Content List Available at ThaiJo

Khon Kaen Agriculture Journal

Journal Home Page : https://li01.tci-thaijo.org/index.php/agkasetkaj

Genetic diversity of chlorophyll fluorescence in Jerusalem artichoke (*Helianthus tuberosus* L.) germplasm under different water regimes

Anon Janket[1], Nimitr Vorasoot[2], Ruttanachira Ruttanaprasert[3] and Sanun Jogloy[2,4]*

[1] *Department of Agronomy, Faculty of Agriculture, Ubon Ratchathani University, Ubon Ratchathani, 34190, Thailand*
[2] *Department of Agronomy, Faculty of Agriculture, Khon Kaen University, Khon Kaen, 40002, Thailand*
[3] *Department of Plant Science Textile and design, Faculty of Agriculture and Technology, Rajamangala University of Technology, Surin Campus, 32000, Thailand*
[4] *Peanut, Jerusalem Artichoke and Cassava Research Group, Khon Kaen University, Khon Kaen 40002, Thailand*

ABSTRACT: Genetic diversity plays a critical role in crop improvement, but information on genetic diversity for chlorophyll fluorescence is rare regarding the Jerusalem artichoke (JA). This study aimed to investigate genetic variations for chlorophyll fluorescence in JA accessions and to identify superior genotypes under different water gradient conditions. A field experiment was conducted in a strip plot design with four replications. A horizontal factor was three different water regimes (W1= 100% of the crop water requirement, W2 = 50%, and W3=25% of the crop water requirement) and a vertical factor consisted of forty JA genotypes. Chlorophyll fluorescence and relative water content were recorded at 40, 60, and 70 days after transplanting (DAT). Results indicated that there were significant genetic variations in chlorophyll fluorescence and there was no significant interaction between genotypes and water regimes for this trait. The genotypes CN52867, JA70, HEL257, JA125, and JA92 showed significantly higher F'v/F'm than the other genotypes at all plant ages, whereas the CN52867 genotype showed the highest Fv/Fm at all plant ages. These genotypes would be profitable genetic resources for improving the efficiency of the photosystem of JA in the future.
Keywords: breeding; genotypic variation; Jerusalem artichoke; sunchoke; water stress

Introduction

Helianthus tuberosus L. or Jerusalem artichoke (JA), is a tuber crop native to North America. It is closely related to the sunflower (*Helianthus annus*), and they are only the species in the genus under commercial cultivation. Jerusalem artichoke is an herbaceous, tuberous, and inulin-producing plant (Cosgrove et al., 2000). Inulin is beneficial to health, and it is classified as a prebiotic substance that enhances immunity while increasing the absorption of calcium and magnesium (Roberfroid, 2005). It can also help with the treatment of a variety of health problems, including osteoporosis, atherosclerosis, dyslipidemia, obesity, type 2 diabetes, and constipation (Roberfroid, 2000). Tubers of JA also can be used as an ingredient for antibiotics in animal feed, as inulin suppresses pathogenic microbes, balances gut microflora, enhances nutrient digestion and absorption (Summart et al., 2021), and serves as a raw material for bio-ethanol production (Cosgrove et al., 2000; Onsoy et al., 2007).

Drought is one of the most severe environmental stresses affecting JA productivity (Ruttanapraseart et al., 2014; Chaimala et al., 2020, 2021). An empirical study revealed that a supply of 75% and 45% of the water

* Corresponding author's email: sjogloy@gmail.com
Received: date; May 17, 2022 Accepted: date; March 15, 2023 Published: date

requirement reduced the tuber dry weight by 28.3% and 51.7%, respectively compared to fully irrigated conditions (Ruttanapraseart et al., 2014). The tuber yield of JA was more greatly reduced under a long duration of drought than under a short duration of drought. Chaimala et al. (2020) noted that a short-term drought duration occurring at 60 days after transplanting (DAT) until harvest reduced tuber dry weight by 42.5% compared to fully irrigated conditions, whereas long-term drought duration at 45 DAT until harvest reduced tuber yield by 62.6%. Among inulin-containing crops, JA is more susceptible to water stress than sugar beet and chicory (Schittenhelm, 1999).

Although many farmers are seeking water resources to solve the drought problem, high investment is required. Moreover, the construction of reservoirs destroys large areas of forest. The use of JA varieties with a high level of drought resistance is inevitably the last choice to combat the drought problem. Breeding for drought resistance is an important strategy to alleviate the drought problem and sustain crop productivity under drought conditions. In the breeding program, the identification and selection of superior genotypes is the first and most important step for choosing parental genotypes. In general, the selection of drought-resistant varieties has been based mainly on yield per se and low yield reduction under drought conditions. However, yield is controlled by several genes, and high genotype and environment interactions are usually found. These affect the efficiency of selection in a breeding program (Dinh et al., 2014). The use of other physiological traits, which are simple and rapid as surrogate traits for drought resistance, would be more effective and efficient.

