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Genotypic variability for tuber yield, biomass, and drought tolerance in Jerusalem artichoke germplasm

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Abstract: Jerusalem artichoke could be an alternative feedstock for bioenergy during times when there are shortages of other raw materials for the ethanol industry. However, insufficient water under rainfed conditions is a major cause of Jerusalem artichoke losses. Genetic variation for drought tolerance is an essential prerequisite for the development of Jerusalem artichoke cultivars with improved drought tolerance. The objectives of this study were to determine the effects of drought stress on tuber dry weight and biomass and to investigate the genotypic variability in Jerusalem artichoke germplasm. The line-source sprinkler technique was used to compare moisture responses of a range of 40 Jerusalem artichoke genotypes grown using 3 water levels. Experiments were conducted on a Yasothon soil series in Northeast Thailand during 2010/11 and 2011/12 and included extended dry periods. Drought reduced tuber dry weight and biomass, and the reductions in tuber dry weight and biomass were greater under severe drought than moderate drought conditions. Over both seasons, CN 52867, HEL 53, HEL 231, HEL 335, JA 76, HEL 65, and JA 102 × JA 89 (8) had consistently high tuber dry weight (1.3 to 4.5 t ha^{-1}) and HEL 53, HEL 61, HEL 231, HEL 335, JA 76, JA 15, JA 89, HEL 65, HEL 256, and JA 102 × JA 89 (8) had consistently high biomass (2.0 to 6.8 t ha^{-1}). These Jerusalem artichoke genotypes are promising parents in breeding for drought tolerance.

Key words: Drought, bioethanol, inulin

1. Introduction

High oil prices stimulated interest in bioethanol as a potential liquid fuel for transportation (Margaritis and Pratima, 1983). Bioethanol is currently produced using carbohydrate sources in many countries. Common feedstocks for ethanol production are sugarcane, cassava, corn grain, and many other agricultural raw materials rich in fermentable carbohydrates. These feedstocks are then chemically converted to yield fermentable sugars (Lin and Tanaka, 2006). Corn, sorghum, Jerusalem artichoke, potato, and lignocellulosic biomass are sources of feedstock with great potential for ethanol production (Azhar and Hamdy, 2003).

Mainstream raw materials such as sugarcane, cassava, and corn grain have limited harvest times and are rarely available for year round production. Nonconventional feedstocks such as sweet sorghum and Jerusalem artichoke can diversify raw materials and extend production times for the bioethanol industry (Walker, 2010). Of these nonconventional raw materials, Jerusalem artichoke is one of the most interesting (Szambelan et al., 2005). The ethanol yield from Jerusalem artichoke tubers is equivalent to that obtained from sugar beets and 2-fold that of corn (Azhar and Hamdy, 2003). Jerusalem artichoke has high carbohydrate yield, ranging between 5 and 14 t ha^{-1} (Stephen et al., 2006). Because of its high carbohydrate yield, Jerusalem artichoke has been evaluated as a potential crop for ethanol production (Denoroy, 1996). About 4.0 to 4.7 t ha^{-1} of bioethanol was produced from Jerusalem artichoke (Walker, 2010). Jerusalem artichoke is also a promising candidate for inulin production in the tropics. The possibility of growing Jerusalem artichoke for energy has stimulated scientific interest in this crop (Kim et al., 2013; Li et al., 2013). Although Jerusalem artichoke grown in the tropics is not as productive as that grown in temperate regions, it can be grown successfully and profitably. Agronomic studies and breeding efforts for Jerusalem artichoke are ongoing at Khon Kaen University.

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Production of Jerusalem artichoke in Northeast Thailand is usually under rainfed conditions with low annual rainfall, poor rain distribution, and insufficient water supply. Therefore, drought stress is a major limitation to crop production. Although effective irrigation scheduling may increase water savings for irrigated crops in the short-term, the breeding and selection of drought-tolerant genotypes that are more efficient, with high yield under drought conditions, may be a long-term solution to the problem. The use of drought-tolerant genotypes would be a means to increase Jerusalem artichoke productivity under tropical growing conditions, and this might be possible if diverse germplasm sources are screened and drought-resistant genotypes are identified.

The previous studies on drought tolerance in Jerusalem artichoke have been conducted only in temperate regions with few genotypes and water regimes (Conde et al., 1991; Losavio et al., 1997; Schittenhelm, 1999; Monti et al., 2005; Liu et al., 2012). Drought can severely reduce the tuber yield of Jerusalem artichoke; however, the crop shows a certain acclimation to water stress, decreasing yield by only 20% when optimum irrigation was reduced by 50% and evenly supplied throughout the year (Conde et al., 1991). Under a Mediterranean climate, a supply of 50% of Jerusalem artichoke's water requirement also reduced yield by only 20% (Losavio et al., 1997).

The objectives of this study were to determine the effects of drought stress on tuber dry weight and biomass under tropical conditions and to evaluate the genotypic variability in Jerusalem artichoke germplasm. This information will be useful for both breeding and production of Jerusalem artichoke, aiming to increase the productivity of this crop, especially under drought conditions.

2. Materials and methods

2.1. Experimental design, treatments, and crop management

Forty genotypes of Jerusalem artichoke with differences in morphological and physiological traits (harvest date, plant height, and biomass) were screened for drought tolerance using a line-source sprinkler system (Hank et al., 1976). The experiment was set up in a strip plot design with 4 replications for 2 years in the dry season from October 2010 to January 2011 and October 2011 to January 2012 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 soil type was Yasothon series (Yt: fine-loamy; siliceous, isohypothermic, Oxic Paleustults). Three water gradients (defined as W1, W2, and W3, respectively) were assigned in horizontal plots and 40 Jerusalem artichoke accessions (Table 1) were randomly assigned in vertical plots. W1 (control treatment) was the full crop water requirement [evapotranspiration (ET) crop], W2 was slight drought, and W3 was the most severe drought. The water gradients were set up in strip plots along the line source sprinkler at distances of 1–5, 5–9, and 9–13 m, respectively. Water content of each level was measured by catch cans (24 cans for each water regime treatment).

Seed tubers were cut into small pieces with 2 to 3 buds per piece. These tuber pieces were then presprouted in coconut peat medium under ambient conditions for 4 to 7 days and then were transferred to germinating plug trays with mixed medium containing burnt rice husk and soil for 7 days for complete sprouting. The healthy seedlings were then ready for transplantation. Conventional tillage was practiced for soil preparation, including primary plowing, secondary plowing, harrowing, and leveling. Plot size was 2 × 4 m with a spacing of 50 × 30 cm for the 4 rows per plot for each genotype. Manual weeding was performed at 14 days after transplanting (DAT), and single-dose fertilization of N-P_2O_5-K_2O formula 15-15-15 at the rate of 156.25 kg ha^{-1} was spread over the plots at 30 DAT.

