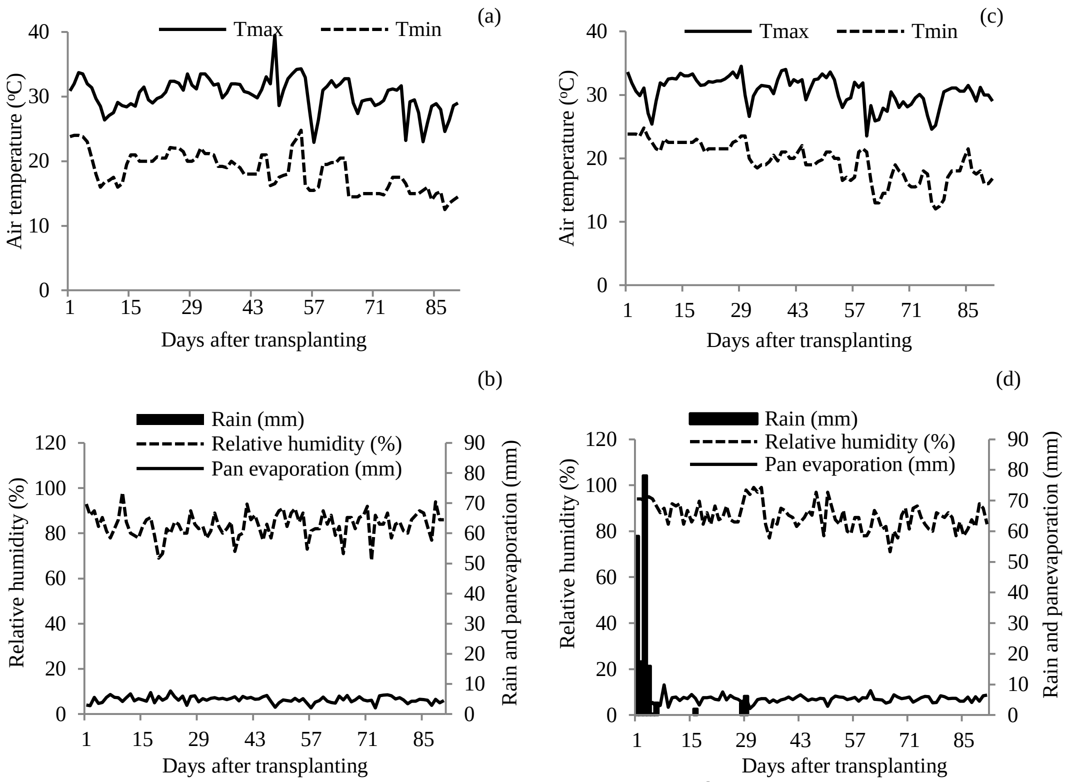

Fig 1. Maximum air temperatures (T-max), minimum air temperatures (T-min) (^{O}C), rainfall (mm), pan evaporation (mm) and relative humidity(RH) (%) during the crop growth period of Jerusalem artichoke in the dry season 2010/11 (a),(b) and the dry season 2011/12 (c),(d)

conducted so far have been limited to 6 Jerusalem artichoke genotypes (Yang et al., 2010). Studies on a wide range of diverse genotypes are required to fully exploit genetic variations in these characters. The objectives of this study were to compare water use efficiency among Jerusalem artichoke genotypes under different water gradient conditions and to identify Jerusalem artichoke genotypes with high water use efficiency. The information obtained in this study will be useful for irrigation management of Jerusalem artichoke and breeding of Jerusalem artichoke for high water use efficiency.

Results

Meteorological conditions, soil moisture status and variation of plant water status

Average daily maximum (T-max) and minimum temperature (T-min) were slightly different between years. Means of T-max in the first year and the second year were 30.3 ^{o}C and 30.5 ^{o}C, respectively. Means of T-min in the first year and the second year were 18.4 ^{o}C and 19.5 ^{o}C, respectively. Daily pan evaporations ranged from 2.0 to 7.7 mm in the first year and 2.2 to 9.8 mm in the second year.

Table 2. Ten selected genotypes with the highest water use (WU), water use efficiency for biomass (WUEb) and water use efficiency for tubers (WUEt) and 10 selected genotypes with the lowest performance for these traits and drought tolerance index (DTI) selected from 40 Jerusalem artichoke genotypes in the dry seasons 2010/11.