Previously, genotypic and phenotypic variations among JA genotypes under different water regimes have been reported in terms of biomass, tuber yield (Ruttanaprasert et al., 2016a), water use, water use efficiency (Janket et al., 2013), yield components, days to harvest (Janket et al., 2016), specific leaf area, SPAD chlorophyll meter reading (SCMR), and harvest index (Ruttanaprasert et al., 2016b). These previous studies were successfully performed with field line-source sprinklers to create different water gradient conditions in a large area for the evaluation of a large JA germplasm. Incidentally, there are many physiological traits that are related to the yield of JA under drought conditions, such as relative water content, stomatal conductance, specific leaf area (Chaimala et al., 2021), SCMR (Ruttanaprasert et al., 2012; 2016b), root length (Ruttanaprasert et al., 2015; Puangbut et al., 2018), and leaf area (Puangbut et al., 2022). The relationship between SCMR and photosynthetic capacity was also observed, which showed that the higher performance of these physiological traits could contribute to a higher biomass of JA (Puangbut et al., 2017). Currently, plant photosynthetic efficiency is one of the alternative physiological traits that can be used to evaluate the performance of crops under various unfavorable growing conditions.

Chlorophyll fluorescence is light re-emitted by chlorophyll molecules during the return from excited to non-excited states in photosystem II during the process of photosynthesis (Kalaji and Guo, 2008). It is one of the most powerful and widely-used techniques for studying photosynthetic responses to stress (Guidi et al., 2019). Many empirical studies suggested that the quantum efficiency of photochemistry values (Fv/ Fm and Fv′/Fm′) could be useful criteria in the selection for drought tolerance in the crops (Guidi et al., 2019; Sawatraksa et al., 2018). An earlier study in sunflower (*Helianthus annuus*) showed that the values of Fv/Fm for non-stressed plants were 0.78–0.80 and decreased to 0.45-0.62 when the crop was subjected to abiotic stresses (drought and heavy metal) (Plesni˘ar et al., 1994; Azevedo et al., 2005; Yalcin et al., 2016). Unfortunately, genotypic variation in

chlorophyll fluorescence under different water regimes is lacking for JA. Therefore, the aims of this study were to (i) investigate the genotypic variation in chlorophyll fluorescence of 40 JA genotypes under different water regimes and (ii) to identify JA genotypes with high chlorophyll fluorescence. The identified genotypes will be useful in future breeding programs for drought tolerance.

Materials and Methods

Plant materials and experimental details

The experimental field site was located at the Agronomy farm at Khon Kaen University, Thailand (16° 28′ N, 102 ° 48′ E, 200 m above sea level), during the dry season from October to February. A strip-plot design with four replications was used. The horizontal factor involved three water regimes created by a line source sprinkler irrigation system consisting of 100%, 75%, and 45% of crop water requirement (ETcrop) (Hank et al., 1976), and the 40 JA genotypes with differences in yield and plant characteristics from three diverse sources were assigned as the vertical factor **(Table 1)**.

Seedlings were prepared by cutting the tubers into small pieces with 2-3 buds each and immersing them in hydrous fungicide (carboxamide) at the rate of 1 g per 2 liters of water to prevent fungal infections in the tuber pieces. The tuber pieces were then incubated in burnt rice husk mixed with *Trichoderma* (1:1) in plastic boxes for 5-7 days to stimulate germination. *Trichoderma* was used for preventing stem rot disease caused by *Sclerotium rolfsii*. After germination, the seedlings were transferred into plug trays containing a mixed medium of soil, burnt rice husk, and *Trichoderma* at the ratio of 3:3:2. Water was supplied regularly to the seedlings to avoid water stress until the seedlings had 2-3 leaves or about 7-10 days after transfer. The seedlings were then suitable for transplantation into the field.

The breakup of the hardpan was carried out by a subsoiler at a depth of 60 cm, and the soil was plowed twice using a disc plow tractor. A line source sprinkler system consisting of two modules was installed at the center of the experimental field, and PVC tubes 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, but the system was not operated until the crop was established well.

Prior to transplantation, 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 pressure values and water meters were fitted separately for all replications to ensure a uniform supply of water. An aluminum access tube was installed in the middle of each plot border water level to measure changes in soil moisture.

Plot size was 2 m wide and 4 m long, with a spacing of 50 cm between rows, and 10 cm between plants within a row. The healthy and uniform seedlings were then transplanted, and an inoculum of *Trichoderm*a spp. was applied to each hill before planting. Supplementary irrigation was supplied immediately for 10 days after transplanting (DAT) by drip irrigation at field capacity (FC) level to facilitate establishment. Manual weeding was performed at 14 DAT, and mixed fertilizer of N – P_2O_5 –K_2O (15-15-15) at the rate of 156.25 kg/ha was applied at 30

DAT. After 14 DAT, water was supplied through a line source sprinkler irrigation system until harvest to create the difference in soil water regimes.

W1 was nearest to the line source sprinkler, with a distance of 1 to 5 m and the amount of water that was supplied to the plots was equivalent to the ETcrop following the equation of Doorenbos and Pruitt (1992), where,

ETcrop = ETo x Kc

ETcrop = crop water requirement (mm/day)

ETo = evapotranspiration of a reference plant under specified conditions calculated by the pan evaporation method

Kc = the crop water requirement coefficient, which varies depending on varieties and growth stages. As the Kc of JA was not found in the literature, the Kc for sunflowers was used (Janket et al., 2013; Ruttanaprasert et al., 2016ab).

W2 was 5 to 9 m away from the center of the line source sprinkler, and the amount of water was 75% of the crop water requirement. W3 was the driest treatment, with a distance of 9 to 13 m from the center of the line source sprinkler, and the water supplied to the plot was 45% of the crop water requirement. In this study, the water supplied was monitored by catch cans, which were installed in all replications of water treatments.