Prior to planting, water was supplied uniformly to the experimental field to water-holding field capacity at the depth of 10 cm using drip irrigation to facilitate uniform plant stand and crop establishment until 10 DAT. Different water gradients were supplied by the line source sprinkler system to the crop at 14 DAT until harvest. W1 was used as a control treatment and maintained at crop water requirement until harvest.

The amount of crop water requirement used was calculated as described by Doorenbos and Pruitt (1992), using the following relationship:

$$ETcrop = kc \times ETo,$$

where ETo is evapotranspiration of the reference crop and kc is the coefficient of the crop at different growth stages. The crop coefficient (kc) of Jerusalem artichoke was not found in literature, so the kc of sunflower was used (Monti et al., 2005).

2.2. Data collection and statistical analysis

Rainfall, humidity, evaporation (E_0), and maximum and minimum temperatures (Figure 1) were recorded daily from transplanting until harvest by a weather station located 100 m away from the experimental field. The soil in 2010/11 was Yasothon series (loamy sand in 2010/11 and sand in 2011/12) with the chemical and physical properties presented in Table 2. In each plot, relative water content (RWC) was measured at 40, 60, and 70 DAT to estimate plant water status. RWC was measured following Kramer (1980), using the second leaf from the top of the main stem and 5 plants for each plot. The leaf was bored by a disc borer with 1 cm^2 in leaf area. RWC was calculated as shown below.

Table 1. Forty genotypes of Jerusalem artichoke used in the experiment, their characteristics, and their sources of origin.

Genotypes	Characteristics			Sources of origin
	Maturity	Plant height	Biomass	
JA 1, JA 4, JA 6, JA 36, JA 70, JA 92, JA 114	Early	Short	Low	PGRC[1], Canada
JA 3, JA 16, JA 21, JA 37, JA 38, JA 97, JA 132	Early	Short	High	PGRC, Canada
JA 5, JA 122	Early	High	Low	PGRC, Canada
HEL 324	Early	High	Low	IPK[2], Germany
HEL 53, HEL 61, HEL 231, HEL 335	Early	High	High	IPK, Germany
CN 52867	Early	High	High	PGRC, Canada
KKUAc001	Early	High	High	Jowaman Khajarern[3]
JA 61	Early	High	High	PGRC, Canada
JA 46, JA 60, JA 109	Late	Short	Low	PGRC, Canada
JA 76, JA 77	Late	Short	High	PGRC, Canada
HEL 62	Late	Short	High	IPK, Germany
HEL 246, HEL 257	Late	High	Low	IPK, Germany
JA 15, JA 67, JA 125	Late	High	High	PGRC, Canada
JA 89	Late	High	High	PGRC, Canada
HEL 65, HEL 253, HEL 256	Late	High	High	IPK, Germany
JA 102 × JA 89 (8)	Late	High	High	Jerusalem Artichoke Research Project[4]

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

Saturated weight was determined by putting the leaf sample in water for 8 h, blot-drying the outer surface, and then measuring leaf weight.

The plants were harvested at maturity. The mature plants determined by defoliation and 50% stem browning were cut at the soil surface and separated into shoots and tubers. The plants at the 2 ends of the rows were discarded. As plants were bordered by adjacent plots, 14 plants in an area of 2.1 m^2 were harvested. The tubers were washed in tap water to remove soil and potting medium and were counted. Tuber number per plant was then determined. The samples were oven-dried at 80 °C for at least 72 h or until the weights were constant. Tuber dry weight and biomass including shoot dry weight and tuber dry weight were recorded.

Analysis of variance was performed for each character following a strip plot design (Gomez and Gomez, 1984). When the differences of main effects were significant ($P \leq 0.05$), Duncan's multiple range test was used to compare means. All calculations were performed using the MSTAT-C package. Simple linear response in tuber dry weight and biomass to 3 different water regimes was also calculated to determine average reductions for tuber dry weight and biomass of each genotype due to water stress.

3. Results

3.1. Climate, soil moisture, and plant water status

The meteorological data are shown in Figure 1. Average air temperatures in the first and the second years were 18.4–30.3 °C and 19.5–30.5 °C, respectively (Figure 1a). 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 (Figures 1b and 1c). The relative humidity values were 84.0% and 86.6% in the first and second years, respectively. There was no rainfall in 2010/11, whereas a rainfall of 174.6 mm in 2011/12 was recorded at the beginning of the growing cycle from 1–6 DAT (Figures 1b and 1c).

Soil moisture contents of the 3 water regimes were compared at weekly intervals during growing seasons at the soil depths of 30, 60, and 90 cm (Figure 2). Soil moisture content at the soil depth of 0–30 cm for W1 was slightly higher than that for W2 in 2010/11, but they were generally higher than those for W3. However, soil moisture