Group	No.	Water use (WU) (mm)				DTI		Water use efficiency for biomass (WUEb) (kg mm^{-1} ha^{-1})				DTI[a]		Water use efficiency for tubers (WUEt) (kg mm^{-1} ha^{-1})				DTI	
		Genotypes	W1	W2	W3	W2	W3	Genotypes	W1	W2	W3	W2	W3	Genotypes	W1	W2	W3	W2	W3
High	1	HEL 62	217.5 a	161.8 a	93.3 b	0.74	0.43	HEL 53	32.7 a	36.6 a	31.4 a	1.12	0.96	HEL 53	24.8 a	27.2 a	32.0 a	1.10	1.29
	2	HEL 246	211.2 ab	157.7 ab	114.7a	0.75	0.54	HEL 253	32.0 a	28.5 b	31.9 a	0.89	1.00	HEL 335	24.3 a	18.9 ab	13.2 g-k	0.78	0.54
	3	KKUAc001	210.3 abc	158.3 ab	93.1 b	0.75	0.44	HEL 335	30.7 ab	20.4 e-h	19.2 e-i	0.66	0.62	HEL 65	22.5 ab	15.9 c-f	22.8 c	0.70	1.01
	4	HEL 256	209.6 a-d	158.7 ab	93.3 b	0.76	0.44	HEL 256	30.7 ab	24.0 cde	26.9 a-d	0.78	0.88	HEL 256	22.1 abc	12.9 e-i	14.5 e-j	0.58	0.66
	5	JA 125	209.3 a-d	155.8 a-e	92.4 b	0.74	0.44	HEL 61	28.7 bc	22.1 bc	22.8 c-f	0.77	0.79	HEL 61	22.1 abc	15.7 c-f	17.9 def	0.71	0.81
	6	HEL 257	209.0 a-d	155.4 a-f	92.6 b	0.74	0.44	HEL 65	28.3 bc	21.1 efg	28.5 ab	0.75	1.01	HEL 253	22.0 abc	16.1 cde	20.1 cd	0.73	0.91
	7	JA 77	208.9 a-d	158.0 ab	92.3 b	0.76	0.44	JA102XJA89(8)	28.0 bc	21.5 ef	28.4 ab	0.77	1.01	JA 89	21.4 a-d	20.9 b	26.7 b	0.98	1.25
	8	JA 67	208.9 a-d	157.1 abc	92.3 b	0.75	0.44	JA 89	25.7 cd	27.5 bc	27.7 ab	1.07	1.08	JA102XJA89(8)	20.4 a-e	16.1 cde	17.9 def	0.79	0.88
	9	HEL 53	208.7 a-d	157.8 ab	93.1 b	0.76	0.45	HEL 231	25.7 cd	26.1 bcd	24.3 b-e	1.02	0.95	HEL 231	19.7 a-f	16.0 c-f	19.5 cd	0.81	0.99
	10	HEL 335	208.1 a-d	158.1 ab	93.4 b	0.76	0.45	KKUAc001	24.0 d	22.7 de	27.2 abc	0.95	1.33	KKUAc001	17.3 a-g	20.5 b	19.7 cd	1.19	1.14
Low	1	HEL 253	194.7 b-f	157.9 ab	93.4 b	0.81	0.48	JA 125	10.2 m-p	13.7 j-o	13.3 jp	1.35	1.31	JA 36	8.4 g-j	5.1 pq	7.1 n	0.60	0.85
	2	JA 21	194.5 b-f	146.6 i-m	86.8 b	0.75	0.45	JA 36	9.9 n-q	9.2 p-s	8.5 p	0.93	0.86	HEL 62	8.3 a-j	8.4 k-p	8.4 lmn	1.01	1.01
	3	HEL 65	194.5 b-f	156.5 a-d	91.1 b	0.80	0.47	JA 60	9.4 n-r	10.7 n-r	10.1 nop	1.14	1.07	JA 125	8.3 g-j	10.1 g-n	11.3 j-n	1.22	1.36
	4	HEL 324	193.7 b-f	145.6 j-m	86.5 b	0.75	0.45	JA 109	9.3 n-r	13.7 j-o	20.3 e-h	1.47	2.17	JA 60	7.8 g-j	9.1 i-o	10.7 j-n	1.17	1.37
	5	JA 3	193.3 b-f	144.7 klm	86.4 b	0.75	0.45	JA 46	8.8 n-r	10.9 m-r	12.2 k-p	1.23	1.39	JA 109	6.8 g-j	9.6 h-o	17.2 d-h	1.41	2.53
	6	JA 76	192.5 c-f	156.6 a-d	93.1 b	0.81	0.48	JA 97	8.6 o-r	8.7 qrs	15.5 h-n	1.01	1.80	JA 61	6.5 a-j	6.1 opq	9.5 k-n	0.93	1.45
	7	JA 36	191.7 c-f	143.4 lm	85.5 b	0.75	0.45	JA 77	7.5 pqr	8.5 qrs	8.5 p	1.13	1.12	JA 77	6.3 hij	7.1 l-q	7.1 ln	1.12	1.12
	8	JA 6	191.5 def	146.6 i-m	86.6 b	0.77	0.45	JA 1	6.9 qr	5.6 s	9.1 p	0.82	1.33	JA 97	6.0 ij	6.8 m-q	11.5 j-n	1.13	1.92
	9	JA 16	188.9 ef	141.8 m	84.7 b	0.75	0.45	JA 70	6.8 qr	7.9 rs	10.3 m-p	1.16	1.52	JA 1	5.8 ij	4.7 q	7.9 mn	0.82	1.36
	10	JA 15	181.8 f	148.6 e-m	85.2 b	0.82	0.47	JA 61	6.3 r	7.1 rs	9.4 op	1.12	1.48	JA 70	5.5 j	6.6 n-q	8.4 lmn	1.19	1.52
Mean			201.8 A	152.5 B	90.5 C	0.76	0.45		16.9 AB	15.7 B	17.7 A	0.97	1.21		13.45 A	12.15B	14.27A	0.94	1.14
Min			181.8	141.8	84.7	0.73	0.43		6.3	5.6	8.5	0.66	0.62		5.5	4.7	7.1	0.58	0.54
Max			217.5	161.8	114.7	0.82	0.54		32.7	36.6	31.9	1.47	2.17		24.8	27.2	32.0	1.41	2.52

Maximum, minimum and mean values were calculated from 40 genotypes, For comparison among Jerusalem artichoke genotypes and for comparison among water regimes, Means in the same column followed by the same letter(s) are not significantly different at $P < 0.05$ probability levels by Duncan's multiple range test (DMRT).

[a]DTI = Drought tolerance index was calculated by the ratio of stressed conditions / non stressed conditions.

W1= 100%ET, W2= 75%ET and W3=45%ET

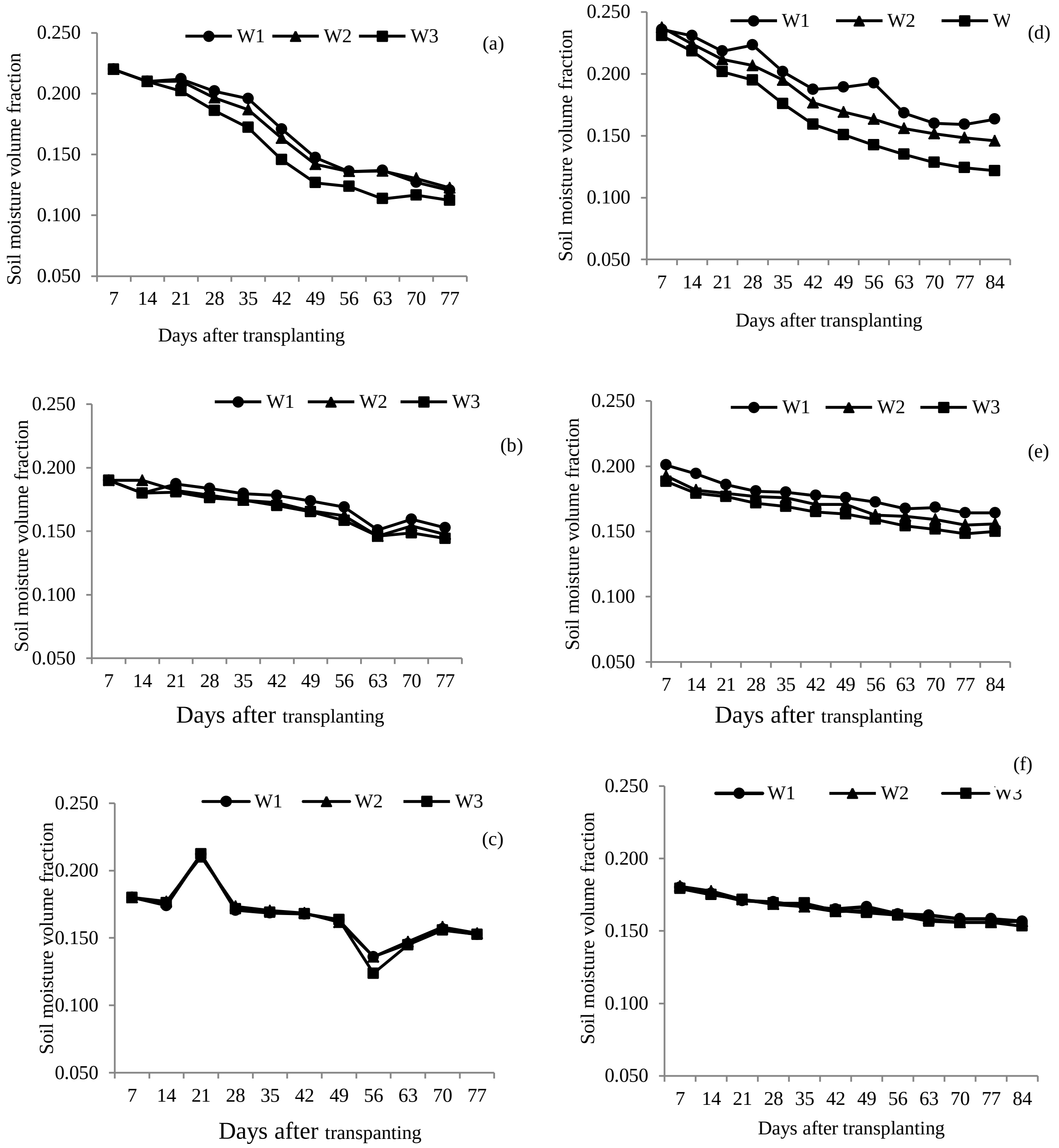

Fig 2. Soil moisture volume fractions for three soil water regimes (W1= 100%ET, W2= 75%ET and W3= 45%ET) of three soil depths at 30 cm (a), 60 cm (b) and 90 cm (c) in the dry seasons 2010/11 and the dry season 2011/12 (d-f).