Table 1 Forty genotypes of Jerusalem artichoke were used in the experiment; their characteristics and sources of origin are as follows:

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

[4]Jerusalem Artichoke Research Project, Khon Kaen University, Thailand

Data collection

Soil and weather conditions

Prior to planting, soil samples were randomly collected from 10 points for each replication at depths of 0-30 cm. After air drying, the bulked soil samples were used to determine the soil's physical characteristics (the texture, pH, electrical conductivity, cation exchange capacity) and chemical properties (total nitrogen, available phosphorus, and exchangeable potassium). A pressure plate extractor was used to estimate water content in percentages at FC and the permanent wilting point (PWP). The soil moisture volume fraction at 7-day intervals from transplantation until harvest at depths of 30, 60, and 90 cm, were measured by a neutron probe (Type I.H. II SER. No NO152, Ambe Diccot Instruments Co., Ltd., England). Weather conditions (evaporation, maximum and minimum temperatures, rainfall, and relative humidity) were also recorded by a weather station located in the experimental field.

The soil in the experiment was loamy sand. The soil type is the Yasothon series with the following chemical properties: pH of 6.08, poor organic matter (0.44%), total nitrogen (N) (0.02%), available phosphorus (P)

(23.95 mg/kg), exchangeable potassium (K), and calcium (Ca) (33.09 and 418.33 mg/kg, respectively) with electric conductivity at (EC) (0.03 dS/m) **(Table 2)**. Maximum temperatures (Tmax) ranged from 22.9-39.5 °C and minimum air temperatures (Tmin) ranged from 12.5-24.4 °C **(Figure 1a)**. Daily pan evaporation ranged from 2.0 to 7.70 mm, and the relative humidity values ranged from 68-98% **(Figure 1b)**. There was no rainfall during the growing season.

Table 2 Soil physical and chemical properties in the experimental fields at the depth of 0-30 cm

Chemical and physical properties	Values
pH (1:1 H_2O)	6.08
Organic matter (%)	0.44
Total N (%)	0.02
Available phosphorus (mg/kg)	23.95
Exchangeable potassium (mg/kg)	33.09
Electrical conductivity (EC., dS/m) (1:5 H_2O)	0.03
Cation exchange capacity (CEC) (c mol/kg)	5.22
Exchangeable Ca (mg/kg)	418.33
Texture class	Loamy sand

Chlorophyll fluorescence and relative water content

Chlorophyll fluorescence parameters were determined on the healthy leaf blade of the second or third fully expanded leaf from five bordered plants for each subplot. The measurements were done from 9 to 11 a.m. at 30, 60, and 90 DAT using the Mini PAM-II Photosynthesis Yield Analyzer (Heinz Walz GmbH, Effeltrich, Germany). Care was taken to ensure that the sensor fully covered the leaf lamina and interference from veins and midribs was avoided. The photosynthetic quantum yield of the reaction center of photosystem II (PSII) was measured under natural light conditions (F'v/F'm). The minimal fluorescence yield of the dark-adapted state (F_0) was determined in complete darkness at predawn from 3.00-4.30 a.m. (Santanoo et al., 2019). Maximal fluorescence of the dark-adapted state (F_m) was achieved following a saturating pulse of 4000 μmol/m^2/second lasting 0.8 seconds. The maximal quantum yield of PSII photochemistry (Fv/Fm) was calculated as follows: All measurements were measured under natural temperature condition.

$Fv/Fm = (F_m - F_0)/F_m$.

Relative water content (RWC) was also evaluated at 40, 60, and 70 DAT based on the Krammer method (Krammer, 1980). Five leaf discs per plot from five individual plants were cut at the second or third expanded leaves from the top of the main stem using a disc borer (1 cm^2 in leaf area). After determining fresh weight, leaf samples were kept in distilled water for 8 h at room temperature (25 °C) to attain turgidity, and then the turgid weight was recorded. The leaf discs were then oven-dried at 80 °C for at least 48 h or until the weight was constant, and the leaf dry weight was recorded. The relative water content was calculated as follows:

RWC =[(FW-DW)/ (TW- DW)] x 100,

where FW: sample fresh weight, TW: sample turgid weight, and DW: sample dry weight.

We noted that the difference among water regimes in soil moisture volume fractions was clearly observed at a soil depth of 30 cm only **(Figure 2a)**, which started occurring at 21 DAT after drought conditions were imposed on the crop by a line-source sprinkler irrigation system for a week. Considering the soil depth of 30 cm, the soil moisture volume fraction for W1 was higher than W2, and W2 was higher than W3 throughout the growing season. In this study, the difference in soil moisture volume fraction among water regimes was slightly observed at a soil depth of 60 cm but not observed at 90 cm **(Figure 2bc)**.

The means of RWC for all JA genotypes at 40, 60, and 70 DAT for W1 ranged from 74.3-78.9%, W2 ranged from 64.9-75.0%, and W3 ranged from 57.8-73.1%. It was noted that the relative water content for W1 was significantly higher than W2, and W2 was significantly higher than W3 for all plant ages **(Table 3)**.

Table 3 The relative water content (%) of second or third expanded leaves at 40, 60, and 70 days after transplanting (DAT) of 40 Jerusalem artichoke genotypes grown in different water regimes

Water regimes	Relative water content (%)		
	40 DAT	60 DAT	70 DAT
W1	78.9±0.6a	78.9±0.6 a	74.3±0.9a
W2	75.0±0.6 b	71.1±0.6b	64.9±0.7b
W3	73.1±0.6c	64.7±0.7 c	57.8±0.6c

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). Data are presented as means ±SD (n=4). W1= 100%ETcrop, W2= 75%ETcrop and W3=45%ETcrop.