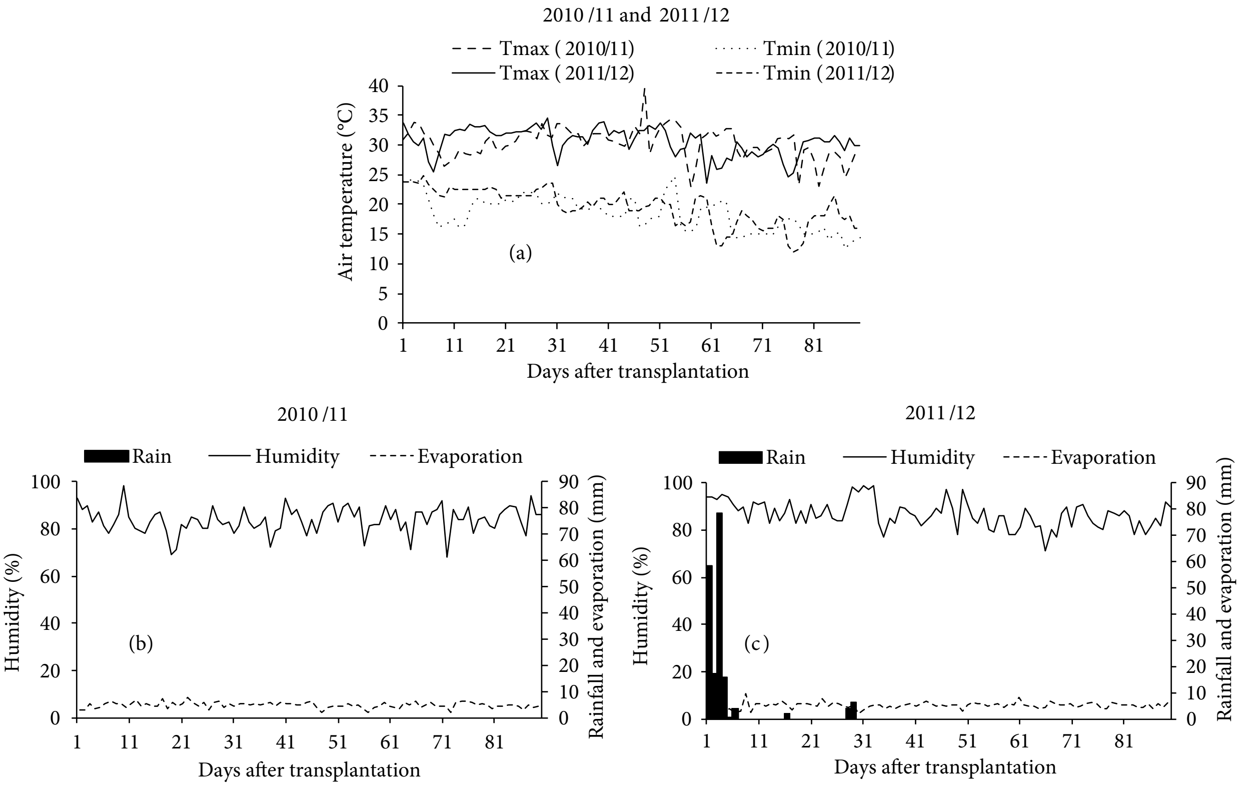

Figure 1. Maximum (Tmax) and minimum (Tmin) air temperatures (°C) in the dry periods of 2010/11 and 2011/12 (a); rainfall (mm), evaporation (mm), and humidity (%) in the dry seasons 2010/11 (b) and 2011/12 (c).

contents at a soil depth of 30 cm for W1, W2, and W3 were clearly different in 2011/12. At the soil depth of 60 cm, the soil moisture contents of the 3 water regimes were similar throughout the growing seasons, and, at the soil depth of 90 cm, soil moisture contents for W1, W2, and W3 were not different throughout the growing seasons. In general, clear differences among water regimes were only observed at the soil depth of 30 cm, and were particularly evident in 2011/12.

Table 2. Soil texture and chemical properties for field experiments in 2010/11 and 2011/12.

Soil texture	2010/11	2011/12
Sand	85%	90%
Silt	7%	8%
Clay	8%	2%
Texture class	Loamy sand	Sand
Soil chemical properties	2010/11	2011/12
pH	6.08	6.12
EC (dS m^{-1})	0.03	0.03
CEC (cmol kg^{-1})	5.22	5.93
OM (%)	0.44	0.42
Total N (%)	0.02	0.01
Available P (mg kg^{-1})	23.95	37.97
K (mg kg^{-1})	33.09	37.83
Ca (mg kg^{-1})	418.33	448.75

Plant water status for W1, W2, and W3 was evaluated at 40, 60, and 70 DAT (Table 3). Clear differences among the 3 water regimes were observed for RWC at 40, 60, and 70 DAT, and RWC values ranging from 57.8 to 86.1 were observed. RWC values for W1 were significantly higher than those for W2, whereas RWC values for W2 were significantly higher than those for W3.

3.2. Combined analysis of variance

Years were significantly different for tuber fresh weight and biomass. Genotypes and water regimes had a significant influence on tuber fresh weight, tuber dry weight, and biomass (Table 4). Genotype contributed to a large portion of total variation for tuber fresh weight (18%), tuber dry weight (21.4%), and biomass (26.3%). Similarly, water regime was also a great source of the total variation for tuber fresh weight (43.6%), tuber dry weight (35.9%), and biomass (33.5%). Year contributed rather small portions of variation for tuber fresh weight (7.7%), tuber dry weight (7.3%), and biomass (11.6%). The variation of replication