Daily maximum relative humidity ranged from 69 to 98 % in the first year and 71 to 99% in the second year (Fig. 1a,c). There was no rainfall during the experimental period in 2010/11 but rainfall of 174.6 mm was recorded in 2011/12 at 1–6 days after transplanting (DAT) (Fig. 1b,d). The rainfall did not cause significant difference among water treatments because it occurred during pre-treatment period, when all treatments received the same amount of water. Soil moisture contents of different water regimes (W1–W3) were clearly different at the soil depth of 30 cm, starting from 21 DAT when water was supplied to the crop by line- source sprinkler irrigation system for a week (Fig. 2 a,d). Soil moisture content for W1 was slightly lower than field capacity but higher than W2 because deep water loss was ignored and the soil is well-drained. The differences in soil moisture content among water regimes were significant, but differences in soil moisture content were reduced with the depth of the soil profile (Fig 2 b,e). There was no difference in soil moisture at 90 cm depth (Fig. 2 c,f). Relative water contents (RWC) at 40, 60 and 70 DAT for W1 were higher than those for W2, and relative water contents for W2 were higher than those for W3 in both years, indicating that the control of water supply for all water regimes was reasonably good (Fig 3).

Combined analysis of variance

Combined analysis of variance showed significant differences between water regimes (W) and Jerusalem artichoke genotypes (G) for WU, WUEb and WUEt (Table 1). The difference in years (Y) was significant for most characters ($P<0.01$) except for WU, and the differences among genotypes for WU were significant but accounted for only 1.5% of total variation. Year × water interactions were not significant for all characters, whereas the interactions between water and genotypes were significant for all characters. Y × G interactions for WUEb (10.4% of SS) and WUEt (16.4% of SS) were much larger than that for WU (1.5% of SS), the variations among genotypes for these traits were also higher (49.0% of SS for WUEb and 43.7% of SS for WUEt). Year × water × genotype interactions were significant for WUEb and WUEt ($P \leq 0.01$) but not for WU. Water regimes accounted for small percentages of variations in WUEb and WUEt (1.1–1.4%). The contribution of genotype × water regime interaction was higher than that of water regimes but it was still lower than the contribution of genotypic differences to WUEb and WUEt.

Water use and water use efficiency

As the interactions between genotype and year were significant for WU, data were analyzed by year (Tables 2 and 3). WU in both years depended largely on water regimes, in which the highest WU was observed for W1 and the lowest WU was recorded for W3. Genotypic variations for WU were low for all water regimes in both years, and the variations were lowest for W3. Drought tolerance indices for WU were higher for W2 in both years, indicating that under water stress less water used by plants. The identification of superior genotypes for WU was difficult because of low variation for this trait and high Y × G interaction. As the interactions for WUEb and WUEt between genotype and year, genotype and water regime and secondary level of interaction were high but much lower than that for genotype main effect, the data for two years were analyzed separately (Tables 2 and 3). The variations in these traits were due largely to variations in genotypes. Water regime contributed less to total variations compared to genotype main effect, but the differences in water regimes did not show consistent patterns between years. Drought tolerance indices across years for WUEb and WUEt for W3 in general were consistently higher than those for W2. The data indicated that W3 could somewhat increase water use efficiency. The genotypes with high or low WUEb and WUEt could then be identified. HEL 53, JA 89, KKUAc001, JA102×JA89(8), HEL 253, HEL 231, HEL 65 and HEL 61 had consistently high WUEb and WUEt across water regimes in 2010/11. HEL 335 had consistently high WUEb and WUEt under W1 and W2, whereas HEL 256 had high WUEb across water regimes but WUEt exhibited high water use efficiency under W1 only. JA 61, JA 70, JA 1, JA 77, JA 97, JA 46, JA 109, JA 60, JA 36 and JA 125 had low WUEb under W1 in 2010/11, whereas JA 61, JA 70, JA 1, JA 77, JA 60 and JA 36 had consistently low WUEb across water regimes. The genotypes with low WUEb also had low WUEt except for HEL 62 showing low WUEt only and JA 46 showing low WUEb only. JA 70, JA 1, JA 77, JA 61 and JA 36 showed consistently low WUEb and WUEt across water regimes. In the experiment in 2011/12, HEL 256, JA 89, JA 6, HEL 231, HEL 65, CN 52867, KKUAc001, HEL 324, JA102×JA89(8) and JA 16 had high WUEb under W1, and, among these genotypes, JA 6, HEL 231, HEL 65 and JA102×JA89(8) had high water use efficiency across water regimes. HEL 256, JA 89, JA 6, HEL 65, HEL 257, CN 52867 , JA 122, JA 16, HEL 324 and JA102×JA89(8) had high WUEt under W1. Among these accessions, there were 3 genotypes (JA 6, HEL 65 and CN 52867) with high water use efficiency across water regimes. The genotypes with low WUEb under W1 were JA 1, JA 70, JA 36, JA 109, HEL 62, JA 60, JA 46, JA 61, JA 125, JA 92, and the genotypes showing consistently WUEb across water regimes were JA 1, JA 92, JA 70, JA 36, JA 109, JA 60, JA 46 and HEL62. Most genotypes showing low WUEb also had low WUEt. However, JA 125 and JA 61 had low WUEb but their WUEt was relatively high under W1. In contrast, JA 67 and JA 77 had low WUEt but WUEb was relatively high. JA 70, JA 109, HEL 62 and JA 36 showed consistently low WUEt across water regimes. JA 89, KKUAc001, JA102×JA89(8), HEL 231 and HEL 65 had high WUEb across years under W1, whereas JA 89, JA102 × JA89(8) and HEL 65 had high WUEt. Three genotypes (HEL 231, HEL 65 and JA102×JA89(8)) had consistently high WUEb across water regimes and years, and HEL 65 had high WUEt across water regimes and years. There were 6 genotypes (JA61, JA 70, JA 1, JA 109, JA 60 and JA 36) showing consistently low WUEb across years under W1 and 7 genotypes (JA 70, JA 1, JA 109, HEL 62, JA 36, JA 60 and JA 77) showing consistently low WUEt under W1. However, there were only four genotypes (JA 70, JA 1, JA 60 and JA 36) with consistently low WUEb across water regimes and years and three genotypes (JA 70, HEL 62 and JA 36) with consistently low WUEt across water regimes and years. Correlation coefficients between the data of two years (2010/11 and 2011/12) for water use efficiency for biomass WUEb and water use efficiency for tuber yield (WUEt) were calculated for three water regimes (Fig. 4). Correlation coefficients for (WUEb) were positive and significant for all water regimes, being 0.71**, 0.57** and 0.48** for W1, W2 and W3, respectively (Fig. 4 a,b,c). Correlation coefficients for WUEt were lower but positive and significant, being 0.59**, 0.29* and 0.31* for W1, W2 and W3, respectively (Fig. 4 d,e,f). Correlation coefficients between years for WUEb and WUEt were lower in the drought treatments of W2 and W3 (Fig. 4 b,c and e,f), and correlation coefficients for WUEb were higher than for WUEt for all water regimes. Drought at moderate level (W2) caused 7.1 and 9.6% reductions in WUEb and WUEt, respectively, but drought at severe level (W3) caused slight increases in WUEb (4.2%) and WUEt (5.4%). The reductions in 2010/11 were higher than in 2011/12 (data not shown). In 2010/11, the DTI ranged in all drought conditions from 0.54 to 2.52 (Table 2). The genotypes showing high DTI for WUEb and WUEt were JA 109, JA 97, HEL 324, JA 70 and JA 61 in W3 ranged from 1.44 to 2.52. In the experiment in 2011/12, the DTI ranged in all drought conditions from 0.54 to 1.73 (Table 3). The genotypes with high DTI for WUEb were JA 3, JA 15, HEL 253, JA 38 and JA 61 in W3 ranged from 1.33 to 1.57 and DTI for WUEt the genotypes with high DTI were JA 3, JA 67, JA 38, JA 132 and JA 92 ranged from 1.30 – 1.73.