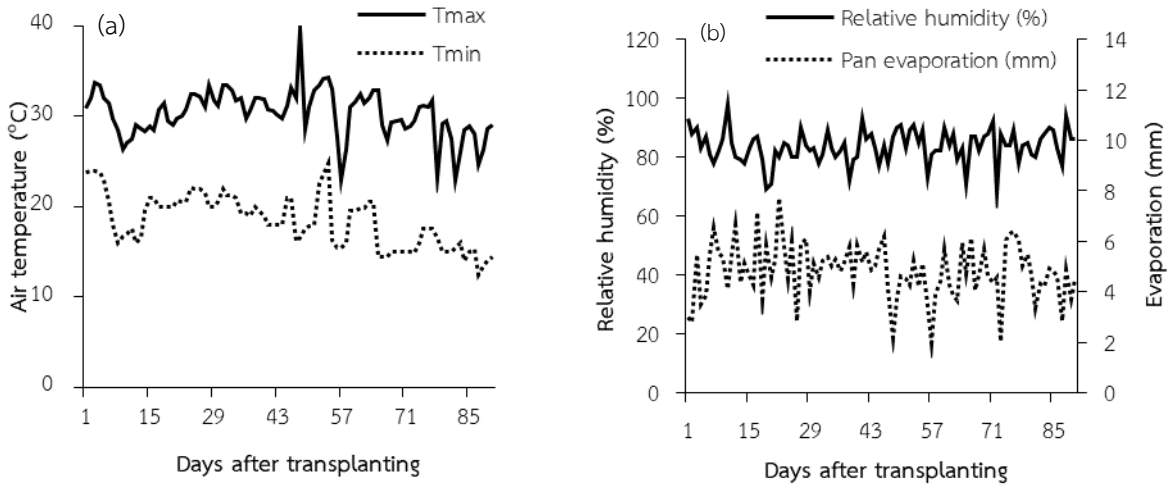

Figure 1 Maximum temperatures (T-max), minimum air temperatures (T-min) (^{O}C) (a), rainfall (mm), pan evaporation (mm), and relative humidity (%) (b) during the growing periods

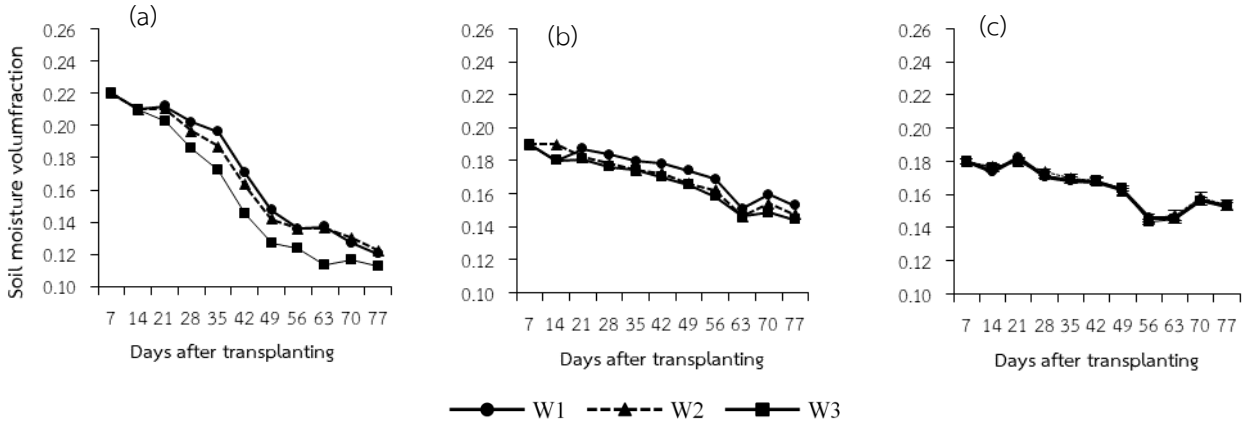

Figure 2 Soil moisture volume fractions for three soil water regimes at three soil depths of 30 cm (a), 60 cm (b), and 90 cm (cm) during the dry season

Biomass and tuber yield

At the harvesting stage, biomass and tuber yield were also determined from fourteen bordered plants in each subplot. Crop maturity was determined by leaf senescence of 50% and stem browning, with differences among genotypes and water regimes (Janket et al., 2016). Plants were cut at the soil surface and separated into leaves, stems, and tubers. Tubers were washed in running tap water to remove adhering soil, and then the fresh weight for all plant parts was determined. At least 10% of all plant parts were then subsampled and oven-dried at 80 °C for at least 72 h or until weights were constant. After drying, the dry weights of individual plant parts were recorded.

The stress tolerance index (STI) and stress susceptibility index (SSI) for biomass and tuber dry weight were calculated as follows:

$STI= (Yp*Ys)/(\hat{Y}p)^2$ and $SSI= 1-(Ys/Yp)/ 1 – (\hat{Y}s / \hat{Y}p)$ where

Yp*Ys are the mean of individual genotypes under non-stress and stress conditions, respectively, and $\hat{Y}p$ and $\hat{Y}s$ are the means of all genotypes under non-stress and stress conditions, respectively. A high STI value indicates greater drought tolerance, whereas a low SSI value (less than 1) is preferred (Hooshmandi, 2019).