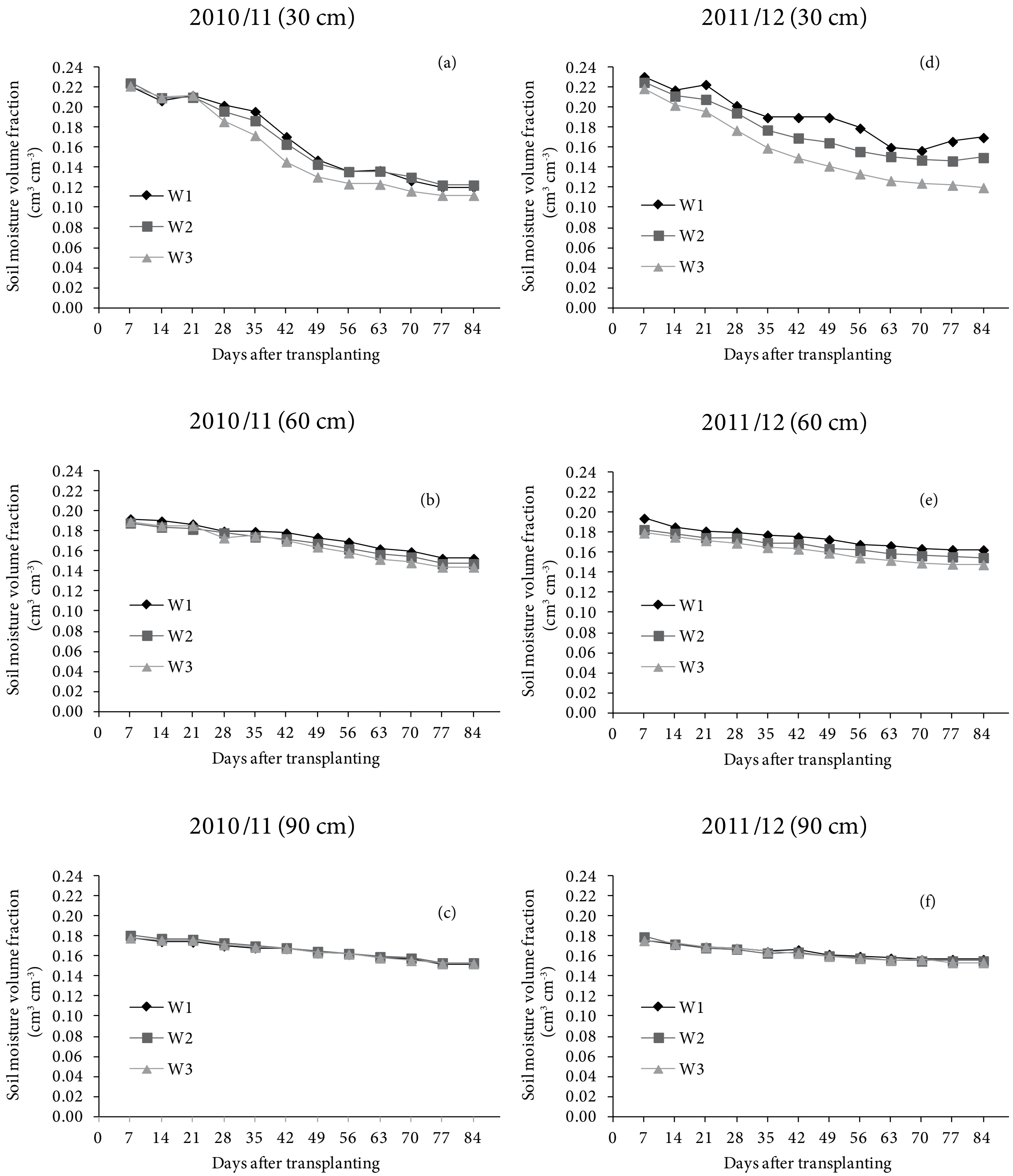

Figure 2. Soil moisture volume fractions for 3 soil water regimes (W1 = 100% ET, W2 = 75% ET, and W3 = 45% ET) at the soil depths of 30 cm (a, d), 60 cm (b, e), and 90 cm (c, f) in the dry seasons of 2010/11 and 2011/12, respectively.

within year for all traits indicated that the blocking procedure used for this large experimental area could also identify the difference among the replications. Interaction effects contributed small portions of variations for tuber fresh weight, tuber dry weight, and biomass, ranging from 0.1% to 0.2% for the interactions between year and water regime and ranging from 3.9% to 5.4% for the interactions between year and genotype. The interaction effects,

Table 3. Leaf relative water content (RWC) under 3 water regimes at 40 days after transplanting (DAT), 60 DAT, and 70 DAT of 40 Jerusalem artichoke genotypes grown under 3 water regimes (W1 = 100% ET, W2 = 75% ET, and W3 = 45% ET) during the dry seasons of 2010/11 and 2011/12.

	RWC (%) in 2010/11						RWC (%) in 2011/12					
	40 DAT		60 DAT		70 DAT		40 DAT		60 DAT		70 DAT	
W1	78.8	a	79.7	a	74.2	a	86.1	a	86.1	a	77.8	a
W2	75.0	b	71.1	b	64.9	b	80.6	b	77.9	b	69.9	b
W3	73.0	c	64.5	c	57.8	c	76.0	c	70.3	c	61.8	c

Means in the same column followed by the same letters are not different at P ≤ 0.01 probability level by Duncan's multiple range test.

Table 4. Mean squares for tuber fresh weight, shoot dry weight, tuber dry weight, and biomass of 40 Jerusalem artichoke genotypes grown under 3 water regimes (W1 = 100% ET, W2 = 75% ET, and W3 = 45% ET) during the dry seasons of 2010/11 and 2011/12.

Source	df	Tuber fresh weight (t ha^{-1})		Tuber dry weight (t ha^{-1})		Biomass (t ha^{-1})	
Year	1	1181.3	(7.7)*	78.0	(7.3)ns	243.3	(11.6)*
Rep within year	6	187.8	(7.4)	13.5	(7.5)	22.5	(6.4)
Water	2	3328.1	(43.6)**	192.5	(35.9)**	352.1	(33.5)**
Year × water	2	4.8	(0.1)ns	0.5	(0.1)ns	1.9	(0.2)ns
Error (a)	12	10.5	(0.8)	0.6	(0.7)	0.8	(0.5)
Genotypes	39	70.6	(18.0)**	5.9	(21.4)**	14.1	(26.3)**
Year × genotypes	39	18.2	(4.6)**	1.5	(5.4)**	2.1	(3.9)**
Error (b)	234	5.2	(7.9)	0.5	(10.5)	0.8	(8.5)
Water × genotypes	78	6.9	(3.5)**	0.6	(4.0)**	1.1	(3.9)**
Year × water × genotypes	78	3.0	(1.6)**	0.2	(1.7)**	0.3	(1.2)**
Error (c)	468	1.6	(4.7)	0.1	(5.4)	0.2	(3.9)
Total	959						
CV% (a)		40		36		30	
CV% (b)		28		32		30	
CV% (c)		15		16		14	

Numbers within the parentheses are percentages of sum squares to total sum of squares.
ns, *, **: Nonsignificant, significant at P ≤ 0.05, and highly significant at P ≤ 0.01, respectively.

although they were significant, were lower than the main effects (genotype, water regime, and year) for these traits.

3.3. Genotypic variation and response of Jerusalem artichoke to water regimes

Since the interactions between genotype and year and the interactions between genotype and water regime were significant for tuber dry weight and biomass, data for the 2 years were analyzed separately (Tables 5 and 6). Drought reduced tuber dry weight and biomass in both years, and the reductions in tuber dry weight and biomass were more severe under W3 than W2. In 2010/11, overall means for tuber dry weight under fully irrigated, moderate, and severe drought conditions were 2.7, 1.8, and 1.2 t ha^{-1}, respectively, whereas overall means for biomass were 3.5, 2.3, and 1.5 t ha^{-1}, respectively (Table 5). In 2011/12, the overall means for tuber dry weight were 3.3, 2.5, and 1.7 t ha^{-1} under fully irrigated, moderate, and severe drought conditions, respectively, whereas overall means for biomass were 4.6, 3.4, and 2.3 t ha^{-1}, respectively (Table 6). The reductions in tuber dry weight and biomass as affected by drought were also indicated by the regression coefficient (b-values) for tuber dry weight and biomass.

Table 5. Mean tuber dry weight and biomass, b-values, and coefficients of determination (R^2) for 40 Jerusalem artichoke genotypes grown under 3 water regimes (W1 = 100% ET, W2 = 75% ET, and W3 = 45% ET) during the dry season of 2010/11.