Cluster analysis

Based on combined data for WUEb and WUEt of two drought levels for two years, a dendrogram could divide 40 Jerusalem artichoke genotypes into five clusters (R-square = 0.85) (Fig. 5). Nine Jerusalem artichoke genotypes formed cluster 1, which was characterized by low water use efficiency under drought conditions. Cluster 2 comprised 7 genotypes, which was characterized by relatively low water use efficiency under drought conditions. Cluster 3 included 12 genotypes, which was characterized by intermediate to relatively high water use efficiency under drought conditions, but a few genotypes had relatively low water use efficiency. Cluster 4 had 5 genotypes, which are characterized by relatively high water use efficiency under drought conditions. Cluster 5 had 7 genotypes, which was characterized by high water use efficiency under drought conditions.

Table 3. Ten selected genotypes with the highest water use (WU), water use efficiency for biomass (WUEb) and water use efficiency for tubers (WUEt) and 10 selected genotypes with the lowest performance for these traits and drought tolerance index (DTI) selected from 40 Jerusalem artichoke genotypes in the dry seasons 2011/12.

Group	No.	Water use (WU) (mm)				DTI		Water use efficiency for biomass (WUEb) (kg mm^{-1} ha^{-1})				DTI[a]		Water use efficiency for tubers (WUEt) (kg mm^{-1} ha^{-1})				DTI	
		Genotypes	W1	W2	W3	W2	W3	Genotypes	W1	W2	W3	W2	W3	Genotypes	W1	W2	W3	W2	W3
High	1	HEL 62	215.9 a	163.5 abc	103.3 abc	0.76	0.48	HEL 256	35.6 a	20.7 j-p	28.1 a-h	0.58	0.79	HEL 256	27.6 a	14.8 g-m	17.5 f-m	0.54	0.64
	2	HEL 65	214.8 ab	164.4 ab	104.5 ab	0.77	0.49	JA 89	32.5 ab	23.9 d-k	26.7 c-j	0.74	0.82	JA 89	23.5 b	16.3 d-j	18.9 d-h	0.69	0.80
	3	HEL 256	212.6 abc	166.4 a	105.6 a	0.78	0.50	JA 6	31.7 bc	31.9 a	31.2 a-d	1.01	0.99	JA 6	23.1 bc	21.1 ab	23.8 abc	0.91	1.03
	4	HEL 253	210.0 a-d	162.9 abc	103.2 abc	0.78	0.49	HEL 231	31.2 bcd	26.7 b-f	31.7 abc	0.86	1.01	HEL 65	22.5 bcd	20.3 ab	21.9 a-e	0.90	0.98
	5	HEL 335	208.6 a-e	163.4 abc	100.8 a-e	0.78	0.48	HEL 65	30.3 b-e	30.3 abc	29.7 a-e	1.00	0.98	HEL 257	21.3 b-e	18.7 b-f	20.7 b-f	0.88	0.97
	6	JA 132	207.3 a-f	158.5 b-e	101.1 a-e	0.76	0.49	CN 52867	29.9 b-e	27.3 b-e	27.3 a-i	0.91	0.91	CN 52867	21.0 b-f	20.3 ab	25.1 a-d	0.97	1.20
	7	JA102XJA89(8)	207.3 a-f	153.7 d-i	99.6 b-g	0.74	0.48	KKUAc001	28.9 b-f	28.0 a-d	26.9 c-i	0.97	0.93	JA 122	20.2 c-g	19.6 abc	17.9 f-k	0.97	0.89
	8	JA 76	206.5 a-g	158.4 b-e	99.9 b-f	0.77	0.48	HEL 324	28.0 c-g	24.1 d-j	29.5 a-e	0.86	1.05	JA 16	19.7 g-h	16.6 c-i	14.4 j-o	0.84	0.73
	9	JA 37	206.0 a-g	158.3 b-e	100.3 b-e	0.77	0.49	JA102XJA89(8)	27.9 d-g	30.1 abc	28.7 a-f	1.08	1.03	HEL 324	19.5 d-i	15.5 f-k	17.7 f-l	0.79	0.91
	10	JA 67	205.8 a-g	160.1 a-d	101.9 a-d	0.78	0.50	JA 16	27.7 d-g	23.9 d-k	20.1 l-m	0.86	0.73	JA102XJA89(8)	19.5 d-i	19.9 abc	18.2 e-j	1.02	0.93
Low	1	JA 114	187.2 l-q	144.6 k-n	93.0 j-o	0.77	0.50	JA 92	18.0 o-u	21.3 h-o	22.7 h-o	1.19	1.26	JA 77	13.3 n-t	15.0 g-l	16.7 f-n	1.13	1.26
	2	CN 52867	187.0 l-q	147.6 h-m	95.0 f-n	0.79	0.51	JA 125	17.5 p-u	16.7 p-s	17.5 o-r	0.96	1.00	JA 46	13.0 o-t	13.1 j-o	14.7 i-o	1.01	1.13
	3	JA 3	186.2 m-q	141.4 lmn	91.8 l-o	0.76	0.49	JA 61	17.4 p-u	19.2 l-q	23.1 h-n	1.10	1.33	JA 92	12.9 o-t	15.6 f-k	16.9 f-n	1.21	1.30
	4	JA 38	186.0 m-q	145.1 j-n	93.8 h-o	0.78	0.50	JA 46	16.9 p-u	17.8 n-s	18.7 n-r	1.06	1.11	JA 67	12.8 o-t	12.9 k-o	18.5 e-i	1.01	1.44
	5	JA 5	185.2 n-q	143.8 k-n	92.7 k-o	0.78	0.50	JA 60	16.5 r-u	14.9 rs	18.9 m-r	0.91	1.15	JA 60	12.5 p-t	11.7 mno	15.0 h-o	0.94	1.20
	6	HEL 324	184.7 n-q	138.7 n	90.6 no	0.75	0.49	HEL 62	16.3 r-u	15.7 qrs	20.3 l-p	0.96	1.24	JA 36	11.6 q-t	11.9 l-o	9.6 q	1.03	0.83
	7	JA 36	181.2 opq	142.1 lmn	91.7 mno	0.78	0.51	JA 109	16.1 stu	16.0 qrs	14.9 qr	0.99	0.92	HEL 62	11.5 rst	11.0 no	13.4 nop	0.96	1.17
	8	JA 122	180.9 opq	141.2 mn	91.9 l-o	0.78	0.51	JA 36	15.9 tu	15.8 qrs	16.1 pqr	1.00	1.01	JA 109	11.3 rst	10.8 o	9.7 q	0.95	0.86
	9	JA 16	179.4 pq	140.1 mn	90.7 no	0.78	0.51	JA 70	14.5 u	14.0 s	13.9 r	0.96	0.95	JA 1	10.9 st	14.1 h-n	8.7 q	1.29	0.80
	10	JA 6	176.6 q	139.0 n	89.9 o	0.79	0.51	JA 1	14.5 u	17.2 o-s	14.3 r	1.19	0.99	JA 70	10.2 t	10.3 o	10.1 pq	1.01	0.99
Mean			196.9 A	152.0 B	97.1 C	0.77	0.49		23.2 AB	22.5 B	24.4 A	0.98	1.07		16.6 AB	16.2 B	17.3 A	0.99	1.06
Min			176.6	138.7	89.9	0.74	0.48		14.5	14.0	13.9	0.58	0.73		10.2	10.3	8.7	0.53	0.63
Max			215.9	166.4	105.6	0.79	0.51		35.6	31.9	32.5	1.19	1.57		27.6	22.4	25.1	1.29	1.73