Statistical analysis

Analysis of variance for each parameter was performed according to strip plot design (Gomez and Gomez, 1984) using the Statistix 10 program. Duncan's multiple range test (DMRT) was used to compare means at a 5% level of probability using the IBM SPSS statistics program. Correlation coefficients between chlorophyll fluorescence (Fv/Fm and F'v/F'm), values with biomass, yield, STI, and SSI were also calculated for each water regime.

Results

Analysis of variance

An analysis of variance revealed that JA genotypes were significantly different in F'v/F'm at 40 DAT and Fv/Fm at all plant ages (40, 60, and 70 DAT) **(Table 4)**. The water regime was not significantly different for all

chlorophyll fluorescence at all plant ages. Moreover, there was no significant interaction between water regimes and genotypes. Therefore, the means for all chlorophyll fluorescence parameters were combined and analyzed across water regimes.

Table 4 The mean squares from the combined analysis of variance for chlorophyll fluorescence (Fv'/Fm' and Fv/Fm) at 40, 60, and 70 days after transplanting (DAT) of 40 Jerusalem artichoke genotypes grown in different water regimes

Source of variance	df	Mean square					
		40 DAT		60 DAT		70 DAT	
		Fv'/Fm'	Fv/Fm	Fv'/Fm'	Fv/Fm	Fv'/Fm'	Fv/Fm
Replication	3	0.21954	0.0025	0.1483	0.0374	0.09735	0.0151
Water regimes (W)	2	0.00362 ^{ns}	0.0010 ^{ns}	0.0049 ^{ns}	0.0054 ^{ns}	0.02226 ^{ns}	0.0054 ^{ns}
Error (a)	6	0.01474	0.0001	0.0194	0.0006	0.03913	0.0026
Genotypes (G)	39	0.00737*	0.0003*	0.0046 ^{ns}	0.0017**	0.01571 ^{ns}	0.0058*
Error (b)	117	0.00478	0.0002	0.0032	0.0005	0.01293	0.0024
W x G	78	0.00309 ^{ns}	0.0001 ^{ns}	0.0029 ^{ns}	0.0002 ^{ns}	0.01043 ^{ns}	0.0015 ^{ns}
Error (c)	234	0.00355	0.0001	0.0034	0.0003	0.01061	0.0014
Total	479	0.21954	0.0002	0.0045	0.0007	0.01251	0.0021
CV(a)		19.4	1.1	20.7	3.0	24.1	7.5
CV(b)		11.0	1.6	8.4	2.7	19.6	7.2
CV(c)		9.5	1.3	8.6	2.0	17.8	5.4

ns, *, ** = non-significant differences, significant differences at $p \leq 0.05$ and $p \leq 0.01$, respectively

Genotypic variation in chlorophyll fluorescence

The means of F'v/F'm at 40 DAT across genotypes among water regimes were 0.625, 0.633, and 0.624 for W1, W2, and W3, respectively. Whereas the means among JA genotypes across water regimes for F'v/F'm at 40 DAT ranged from 0.534 to 0.661. It was noted that JA15, HEL253, JA92, JA60, CN52867, JA70, HEL324 and JA37 had the highest F'v/F'm, whereas HEL62 had the lowest F'v/F'm at 40 DAT. No significant differences among water regimes were also observed for Fv/Fm at 40 DAT. The values for W1, W2, and W3 were 0.846, 0.850, and 0.850, respectively. The means among JA genotypes across water regimes for Fv/Fm at 40 DAT ranged from 0.838 to 0.860. CN52867 had the highest, whereas JA102xJA89(8) had the lowest values for Fv/Fm at 40 DAT **(Table 5)**.

The means for F'v/F'm at 60 DAT across genotypes among water regimes were 0.679, 0.673, and 0.668 for W1, W2, and W3, respectively. There was no significant difference among JA genotypes, with the mean among JA genotypes ranging from 0.624 to 0.713. The results showed that JA38, JA77, and JA70 seemed to be the best genotypes, whereas HEL62 and HEL65 gave the lowest values of F'v/F'm at 60 DAT. The values of Fv/Fm at 60 DAT for W1, W2, and W3, were 0.802, 0.805, and 0.813, respectively, whereas the mean for Fv/Fm among JA genotypes

ranged from 0.776 to 0.828. CN52867, JA16, and JA37, had the highest values, while HEL253, JA132, and JA102xJA89(8) had the lowest values for Fv/Fm at 60 DAT **(Table 5)**.

The means among water regimes for F'v/F'm at 70 DAT were 0.566, 0.586, and 0.587, for W1, W2, and W3, respectively. There was no significant difference among JA genotypes, with the means across water regimes of 0.508 to 0.649. JA77 and JA60 seemed to be better genotypes, whereas JA38 and JA15 tended to have the lowest values of F'v/F'm at 60 DAT. No significant differences among water regimes were also observed for Fv/Fm at 70 DAT. The values of Fv/Fm at 70 DAT for W1, W2, and W3, were 0.680, 0.684, and 0.691, respectively. The mean for Fv/Fm among JA genotypes ranged from 0.620 to 0.727. HEL257, JA125, CN52867, JA77, JA70, JA37, HEL256, JA60, JA109, and JA21 had the highest values for Fv/Fm at 70 DAT, whereas HEL61 had the lowest value **(Table 5)**.