Entry No.	Genotypes	Tuber dry weight (t ha^{-1})						b-value	R^2	Biomass (t ha^{-1})						b-value	R^2
		W1		W2		W3				W1		W2		W3			
1	JA 1	1.2	l	0.7	l	0.7	fg	−0.26	0.82	1.4	m	0.8	h	0.8	h	−0.31	0.84
2	JA 4	2.8	c–i	1.9	b–k	1.0	c–g	−0.88	1.00	3.4	e–k	2.2	d–g	1.3	e–h	−1.05	1.00
3	JA 6	2.8	c–i	1.5	f–l	0.9	d–g	−0.95	0.96	3.5	d–j	2.0	e–h	1.2	f–h	−1.15	0.97
4	JA 36	1.6	j–l	0.9	kl	0.7	fg	−0.42	0.90	1.9	k–m	1.1	gh	0.9	h	−0.50	0.92
5	JA 70	1.1	l	1.0	j–l	0.6	g	−0.22	0.80	1.3	m	1.2	f–h	0.8	h	−0.28	0.88
6	JA 92	2.8	d–j	1.5	f–l	0.9	d–g	−0.92	0.96	3.5	d–j	1.9	e–h	1.1	gh	−1.18	0.97
7	JA 114	2.1	g–l	1.3	i–l	1.0	c–g	−0.56	0.90	2.6	g–m	1.6	e–h	1.2	f–h	−0.70	0.93
8	JA 3	2.0	h–l	1.2	i–l	0.8	e–g	−0.59	0.94	2.3	i–m	1.4	f–h	1.0	h	−0.68	0.96
9	JA 16	2.1	g–l	1.4	g–l	1.0	d–g	−0.59	0.99	2.5	h–m	1.7	e–h	1.1	f–h	−0.68	0.98
10	JA 21	2.1	g–l	1.2	i–l	0.9	d–g	−0.59	0.92	2.5	h–m	1.5	f–h	1.1	gh	−0.70	0.93
11	JA 37	4.0	a–c	2.2	b–i	1.1	c–g	−1.45	0.98	4.7	b–f	2.5	c–f	1.3	e–h	−1.69	0.98
12	JA 38	2.5	e–k	1.5	g–l	0.8	fg	−0.86	0.98	2.9	g–l	1.7	e–h	1.0	h	−0.98	0.98
13	JA 97	2.0	h–l	1.4	g–l	1.0	d–g	−0.50	1.00	2.5	h–m	1.7	e–h	1.2	f–h	−0.66	0.99
14	JA 132	2.6	d–j	2.1	b–j	1.3	a–g	−0.68	0.99	3.3	f–k	2.5	c–f	1.5	c–h	−0.89	1.00
15	JA 5	2.7	d–j	1.7	e–l	0.9	d–g	−0.89	0.99	3.3	f–k	2.1	e–h	1.2	f–h	−1.05	0.99
16	JA 122	2.5	e–k	1.9	b–k	1.2	b–g	−0.63	1.00	3.0	g–l	2.3	d–g	1.5	c–h	−0.78	1.00
17	HEL 324	2.2	f–l	1.7	e–l	1.3	a–g	−0.46	0.99	2.9	g–m	2.1	e–h	1.7	b–h	−0.60	0.98
18	JA 61	2.4	f–k	1.7	e–l	1.2	a–g	−0.57	0.99	2.6	g–m	1.8	e–h	1.4	d–h	−0.63	0.98
19	CN 52867	2.9	c–i	1.8	d–k	1.4	a–f	−0.74	0.96	3.6	d–j	2.2	d–g	1.6	b–h	−0.96	0.95
20	KKUAc001	3.4	a–f	2.4	a–g	1.6	a–e	−0.90	1.00	4.7	b–f	3.4	a–d	2.1	a–e	−1.26	1.00
21	HEL 53	4.5	a	3.2	a	1.9	a	−1.27	1.00	6.2	a	4.4	a	2.7	a	−1.73	1.00
22	HEL 61	4.0	a–c	2.6	a–f	1.7	a–c	−1.11	0.98	5.2	a–c	3.4	a–d	2.3	a–c	−1.48	0.98
23	HEL 231	3.6	a–e	2.5	a–f	1.6	a–d	−0.98	1.00	4.8	a–e	3.5	a–c	2.2	a–d	−1.31	1.00
24	HEL 335	4.1	ab	2.6	a–f	1.3	a–g	−1.37	1.00	5.8	ab	3.7	a–c	2.0	a–g	−1.91	0.99
25	JA 46	1.7	i–l	1.3	h–l	0.7	fg	−0.53	0.99	2.2	j–m	1.6	e–h	0.9	h	−0.64	1.00
26	JA 60	1.7	i–l	1.2	i–l	0.8	fg	−0.46	1.00	2.0	j–m	1.5	e–h	0.9	h	−0.55	1.00
27	JA 109	2.0	h–l	1.4	g–l	0.8	e–g	−0.60	1.00	2.5	h–m	1.7	e–h	1.0	h	−0.75	0.99
28	JA 76	3.4	a–f	2.3	a–h	1.6	a–d	−0.87	0.99	4.1	c–g	2.8	b–e	2.0	a–f	−1.04	0.98
29	JA 77	1.4	kl	1.1	j–l	0.7	fg	−0.34	0.99	1.6	lm	1.3	f–h	0.8	h	−0.43	1.00
30	HEL 62	1.8	i–l	1.1	i–l	0.7	fg	−0.52	0.97	2.5	h–m	1.5	f–h	1.0	h	−0.78	0.96
31	HEL 246	3.2	b–g	1.9	b–k	1.4	a–f	−0.91	0.93	3.9	c–h	2.2	d–g	1.7	b–h	−1.10	0.93
32	HEL 257	2.8	d–j	1.9	b–k	1.0	c–g	−0.87	1.00	3.4	d–j	2.3	d–g	1.3	e–h	−1.09	1.00
33	JA 15	3.1	b–h	1.9	c–k	1.3	a–g	−0.86	0.95	3.8	c–i	2.3	d–g	1.6	b–h	−1.06	0.95
34	JA 67	2.1	g–l	1.3	i–l	1.0	d–g	−0.57	0.91	3.2	f–k	1.8	e–h	1.4	d–h	−0.91	0.92
35	JA 89	3.7	a–d	2.9	ab	1.9	ab	−0.93	0.99	4.9	a–d	3.9	ab	2.5	ab	−1.21	0.99
36	JA 125	1.9	h–l	1.3	h–l	1.0	c–g	−0.43	0.98	2.3	i–m	1.7	e–h	1.2	f–h	−0.54	0.99
37	HEL 65	4.1	ab	2.7	a–e	1.9	ab	−1.11	0.97	5.2	a–c	3.5	a–d	2.4	ab	−1.40	0.98
38	HEL 253	4.1	ab	2.9	a–c	1.9	ab	−1.12	1.00	6.1	ab	3.9	ab	2.7	a	−1.69	0.97
39	HEL 256	4.0	a–c	2.5	a–f	1.7	a–c	−1.12	0.97	5.8	ab	3.7	a–c	2.5	ab	−1.66	0.98
40	JA 102 × JA 89 (8)	3.7	a–d	2.8	a–d	1.9	ab	−0.92	1.00	5.0	a–c	3.8	ab	2.6	a	−1.23	1.00
	Means	2.7		1.8		1.2		−0.76	0.97	3.5		2.3		1.5		−0.98	0.97