Maximum, minimum and mean values were calculated from 40 genotypes, For comparison among Jerusalem artichoke genotypes and forcomparison among water regimes, Means in the same column followed by the same letter(s) are not significantly different at $P < 0.05$ probability levels by Duncan's multiple range test (DMRT). [a]DTI = Drought tolerance index was calculated by the ratio of stressed conditions / non stressed conditions. W1= 100%ET, W2= 75%ET and W3=45%ET.

Table 4. Chemical and physical properties of the soil in the experimental fields at the depth 0-30 cm

Fields	pH (1:1 H_2O)	EC (1:5 H20) (dS/m)	CEC (cmol/kg)	OM (%)	Total N (%)	Available P (mg/kg)	Exchangeable		Particle size, mum (USDA system)			Texture class
							K (cmol/kg)	Ca cmol/kg)	Sand (%) 2.0 – 0.05	Silt (%) 0.05– 0.002	Clay (%) <0.002	
2010/11	6.08	0.03	5.22	0.44	0.02	23.95	0.084	1.043	85.08	7.30	7.62	Loamy sand
2011/12	6.12	0.02	5.93	0.42	0.01	37.97	0.097	1.120	90.29	8.05	1.66	Sand

EC = Electrical conductivity, CEC= Cation exchange capacity and OM = Organic matter.

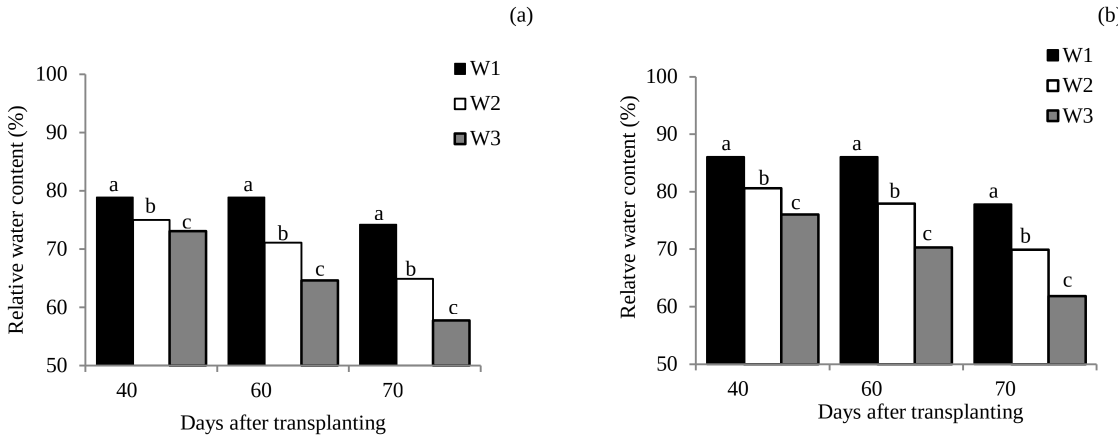

Fig 3. Relative water content (%) at 40, 60 and 70 days after transplanting (DAT) of 40 Jerusalem artichoke genotypes grown under different water regimes in the dry season 2010/2011 (a) and the dry season 2011/2012 years (b) Means in the same date with the same letter are not significant at $P < 0.05$ probability level by DMRT.