In this study, when the top-ten genotypes with the highest chlorophyll fluorescence parameters were considered, CN52867, JA70, HEL257, JA125, and JA92, had consistently high values across plant ages. However, only JA70 showed a consistently statistically significant high F'v/F'm at all plant ages, while only CN52867 showed a consistently statistically significant high Fv/Fm at all plant ages with the highest values.

Relationships between chlorophyll fluorescence parameters with yield and drought tolerance traits

The correlations between chlorophyll fluorescence parameters with yield, biomass, and drought tolerance indices were separately analyzed under well-watered **(Table 6)** and drought conditions **(Table 7)**. There were no correlations between F'v/F'm and Fv/Fm at 40 DAT with yield and biomass under well-watered conditions **(Table 6)**. It was noted under "well-watered" that there was a negative and significant correlation between Fv/Fm at 60 DAT with tuber dry weight (r=-0.28**) and biomass (r=0.29**). Likewise, negative and significant correlations were also observed between Fv'/Fm' at 70 DAT with tuber dry weight (r = -0.20**) and biomass (r=-0.19*). There were negative and significant correlations between Fv/Fm at 70 DAT and tuber dry weight (r = -0.28**) and between Fv/Fm at 70 DAT and biomass (r = -0.29**) under well-watered conditions.

Under drought conditions, there were no correlations between F'v/F'm for all plant ages (40, 60, and 70 DAT) and Fv/Fm at 40 DAT with STI for tuber dry weight and STI for biomass, tuber dry weight, and biomass, for both moderate (W2) and severe drought stress (W3) conditions **(Table 7)**. The correlations between Fv/Fm at 70 DAT with STI for tuber dry weight, STI for biomass, tuber dry weight, and biomass, were also not observed under W3 but not for W2. It was noted under moderate drought stress that positive and significant correlations were observed between Fv/Fm at 60 DAT and 70 DAT with STI for tuber dry weight (r=0.38** and 0.28*) and STI for biomass (r=0.36** and 0.28**). Likewise, the values of Fv/Fm at 60 DAT and 70 DAT were negatively significantly correlated with tuber dry weight (r=-0.36* and -0.18*) and biomass (r=-0.39** and -0.26*). However, under severe drought stress, the correlation coefficients between Fv/Fm with STI for tuber dry weight (r= 0.42**) and STI for biomass (r=0.47**), tuber dry weight (r=-0.45**), and biomass (r=-0.46**), were significant at 60 DAT only.

In this study, the values of SSI for tuber dry weight and SSI for biomass were not correlated with all chlorophyll fluorescence parameters (Fv/Fm and F'v/F'm) at all plant ages for both moderate and severe drought stress conditions **(Table 7)**

Table 5 Genetic diversity of chlorophyll fluorescence (Fv'/Fm' and Fv/Fm) at 40, 60 and 70 days after transplanting (DAT) of 40 Jerusalem artichoke genotypes across 3 water regimes