Means in the same column followed by the same letters are not different at P ≤ 0.01 probability level by Duncan's multiple range test.

Table 6. Mean tuber dry weight and biomass, b-values, and coefficient of determinations (R^2) for 40 Jerusalem artichoke genotypes grown under 3 water regimes (W1 = 100% ET, W2 = 75% ET, and W3 = 45% ET) during the dry season 2011/12.

Entry no.	Genotypes	Tuber dry weight (t ha^{-1})						b-value	R^2	Biomass (t ha^{-1})						b-value	R^2
		W1		W2		W3				W1		W2		W3			
1	JA 1	2.2	j–l	2.0	g–k	1.2	f–h	−0.49	0.93	3.0	m–o	2.5	j–m	1.6	j–n	−0.69	0.98
2	JA 4	3.6	b–i	2.4	c–j	1.9	b–e	−0.83	0.95	4.9	c–h	3.3	b–k	2.6	b–h	−1.19	0.96
3	JA 6	3.9	a–f	3.2	a–c	2.0	a–e	−0.96	0.98	5.6	a–e	4.5	a	2.8	b–e	−1.40	0.99
4	JA 36	2.1	kl	1.7	i–k	1.1	gh	−0.49	0.99	2.9	no	2.3	lm	1.5	l–n	−0.71	0.99
5	JA 70	2.0	l	1.5	k	1.0	h	−0.50	0.99	2.8	o	2.1	m	1.3	n	−0.73	1.00
6	JA 92	3.4	b–i	2.4	c–j	1.6	c–g	−0.89	0.99	4.4	d–l	3.3	b–l	2.2	d–m	−1.13	1.00
7	JA 114	2.5	i–l	2.3	e–k	1.6	d–h	−0.46	0.93	3.8	g–o	3.1	e–l	2.1	e–m	−0.83	0.99
8	JA 3	3.0	c–l	2.5	b–i	1.9	b–e	−0.54	1.00	4.2	e–n	3.2	b–l	2.6	b–h	−0.84	0.99
9	JA 16	3.2	c–k	2.3	d–j	1.6	d–h	−0.81	1.00	4.4	d–l	3.1	e–l	2.1	e–n	−1.19	1.00
10	JA 21	3.5	b–i	2.9	a–e	2.1	a–d	−0.68	0.99	4.5	d–l	3.6	a–h	2.6	b–g	−0.95	1.00
11	JA 37	3.2	c–k	2.5	b–i	1.4	e–h	−0.93	0.98	4.1	f–o	3.1	d–l	1.8	h–n	−1.11	0.99
12	JA 38	3.3	c–j	2.6	a–g	2.1	a–d	−0.64	1.00	4.5	d–l	3.6	a–i	2.8	b–e	−0.84	1.00
13	JA 97	3.6	b–i	3.1	a–d	1.8	b–f	−0.89	0.93	4.7	d–l	3.9	a–g	2.3	c–k	−1.18	0.96
14	JA 132	3.3	c–j	2.7	a–g	1.8	b–g	−0.79	0.99	4.8	c–i	3.5	a–i	2.4	c–i	−1.23	1.00
15	JA 5	3.2	c–k	2.5	b–i	1.5	d–h	−0.85	0.99	4.3	e–m	3.3	b–j	2.1	e–n	−1.13	0.99
16	JA 122	3.7	a–i	3.0	a–e	1.7	c–g	−1.00	0.96	4.9	c–i	3.9	a–g	2.1	e–n	−1.39	0.97
17	HEL 324	4.1	a–d	2.4	c–j	1.6	d–h	−1.24	0.96	5.6	a–de	3.6	a–i	2.5	c–i	−1.59	0.97
18	JA 61	2.7	f–l	2.3	d–j	1.5	d–h	−0.64	0.96	3.5	h–o	2.9	f–m	1.8	h–n	−0.85	0.97
19	CN 52867	4.1	a–c	2.7	a–g	1.7	c–g	−1.20	0.99	5.3	b–f	3.6	a–i	2.4	c–j	−1.49	0.99
20	KKUAc001	3.2	c–k	2.6	a–h	1.5	d–h	−0.84	0.98	5.1	c–g	4.0	a–f	2.4	c–i	−1.31	0.99
21	HEL 53	3.3	c–j	2.7	a–g	2.0	a–e	−0.69	0.99	5.6	a–e	4.2	a–c	3.0	a–c	−1.26	1.00
22	HEL 61	2.9	d–l	2.5	b–i	1.9	a–e	−0.49	0.99	4.6	d–l	3.7	a–g	2.9	a–e	−0.89	1.00
23	HEL 231	3.9	a–f	2.9	a–f	2.3	a–c	−0.83	0.98	6.1	a–c	4.2	a–c	3.3	ab	−1.43	0.96
24	HEL 335	4.5	ab	3.0	a–e	1.7	c–g	−1.39	1.00	6.6	ab	4.2	a–d	2.5	b–h	−2.01	0.99
25	JA 46	2.5	i–l	2.0	g–k	1.2	f–h	−0.65	1.00	3.3	k–o	2.4	j–m	1.6	k–n	−0.88	1.00
26	JA 60	2.5	i–l	1.8	h–k	1.5	d–h	−0.51	0.96	3.3	l–o	2.3	k–m	1.9	g–n	−0.71	0.95
27	JA 109	2.1	kl	1.6	jk	1.0	h	−0.59	1.00	3.0	m–o	2.4	j–m	1.4	mn	−0.81	0.99
28	JA 76	3.9	a–e	3.3	ab	2.0	a–e	−0.95	0.97	5.6	a–de	4.2	a–d	2.7	b–f	−1.46	1.00
29	JA 77	2.7	g–l	2.3	d–j	1.9	b–e	−0.39	0.99	3.4	j–o	2.9	g–m	2.3	c–k	−0.54	1.00
30	HEL 62	2.5	i–l	1.8	h–k	1.2	f–h	−0.65	1.00	3.5	i–o	2.6	i–m	1.7	i–n	−0.89	1.00
31	HEL 246	3.8	a–h	3.0	a–e	1.5	d–h	−1.14	0.97	5.0	c–g	3.9	a–g	2.2	d–l	−1.38	0.99
32	HEL 257	3.8	a–g	2.9	a–e	2.4	ab	−0.73	0.97	4.8	c–j	3.6	a–i	3.0	a–d	−0.91	0.97
33	JA 15	3.2	c–k	2.9	a–f	2.5	a	−0.35	1.00	4.6	d–l	4.1	a–e	3.6	a	−0.51	1.00
34	JA 67	2.6	h–l	2.1	f–k	1.6	d–h	−0.53	1.00	4.1	f–o	3.2	c–l	2.3	c–k	−0.90	1.00
35	JA 89	4.2	a–c	2.4	c–i	1.9	b–e	−1.13	0.91	5.9	a–d	3.6	a–i	2.8	b–e	−1.53	0.92
36	JA 125	2.8	e–l	2.1	f–k	1.6	d–h	−0.61	0.98	3.5	i–o	2.6	h–m	2.0	f–n	−0.78	0.99
37	HEL 65	4.0	a–d	3.4	a	2.0	a–e	−0.99	0.96	5.6	a–e	4.5	a	2.8	a–e	−1.40	0.99
38	HEL 253	3.0	c–l	2.0	g–k	1.7	c–g	−0.69	0.90	4.7	d–k	3.3	b–k	2.7	b–f	−0.99	0.95
39	HEL 256	4.8	a	2.5	b–i	1.6	d–h	−1.61	0.93	6.8	a	3.7	a–g	2.5	b–i	−2.16	0.94
40	JA102 × JA 89 (8)	3.6	b–i	2.8	a–f	1.8	b–f	−0.91	0.99	5.5	b–f	4.3	ab	2.7	b–f	−1.38	0.99
	Means	3.3		2.5		1.7		−0.79	0.98	4.6		3.4		2.3		−0.78	0.98