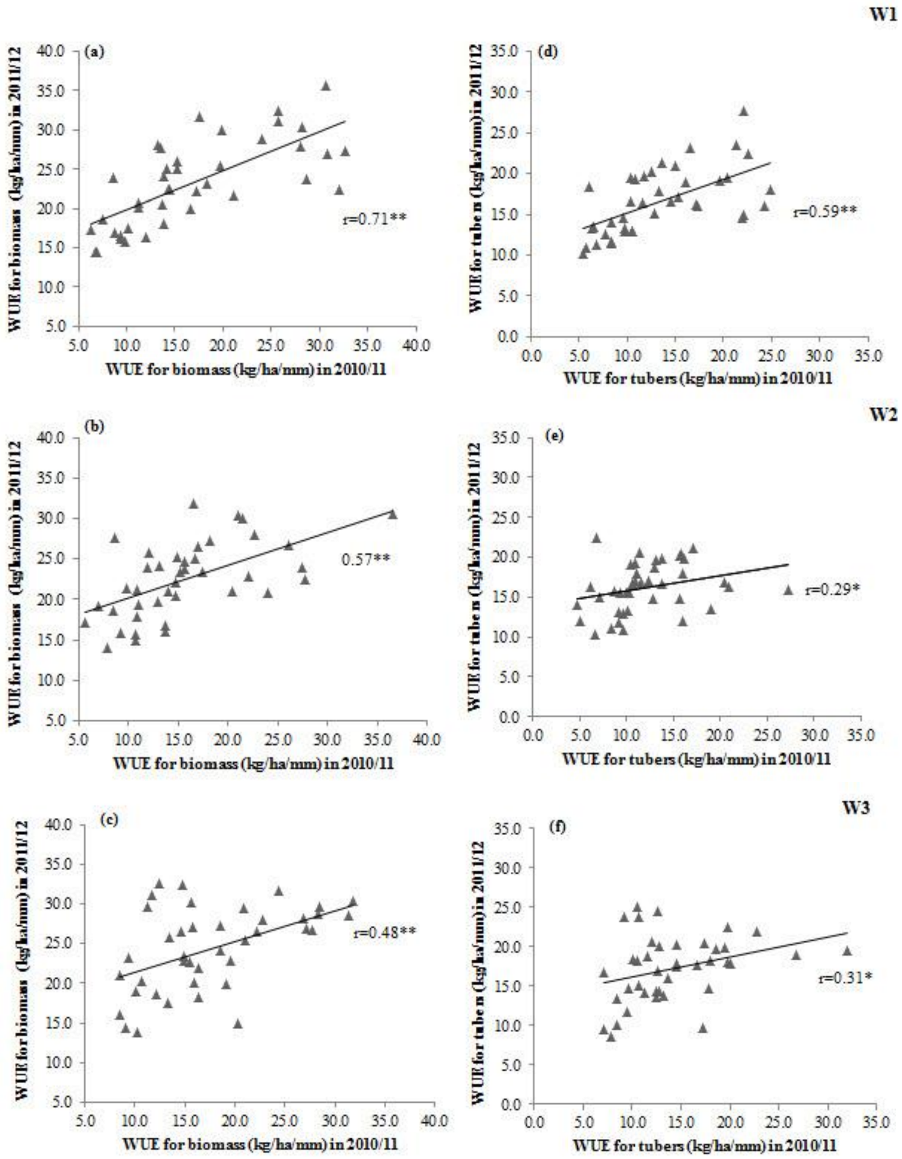

Fig 4. Relationships between years for water use efficiency for biomass (a-c) and water use efficiency for tubers (d-f) of 40 Jerusalem artichoke genotypes under three water regimes in 2010/11 and 2011/12.

Discussion

The soil chemical and physical properties were slightly different among experimental years (Table 4). The soil in the second experiment (2011/12) was higher in pH, available phosphorus (P), exchangeable potassium and exchangeable calcium (Ca) than in the first experiment (2010/11). The chemical properties indicated that soil fertility was lower than optimum conditions for production of Jerusalem artichoke. EC values in both years were lower than 0.03 dS/m, indicating that the soil was not saline (Geng-mao et al., 2008), and P values were higher than 15 mg/kg which should be sufficient for normal growth of Jerusalem artichoke (Lebot, 2009). Potassium values were intermediate and nitrogen values were low. As the nutrient values fell into the same ranges and basal dose was also applied, the difference in nutrients among years would not cause significant differences in water use efficiency. Differences were found among the experiments in the ranking of the genotypes, showing the significance of genotypes by environmental interactions. The differences between years were likely due to higher rain fall and air temperature in 2011/12 that enhanced performance of genotypes. In the first year, maximum and minimum air temperatures ranged from 18.4–30.3 ^{o}C, which was lower than the second year which ranged from 19.5–30.5 ^{o}C. Because Jerusalem artichoke in this study was grown in the tropics, the growing temperatures were much higher than optimum temperatures for this species. Most Jerusalem artichoke cultivars require an average annual temperature between 18–26 ^{o}C under temperate conditions (Cosgrove et al., 1991). However, Jerusalem artichoke grown under temperate conditions and tropical conditions requires a similar number of heat units. In tropical regions, heat units between 2245 and 4242 were reported (Ruttanaprasert et al., 2013), while heat units between 2106 and 4123 were reported in temperate regions (Kocsis et al., 2007). The difference is that the crop in temperate regions takes nine months to accumulate these heat units but it takes only three months in the tropics. The rainfall did not cause significant differences among water treatments because all treatments received uniform water during the crop establishment period, but rainfall during the early growing season in 2011/12 promoted better establishment of the crop and subsequent crop performance than in 2010/11. Differences in WU were largely due to the differences in amount of water applied to the crop, which accounted for 88.4% of total variation for water use. Genotype and genotype by year interaction gave small contribution to total variation for WU (1.5% for both). Improvement of WU in this population was not expected to yield significant results as the genetic variation for this trait was rather low. Genotypes contributed significant proportions of the total variations in WUEb (49.0%) and WUEt (43.7%). The contributions were generally 1- to- 4 fold larger than those for variation by years, water regimes and other interactions. Water use efficiency is important for crop improvement for drought resistance. In peanut, genotype contributed a large portion to the variations in water use efficiency (Jongrungklang et al., 2008; Mattews et al., 1988). Similar results were also reported in cassava (Manickasundaram et al., 2002). Therefore, improvement of these traits in this Jerusalem artichoke population is promising. Other agronomic traits are also important for improvement of Jerusalem artichoke for drought resistance. Variations in fresh tuber yield, biomass and inulin content have also been reported (Puttha et al., 2012), and the genotypic variation in inulin content was consistent across planting dates (Puangbut et al., 2011). However, water use efficiency for inulin yield has not been investigated, and this trait is also important for Jerusalem artichoke breeding for drought resistance. Water regime contributed to small portions of total variations in WUEb (1.1%) and WUEt (1.4%). The results suggested that any water regime can be used for evaluation of water use efficiency with similar results. Therefore, mimicking of drought conditions may not be necessary. In general, the cultivars with high yield potential under optimum conditions had acceptable yield under stressed environments, but, under a particular environmental stress, cultivars with high potential had lower yield than certain cultivars with lower yield potential (Blum, 2005). Therefore, high yield potential and low yield reduction under water stressed conditions are important for sustaining yield under drought. In some cases, drought stress reduced water use efficiency such as in peanut (Jongrungklang et al., 2008) and dry bean (*Phaseolus vulgaris* L.) (Muñoz-perea et al., 2007). In Jerusalem artichoke, water application of 50% of ET caused yield reductions of lower than 50% (Losavio et al., 1997), and, therefore, drought caused higher water use efficiency. Drought also increased water use efficiency in peanut (Aranyanak et al., 2008), cassava (Olanrewaju et al., 2009), common bean and green gram (Webber et al., 2006). Differences in the results from different studies are due to difference in crop species, times of drought imposition to the crops and drought intensity. As mentioned earlier, genotypic variations accounted for 49.0% for WUEb and 43.7% for WUEt. Genotypes with high water use efficiency could be readily identified. HEL 231, HEL 65 and JA102×JA89(8) had high WUEb across water regimes and years, whereas HEL 65 had high WUEt. As water use efficiency is closely related to yield, these Jerusalem artichoke genotypes also showed high yield under and well-irrigated and drought conditions (Data not reported). Relationships between data for WUEb and WUEt of two years were consistent as indicated by significant correlation coefficients. The results indicated that selection for high water use efficiency in these Jerusalem artichoke collections of genotypes is possible. In previous investigation, Yang et al. (2010) found that JA 6 had high water use efficiency for biomass. It is interesting to note here that JA 6 was commonly used in these studies. However, JA 6 has high water use efficiency for biomass and tuber yield across water regimes in 2011/12 only. JA 70, JA 1, JA 60 and JA 36 had low WUEb, whereas JA 70 and JA 36 had low WUEt. Genotypic variations in water use efficiency are mainly due to genetic variation in WU. Reduction in WU should increase water use efficiency and ultimately improve yield under drought conditions (Blum, 2005; Hamlyn, 2004). So, water use efficiency values depend on the WU and day to harvest in each genotype (Lasovio et al., 1997; Matthews et al., 1988).