Water regimes/ Genotypes	40 DAT		60 DAT		70 DAT	
	Fv'/Fm'	Fv/Fm	Fv'/Fm'	Fv/Fm	Fv'/Fm'	Fv/Fm
W1	0.625±0.190	0.846±0.119	0.679±0.095	0.802±0.100	0.566±0.190	0.680±0.190
W2	0.633±0.185	0.850±0.199	0.673±0.116	0.805±0.092	0.586±0.190	0.684±0.196
W3	0.624±0.199	0.850±0.189	0.668±0.195	0.813±0.198	0.587±0.210	0.691±0.201
F-test	ns	ns	ns	ns	ns	ns
JA1	0.585±0.080 ab	0.843±0.096 ab	0.678±0.061	0.818±0.060 abc	0.625±0.210	0.688±0.176 ab
JA 4	0.645±0.096 ab	0.852±0.091 ab	0.685±0.085	0.799±0.160 a-e	0.526±0.118	0.667±0.155 ab
JA 6	0.640±0.066 ab	0.849±0.057 ab	0.676±0.112	0.801±0.009 a-e	0.557±0.099	0.662±0.122 ab
JA 36	0.637±0.070 ab	0.854±0.045 ab	0.654±0.100	0.809±0.079 a-e	0.554±0.210	0.683±0.190 ab
JA 70	0.652±0.090 a	0.853±0.078 ab	0.707±0.094	0.819±0.112 abc	0.636±0.186	0.710±0.167 a
JA 92	0.657±0.100 a	0.857±0.097 ab	0.695±0.091	0.810±0.187 a-e	0.540±0.148	0.695±0.190 ab
JA 114	0.609±0.091 ab	0.843±0.052 ab	0.665±0.061	0.810±0.119 a-e	0.547±0.221	0.699±0.117 ab
JA 3	0.617±0.063 ab	0.853±0.043 ab	0.677±0.191	0.812±0.096 a-d	0.579±0.233	0.688±0.167 ab
JA 16	0.631±0.050 ab	0.850±0.054 ab	0.668±0.049	0.825±0.088 ab	0.553±0.167	0.680±0.198 ab
JA 21	0.599±0.091 ab	0.854±0.065 ab	0.656±0.065	0.820±0.109 abc	0.603±0.190	0.701±0.211 a
JA 37	0.647±0.044 a	0.853±0.029 ab	0.677±0.011	0.823±0.052 ab	0.592±0.177	0.710±0.089 a
JA 38	0.618±0.051 ab	0.849±0.210 ab	0.713±0.082	0.809±0.119 a-e	0.518±0.113	0.689±0.110ab
JA 97	0.623±0.059 ab	0.852±0.190 ab	0.694±0.096	0.806±0.112 a-e	0.583±0.200	0.688±0.190 ab
JA 132	0.636±0.078 ab	0.840±0.078 ab	0.645±0.048	0.780±0.067de	0.612±0.181	0.6875±0.230 ab
JA 5	0.661±0.045 a	0.857±0.110 ab	0.676±0.088	0.804±0.113 a-e	0.616±0.161	0.658±0.205 ab
JA 122	0.637±0.068 ab	0.848±0.090 ab	0.670±0.079	0.820±0.098 abc	0.572±0.163	0.662±0.199 ab
HEL 324	0.652±0.034 a	0.850±0.098 ab	0.656±0.131	0.792±0.070 b-e	0.558±0.187	0.669±0.111 ab
JA 61	0.614±0.061 ab	0.846±0.068 ab	0.678±0.060	0.805±0.062 a-e	0.555±0.167	0.671±0.134 ab
CN 52867	0.653±0.090 a	0.860±0.060 a	0.660±0.091	0.828±0.045 a	0.570±0.220	0.715±0.190 a
KKUAc001	0.633±0.088 ab	0.844±0.006 ab	0.675±0.088	0.792±0.042 b-e	0.564±0.180	0.690±0.087 ab
HEL 53	0.640±0.093 ab	0.846±0.013 ab	0.651±0.171	0.806±0.065 a-e	0.589±0.229	0.666±0.189 ab
HEL 61	0.603±0.065 ab	0.843±0.096 ab	0.676±0.069	0.812±0.078 a-d	0.528±0.190	0.620±0.167 b
HEL 231	0.659±0.090 a	0.854±0.051 ab	0.673±0.038	0.799±0.099 a-e	0.535±0.145	0.652±0.098 ab
HEL 335	0.619±0.048 ab	0.847±0.049 ab	0.695±0.099	0.805±0.111 a-e	0.605±0.170	0.672±0.150 ab
JA 46	0.636±0.067 ab	0.849±0.063 ab	0.674±0.112	0.812±0.049 a-d	0.623±0.097	0.699±0.290 ab
JA 60	0.656±0.067 a	0.848±0.055 ab	0.693±0.167	0.816±0.038 abc	0.647±0.193	0.709±0.162 a
JA 109	0.612±0.090 ab	0.853±0.076 ab	0.665±0.198	0.812±0.012 a-d	0.600±0.229	0.703±0.210 a
JA 76	0.603±0.080 ab	0.844±0.048 ab	0.668±0.091	0.801±0.077 a-e	0.564±0.090	0.683±0.156 ab
JA 77	0.643±0.100 ab	0.847±0.083 ab	0.710±0.088	0.803±0.043 a-e	0.649±0.210	0.713±0.186 a
HEL 62	0.534±0.090 b	0.846±0.033 ab	0.636±0.067	0.811±0.065 a-e	0.608±0.175	0.696±0.198 ab
HEL 246	0.634±0.091 ab	0.841±0.041 ab	0.680±0.123	0.795±0.018 a-e	0.591±0.143	0.677±0.191 ab
HEL 257	0.643±0.120 ab	0.846±0.030 ab	0.683±0.144	0.817±0.045 abc	0.622±0.159	0.727±0.098 a
JA 15	0.626±0.101 ab	0.842±0.011 ab	0.657±0.198	0.817±0.123 abc	0.508±0.197	0.648±0.199 ab
JA 67	0.624±0.101 ab	0.850±0.032 ab	0.693±0.181	0.801±0.111 a-e	0.592±0.096	0.699±0.234 ab
JA 89	0.607±0.095 ab	0.849±0.012 ab	0.692±0.090	0.805±0.099 a-e	0.538±0.114	0.674±0.178 ab
JA 125	0.603±0.064 ab	0.854±0.042 ab	0.675±0.148	0.817±0.060 abc	0.616±0.089	0.716±0.091 a
HEL 65	0.640±0.055 ab	0.853±0.039 ab	0.624±0.091	0.793±0.075 b-e	0.581±0.191	0.667±0.134 ab
HEL 253	0.638±0.048 ab	0.850±0.054 ab	0.671±0.099	0.776±0.090 e	0.541±0.154	0.677±0.156 ab
HEL 256	0.590±0.050 ab	0.845±0.090 ab	0.640±0.144	0.814±0.190 a-d	0.598±0.221	0.709±0.183 a
JA102XJA89(8)	0.630±0.071 ab	0.838±0.010 b	0.673±0.099	0.785±0.081 cde	0.587±0.178	0.675±0.176 ab
F-test	*	*	ns	**	ns	*
W*G	ns	ns	ns	ns	ns	ns

ns, *, ** = non-significant differences, significant differences at $p \leq 0.05$ and $p \leq 0.01$, respectively. Data are presented means ±SD (n=20).