Means in the same column followed by the same letters are not different at $P \leq 0.01$ probability level by Duncan's multiple range test.

Significant differences among Jerusalem artichoke genotypes for tuber dry weight were observed under fully irrigated (W1), moderate (W2), and severe drought conditions (W3) in 2010/11 (Table 5). The ranges of phenotypic variations for tuber dry weight were from 1.1 to 4.5, 0.7 to 3.2, and 0.6 to 1.9 t ha^{-1} under fully irrigated, moderate, and severe drought conditions, respectively. Slope values (b-value) for all Jerusalem artichoke genotypes were negative, ranging from −0.22 to −1.45, whereas coefficient of determinations (r-squared) ranged from 0.80 to 1.00.

CN 52867, KKU Ac001, HEL 53, HEL 61, HEL 231, HEL 335, JA 76, HEL 246, JA 15, JA 89, HEL 65, HEL 253, HEL 256, and JA 102 × JA 89 (8) had consistently high tuber dry weights across water regimes in 2010/11 (Table 5). In general, high tuber dry weights were associated with high and negative b-values, indicating high reductions in tuber dry weight. Although the reductions in tuber dry weight were high, high tuber dry weights were also observed in these genotypes under severe drought conditions. In contrast, low tuber dry weights were associated with low reductions.

Jerusalem artichoke genotypes were also significantly different for biomass under fully irrigated, moderate, and severe drought conditions in 2010/11 (Table 5). Means for biomass of Jerusalem artichoke genotypes ranged from 1.3 to 6.2, 0.8 to 3.9, and 0.8 to 2.7 t ha^{-1} under fully irrigated, moderate, and severe drought conditions, respectively. All b-values for all genotypes were negative, ranging from −0.28 to −1.91. The results indicated that drought reduced biomass in all genotypes, and the magnitudes of reduction were different among Jerusalem artichoke genotypes. The coefficients of determinations were also high, ranging from 0.84 to 1.00.

KKU Ac001, HEL 53, HEL 61, HEL 231, HEL 335, JA 76, JA 15, JA 89, HEL 65, HEL 253, HEL 256, and JA 102 × JA 89 (8) had consistently high biomass across water regimes in 2010/11 (Table 5). Similar to tuber dry weight, the genotypes with high biomass had generally high reductions in biomass and vice versa. The genotypes with high biomass under drought conditions were those with high biomass under fully irrigated conditions.

Significant differences among Jerusalem artichoke genotypes were also observed for tuber dry weight and biomass across water regimes in 2011/12 (Table 6). Tuber dry weights ranging from 2.0 to 4.8, 1.5 to 3.4, and 1.0 to 2.5 t ha^{-1} were observed under fully irrigated, moderate, and severe drought conditions, whereas variations in biomass ranging from 2.8 to 6.8, 2.1 to 4.5, and 1.3 to 3.6 t ha^{-1} were found under fully irrigated, moderate, and severe drought conditions.

JA 6, JA 21, JA 38, JA 97, JA 132, JA 122, CN 52867, HEL 53, HEL 231, HEL 335, JA 76, HEL 257, HEL 65, and JA 102 × JA 89(8) had consistently high tuber dry weights across water regimes in 2011/12 (Table 6). The slopes for all Jerusalem artichoke genotypes were negative, ranging from −0.46 to −1.61, and coefficients of determination ranged from 0.90 to 1.00. The genotypes with high tuber dry weight under fully irrigated conditions had negative and high b-values and vice versa.

JA 6, JA 97, JA 132, HEL 324, CN 52867, KKU Ac001, HEL 53, HEL 61, HEL 231, HEL 335, JA 76, HEL 257, JA 15, JA 89, HEL 65, HEL 256, and JA 102 × JA 89 (8) had consistently high biomass across water regimes in 2011/12 (Table 6). B-values ranged from −0.69 to −2.16, and the b-values for these Jerusalem artichoke genotypes were also negative and high. Coefficients of determination ranged from 0.92 to 1.00, showing good approximation of the real data points. It is interesting to note that the genotypes with high biomass under well-watered conditions had high reductions in biomass and vice versa.