Cluster analysis based on WUEb and WUEt under drought conditions could reasonably well separate groups of Jerusalem artichoke genotypes with high or low WUEb and WUEt. However, the classification of Jerusalem artichoke genotypes based on the dendrogram was slightly different from that based on the data of three water regimes. The difference could be due to the differential response of Jerusalem artichoke genotypes to drought conditions. The genotypes with high DTI were relatively low-yielding genotypes in well- watered conditions. Genotypes with high water use efficiency were not high DTI genotypes because high DTI genotypes were not the best for yield in drought conditions but rather had low yield reductions under drought conditions. The genotypes identified through this study

Table 5. Forty genotypes of Jerusalem artichoke used in the experiment, their characteristics and sources of origin

Genotypes	Characteristics	Sources of origin
JA 1 , JA 4, JA 6, JA 36, JA 70, JA 92, JA 114	Early and low biomass varieties	PGRC[1], Canada
JA3, JA 16, JA 21, JA 37, JA 38, JA 97, JA 132	Early and high biomass varieties	PGRC, Canada
JA 5, JA 122	Early, tall plant and low biomass varieties	PGRC, Canada
HEL 324	Early, tall plant and low biomass varieties	IPK[2], Germany
HEL 53, HEL 61, HEL 231, HEL 335	Early, tall plant and high biomass varieties	IPK, Germany
CN 52867	Early, tall plant and high biomass varieties	PGRC, Canada
KKUAc001	Early, tall plant and high biomass varieties	Khajarern[3]
JA 61	Early, tall plant and high biomass varieties	PGRC, Canada
JA 46, JA 60, JA 109	Late, short plant and low biomass varieties	PGRC, Canada
JA 76, JA 77	Late, short plant and high biomass varieties	PGRC, Canada
HEL 62	Late, short plant and high biomass varieties	IPK, Germany
HEL 246, HEL 257	Late, tall plant and low biomass varieties	IPK, Germany
JA 15, JA 67, JA 125	Late, tall plant and high biomass varieties	PGRC, Canada
JA 89	Late, tall plant and high biomass varieties	PGRC, Canada
HEL 65, HEL 253, HEL 256	Late, tall plant and high biomass varieties	IPK, Germany
JA102×JA89(8)	Late, tall plant and high biomass varieties	Jerusalem artichoke Research Project[4]

1 The Plant Gene Resource of Canada (PGRC). 2 The Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) of Germany,
3 Department of Animal Science Faculty Agriculture, Khon Kaen University, Thailand. 4 Jerusalem artichoke Research Project, Thailand

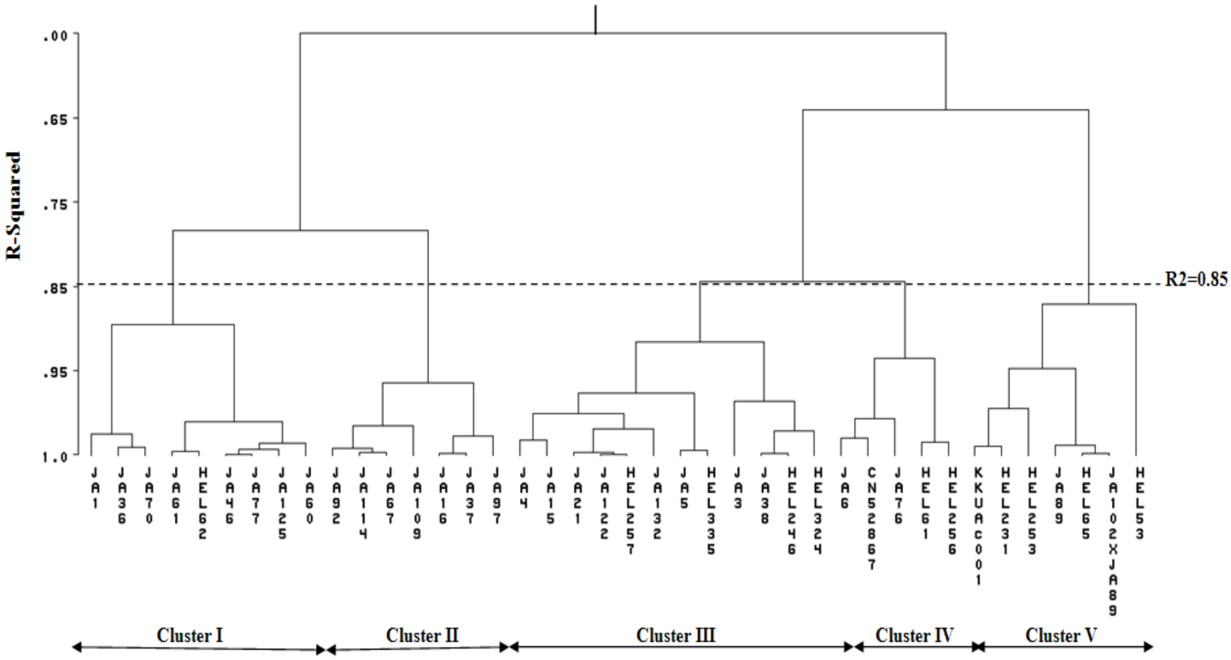

Fig 5. Dendrogram of 40 Jerusalem artichoke genotypes based on water use efficiency for biomass and water use efficiency for tubers under drought conditions for two years

should be useful in future breeding programs for improving drought tolerance.

Materials and methods

Plant materials and experimental design

Field experiments were conducted at the Khon Kaen University's agronomy farm, Khon Kaen, Thailand (16^{O} 28´ N, 102 ^{O} 48´ E, 200 msl) in the dry season for two years during October to February in 2010/2011 and 2011/2012. The soil type was Yasothon series (loamy sand, Oxic Paleustults). Three irrigation levels were assigned in strip plots, 40 Jerusalem artichoke accessions were arranged randomly in subplots, and the treatments were replicated four times.
Twenty-seven accessions were introduced from Plant Gene Resource of Canada (PGRC), 11 accessions were kindly donated from the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) of Germany, one accession was a newly-released variety from the Jerusalem artichoke research project of Thailand and one accession was the first introduced clone in Thailand of unknown origin. The details of Jerusalem artichoke accessions used in the experiment are available in Table 5. A line source sprinkler system was installed to provide three water gradients, which hereafter are referred to as W1, W2 and W3, respectively, and the water gradients were dependent on the distances for the line source, which was installed at the center of the field. The water supplied to W1 was expected to be equivalent to the crop water requirement (ET crop). Water supplied to W2 was estimated as 75% of that supplied to W1, and water supplied to W2 was 45% of that supplied to W1.