4. Discussion

Biomass and tuber yield in 2011/12 were higher than in 2010/11. The differences in biomass and tuber yield between the 2 years may have been due to higher temperatures in 2011/12 than in 2010/11. Lower daily minimum temperature during 7 to 14 DAT (16 to 19.5 °C) in 2010/11 (Figure 1a) may have reduced growth of Jerusalem artichoke. The optimum temperature for growth and yield of sunflower has been reported to range from 21 to 24 °C (Robinson, 1978). Rainfall in 2011/12 may also have contributed to the enhanced performance of the crop. A single rainfall event occurred a few days after planting, which may have promoted better crop establishment in 2011/12. However, the rainfall did not affect the differences among treatments because drought was not imposed on the crop until 14 DAT. In addition, more soil fertility in 2011/12 (Table 2) may have promoted better crop growth than in 2010/11.

Differences in water regimes in 2011/12 were clearer than in 2010/11. This indicated better control of the treatments in 2011/12. The problems for controlling water treatments in 2010/11 were resolved in 2011/12. Irrigation application in 2010/11 was supplied in early morning and evening, but in 2011/12 it was supplied only in the evening. Differences in plant water status as indicated by RWC were also similar to soil water status, as indicated by soil moisture content. The plant and soil water status clearly separated water regimes and drought levels in plants. Clearer differences among water regimes for soil moisture content at 0–30 cm compared to 60 and 90 cm also indicated that moisture at this soil level had larger effects on differences in biomass and tuber yield of Jerusalem artichoke grown under different water regimes. Under drought conditions, however, water at 0–30 cm was depleted and the genotypes with deeper root systems may have had an advantage in mining water in deeper soil (Monti et al., 2005).

Variations between years were rather low for tuber fresh weight, tuber dry weight, and biomass, accounting for 7.7%, 7.3%, and 11.6% of total variations, respectively. This indicated that these traits were rather consistent between years. In contrast to variations between years, greater variations in tuber fresh weight, tuber dry weight, and biomass were found among water regimes, accounting for 43.6%, 35.9%, and 33.5% of total variations for these traits. The results indicated that water management is very important for obtaining high yields. Variations among Jerusalem artichoke genotypes were intermediate among these sources of variations for tuber fresh weight (18.0%), tuber dry weight (21.4%), and biomass (26.3%). This indicated that it is possible to select Jerusalem artichoke genotypes for better performance for these traits. The interactions between year and genotype for tuber fresh weight, tuber dry weight, and biomass, though significant, were very small compared to main effects (year, water regime, and genotype). The interactions between genotype and water regime and the interactions between water regime and year were also low. Low interactions indicated that the genotypes performed rather consistently across years and water regimes and low interactions favor selection of better genotypes.

The biomass of Jerusalem artichoke in this study, ranging from 0.8 to 6.2 t ha^{-1}, was low compared the 16.1 to 35.0 t ha^{-1} seen in temperate regions (Liu et al., 2012). This was mainly caused by shorter crop duration in these tested genotypes. However, these Jerusalem artichoke genotypes can be grown in all seasons, both under rainfed and irrigated conditions, and can supply biomass to the bioethanol industry during seasonal shortage of other raw materials. Tuber dry weights ranging from 0.6 to 4.8 t ha^{-1} (tuber fresh weights ranging from 2.2 to 16.8 t ha^{-1}; data not shown) were observed in this study. In previous investigations in the tropics, fresh tuber yields were recorded, ranging from 3.0 to 38.9 t ha^{-1} (Kays and Nottingham, 2007). However, fresh tuber yields in temperate regions were much higher, ranging from 30.0 to 70.0 t ha^{-1} (Denoroy, 1996), from 24.1 to 65.6 t ha^{-1} (based on tuber dry weight of 7.1 to 18.4 t ha^{-1}) (Rodrigues et al., 2007), and from 3.0 to 38.9 t ha^{-1} (Liu et al., 2012). Maturity in the temperate regions (approximately 6–8 months) is generally longer than in the tropics (approximately 4 months) because crop growth rates near the equator are faster (Kays and Nottingham, 2007). Therefore, growing Jerusalem artichoke in the tropics for 3 crops per year with optimum planting dates is possible (Ruttanaprasert et al., 2013). The results demonstrate that good management of the crop in this specific environment could produce high Jerusalem artichoke biomass.

Severe drought stress resulted in greater reductions of tuber dry weight and biomass than did moderate drought stress. It has previously been reported that water application of 50% of maximum crop evapotranspiration reduced tuber yield by 20% (Conde et al., 1991; Losavio et al., 1997). Yield reductions in this study were higher than 20%, possibly due to sandy soil and higher temperature. Irrigation is important for sustaining high tuber yield; however, development of Jerusalem artichoke varieties with tolerance to drought is another way to sustain yield. The reductions in tuber yield and biomass were dependent on Jerusalem artichoke genotypes. In this study, genotypes with high potential for tuber yield and biomass in general had greater drought-induced reductions than did genotypes with low potential. Therefore, the main criterion for selection of drought-tolerant genotypes in this study was yield under drought stress. A genotype with high tuber yield potential and low reduction in tuber yield under drought stress has been reported (Liu et al., 2012). It would be best to develop adapted cultivars for Thailand that combine high yield potential and low reduction under drought conditions.

Jerusalem artichoke has great potential as a source of biomass for energy because it has a rapid growth rate and the ability to grow on marginal land. It had tuber yield as high as 38.9 t ha^{-1} under favorable conditions in tropical regions (Pimsean et al., 2010). Jerusalem artichoke has relatively low cultivation costs compared to other energy crops, as it generally requires low inputs in terms of irrigation, fertilization, and pesticides (Kays and Nottingham, 2007). The development of adaptive and stress-tolerant cultivars may enable this crop to be used as an important feedstock for bioenergy production in tropical regions.

Drought reduced tuber dry weight and biomass, and the reductions in tuber dry weight and biomass were greater under severe drought than moderate drought conditions. Genotypic variations in tuber dry weight and biomass were observed in this study. Over both seasons, CN 52867, HEL 53, HEL 231, HEL 335, JA 76, HEL 65, and JA 102 × JA 89 (8) had consistently high tuber dry weight (1.3 to 4.5 t ha^{-1}) and HEL 53, HEL 61, HEL 231, HEL 335, JA 76, JA 15, JA 89, HEL 65, HEL 256, and JA 102 × JA 89 (8) had consistently high biomass (2.0 to 6.8 t ha^{-1}). These genotypes could be used to develop high-yielding cultivars with improved drought tolerance.

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