Crop management

Healthy tubers were used as planting materials. The tubers were cut into small pieces with 2 to 3 buds each, and the tuber pieces were immersed into water containing a fungicide (caboximide) at the rate of 10 g per 20 l of water for 40 min. The tuber pieces were then incubated in burnt rice husk mixed (1:1) with a commercial preparation of *Trichoderma* (T9) in plastic boxes for 5 to 7 days to stimulate germination. *Trichoderma* was incorporated into the soil to control stem rot disease caused by *Sclerotium rolfsii*. After germination, the seedlings were transferred into plug trays containing mixed medium of soil, burnt rice husk and *Trichoderma* at the ratio of 3:3:2 V/V. Water was supplied regularly to the nursery to avoid water stress until the seedlings had 2–3 leaves, or about 7–10 days after transferring. The seedlings were then suitable for transplanting into the field. Conventional tillage was practiced for soil preparation. A line source sprinkler system consisting of two modules was installed at the centre of the experimental field, and PVC tubes with 3 inches in diameter were used to supply water to the system. Module 1 supplied water to replications 1 and 2, and module 2 supplied water to replications 3 and 4. A separate control valve was installed for each module, The system was not operated until the crop was well established. Prior to transplanting of Jerusalem artichoke, a subsurface drip irrigation system (Super Typhoon®, Netafim Irrigation Equipment & Drip System, Israel) was installed with a spacing of 50 cm between drip lines and 20 cm between emitters. The drip lines were installed at 10 cm below the soil surface between the rows, and pressure values and water meters were fitted separately for all replications to ensure uniform supply of water. The insecticide carbofuran (2,3–dihydro–2,2–dimethyl benzofuran–7–ylmethylcarbamate 3% G granular) at the rate 62.5 kg ha^{-1} was applied along the drip lines and then the drip lines were covered with soil. An aluminum access tube was installed at the middle of each water level of the plot border to measure soil moisture content. Prior to planting, water was supplied to the soil through drip irrigation at field capacity level. The healthy seedlings were then transplanted to the soil and inoculum of *Trichoderma* was applied to each hill before planting. Plot size was 2 × 4 m in both years with a spacing of 50 cm between rows and 30 cm between plants within row. Manual weeding was done at 14 days after transplanting (DAT) and mixed fertilizer of N – P_2O_5 –K_2O (15–15–15) at the rate of 156.25 kg ha^{-1} was applied at 30 DAT.

Water regimes

Water was supplied to the crop through drip irrigation system at field capacity level from transplanting to 10 DAT, and then drip irrigation system was no longer used. After 14 DAT, water was supplied through a line source sprinkler irrigation system until harvest. Total crop water use for W1 was crop water requirement described by Doorenbos and Pruitt (1992),
Where, ETcrop = ETo × Kc
ETcrop = crop water requirement (mm/day)
ETo = evapotranspiration of a reference plant under specified conditions calculated by pan evaporation method
Kc = the crop water requirement coefficient for sunflower, which varies depending on varieties and growth stages. As crop coefficient for Jerusalem artichoke is not available in the literature, the crop coefficient for sun flower (Monti et al., 2005) is used because sunflower and Jerusalem artichoke are closely related species and their morphological characters are similar. The amounts of water that were supplied to the crop at all moisture levels were monitored by catch can, which were installed in all replications of water treatments (6 cans for each water treatment for a replication).

Data collection

Meteorological conditions

Weather data for both seasons were obtained from nearby meteorological station, Khon Kaen University, Khon Kaen, Thailand. Evaporation (E_0), rainfall, maximum and minimum temperature and relative humidity (RH) were recorded daily form transplanting until harvest.

Soil data and soil moisture content

The field experiment in both years was conducted in the same field. Soil samples were collected before planting in each replication from 8 positions per replication, and the soil samples were air dried. After mixing and bulking, the soil samples were analyzed to determine the physical and chemical properties. The soil chemical and physical properties were slightly different among experimental years. The soil in 2010/11 was loamy sand and in 2011/12 was sand, and clay particle in 2010/11 was slightly higher than in 2011/12 (Table 4). The differences in soil properties could be due to tillage to break hard pan. Soil moisture content was measured by gravimetric methods at transplanting, 14 DAT and harvest at the depths of 30, 60 and 90 cm. Soil moisture content was also measured with a neutron probe (Type I.H. II SER. N^o NO152, Ambe Didcot Instruments Co., Ltd., England), and neutron probe readings were conducted at the depths of 30, 60 and 90 cm (30 cm intervals) at 7–day intervals throughout the course of the experiment.

Crop Data

Relative water content

To evaluate plant water status, the relative water content was measured at 40, 60 and 70 DAT using the second or third expanded leaves from the top of the main stem of five plants from each plot. The leaves were cut with a disc borer 1 cm in diameter, and leaf fresh weight was determined. The leaf discs were placed in distilled water until the leaf was moisture saturated. The turgid weight was determined after keeping the leaf sample in distilled water for 8 hours. The leaf discs were oven-dried at 80 ^{o}C for 48 hours and leaf dry weight was determined. Water content was calculated based on the formula suggested by Kramer (1980) as follows;
RWC =[(FW – DW)/ (TW – DW)] × 100,
Where, FW: sample field weight, TW: sample turgid weight and DW: sample dry weight.

Biomass and tuber yield

At harvest, the plants at two ends of the rows were discarded, all plants in an area of 2.1 m^2 were harvested discarding the border rows, cut at the soil surface and separated into shoots and tubers. Tubers were washed in tap water to remove the potting medium. Fresh shoot weight and tuber fresh weight were determined in the field (Ohaus model PA 413, USA) and then the weights were converted to fresh weights per area. A random shoot fresh weight and tuber fresh weight from 10% of plants in each plot was taken, oven-dried at 80 °C for 72 hours or until constant weight, and weighed. Biomass was calculated from shoot dry weight and tuber dry weight.

Water use (WU) and water use efficiency (WUE) calculation

Total crop water use was calculated by the sum of irrigation applications and rains in each plot ± the difference in soil moisture before transplanting and soil moisture at final harvest. WUE was estimated for biomass and tuber using the formula proposed by Teare et al. (1982):

WUE for biomass (WUEb) = total dry matter /water used in evapotranspiration and

WUE for tubers (WUEt) = tuber dry weight/water used in evapotranspiration.

Drought tolerance index (DTI)

Drought tolerance index was computed for water use, biomass and tuber dry weight ratio by comparing values under stress treatment to values for non–stress treatment as suggested by Nautiyal et al. (2002)

DTI = Data of stress treatment/data of non–stress treatment.

Statistical analysis

Analysis of variance was performed for each character based on a strip plot design (Gomez and Gomez, 1984) using statistix 8 (Statistix8, 2003). Homogeneity of variance was tested for all characters and combined analysis of variance of two-year data was performed. When the differences of main effects were significant ($P \leq 0.05$), Duncan's multiple range test (DMRT) was used to compare means using MSTAT-C package (Bricker, 1989). Cluster analysis was constructed using means of Jerusalem artichoke genotypes for WUEb and WUEt under two drought levels for two years. The cluster analysis based on Ward's method and squared Euclidian distance was performed and the dendrogram was constructed. All calculations were done using computer program SAS 6.12 software (SAS, 2001).

Conclusion

The results show that there were significant genetic variations in WUEb and WUEt in this set of Jerusalem artichoke accessions and, therefore, improvement of drought resistance using these accessions as a germplasm source may be possible. High WU was found in the crop with W1. HEL 231, HEL 65 and JA 102 ×JA89 (8) performed well for WUEb at all water regimes, whereas HEL 65 was identified as the accessions with high WUEt.

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