Table 6 Correlation coefficients between chlorophyll fluorescence with tuber dry weight (TDW) and biomass (BM) of 40 Jerusalem artichoke genotypes under well-watered condition (n=160)

Chlorophyll fluorescence	TDW	BM
Fv'/Fm' at 40 DAT	-0.08 ^{ns}	-0.08 ^{ns}
Fv/Fm at 40 DAT	-0.07 ^{ns}	-0.07 ^{ns}
Fv'/Fm' at 60 DAT	-0.07 ^{ns}	-0.08 ^{ns}
Fv/Fm at 60 DAT	-0.28 **	-0.29**
Fv'/Fm' at 70 DAT	-0.20**	-0.19*
Fv/Fm at 70 DAT	-0.28**	-0.29**

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

Table 7 Correlation coefficients between chlorophyll fluorescence with stress tolerance index (STI), stress susceptibility index (SSI), tuber dry weight (TDW), and biomass (BM) of 40 Jerusalem artichoke genotypes under different drought conditions (n=160)

	STI		SSI			
Physiological traits	TDW	BM	TDW	BM	TDW	BM
W2 (75% ETCrop)						
Fv'/Fm' at 40 DAT	-0.01^{ns}	0.01^{ns}	0.00 ^{ns}	0.02 ^{ns}	-0.04 ^{ns}	-0.02 ^{ns}
Fv/Fm at 40 DAT	-0.11 ^{ns}	-0.10 ^{ns}	-0.07 ^{ns}	-0.06 ^{ns}	-0.07 ^{ns}	-0.07 ^{ns}
Fv'/Fm' at 60 DAT	0.00 ^{ns}	0.00 ^{ns}	-0.07 ^{ns}	-0.05 ^{ns}	0.02 ^{ns}	0.02 ^{ns}
Fv/Fm at 60 DAT	0.38**	0.36**	0.10 ^{ns}	0.15 ^{ns}	-0.36 *	-0.39 **
Fv'/Fm' at 70 DAT	0.15 ^{ns}	-0.14 ^{ns}	-0.15 ^{ns}	-0.11 ^{ns}	-0.12 ^{ns}	-0.13 ^{ns}
Fv/Fm at 70 DAT	0.28*	0.28*	-0.12 ^{ns}	-0.09 ^{ns}	-0.18*	-0.26 *
W3 (45% ETCrop)						
Fv'/Fm' at 40 DAT	0.04 ^{ns}	0.03 ^{ns}	-0.04 ^{ns}	-0.02 ^{ns}	0.06 ^{ns}	0.04 ^{ns}
Fv/Fm at 40 DAT	-0.09 ^{ns}	-0.08 ^{ns}	0.22^{ns}	-0.22 ^{ns}	0.01 ^{ns}	-0.02 ^{ns}
Fv'/Fm' at 60 DAT	-0.09 ^{ns}	-0.06 ^{ns}	-0.06 ^{ns}	-0.07 ^{ns}	-0.07 ^{ns}	-0.07 ^{ns}
Fv/Fm at 60 DAT	0.42**	0.47**	0.03 ^{ns}	0.07 ^{ns}	-0.45**	-0.46 **
Fv'/Fm' at 70 DAT	0.18 ^{ns}	-0.06 ^{ns}	-0.03 ^{ns}	-0.00 ^{ns}	-0.11 ^{ns}	-0.11 ^{ns}
Fv/Fm at 70 DAT	-0.08 ^{ns}	-0.11 ^{ns}	-0.15 ^{ns}	-0.15 ^{ns}	-0.05 ^{ns}	-0.07 ^{ns}

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

Discussion

Knowledge of genotypic variation and the physiological responses to drought stress is important for breeding strategies to enhance drought tolerance. In this study, the soil chemical properties revealed that nitrogen was lower than the optimum requirement for JA growth, whereas potassium, phosphorus, and calcium, were sufficient for normal growth and acceptable yields (Lebot 2009). As chemical fertilizers were applied in the same

ranges for optimal growth, soil fertility would not cause genotypic differences in JA. The growing temperature in this study was much higher than the optimum temperatures for the growth and development of JA. Kays and Nottingham (2008) reported that the optimum air temperature for most JA genotypes ranges between 6 – 26 °C in temperate zones. Leaf relative water content is an important indicator of plant water status and metabolic activity (Sinclair and Ludlow, 1986). Our results revealed that the value of RWC for W1 was significantly higher than W2, and W2 was significantly higher than W3 for all plant ages **(Table 2)**, indicating that the control of water supply for all water regimes was reasonably good, and different levels of plant water stress were clearly separated by water treatment.

Our study showed that there was a significant difference between genotypes of chlorophyll fluorescence (Fv/Fm and F'v/F'm) for most parameters and plant ages **(Table 4)**. In contrast, no significant differences were observed between water regimes and the interaction among genotypes for these parameters. This indicated a similar response of these traits in different water regimes, and the JA genotypes performed stable and consistent performance across water regimes. Accordingly, the evaluation of JA genotypes with chlorophyll fluorescence, thus, possibly requires only a few representative water regimes. Likewise, the high stability of Fv/Fm and F'v/F'm have also been observed in cassava planted under different growing conditions (Sawatraksa et al., 2018) and wheat planted under different water regimes (Lu and Zhang, 1999). These results are consistent with other photosynthetic, physiological, and agronomic traits of JA. Puangbut et al. (2022) studied physiological and photosynthetic responses to drought among six JA genotypes with different levels of drought resistance in field experiments. The authors found that there was no significant interaction between water regimes and genotypes in terms of RWC, SCMR, stomatal conductance, biomass, and tuber yield. A similar result in the pot experiment was also reported by Puangbut et al. (2017).

This is the first report showing the genotypic variation of JA germplasm for chlorophyll fluorescence. From the first application, the dark-adapted value of Fv/Fm or the maximum quantum efficiency of PSII has primarily been used as a sensitive indicator of plant photosynthetic performance (Murchie and Lawson, 2013). A reduction in this trait is indicative of a decrease in PSII efficiency (Guidi et al., 2019). An earlier study in sunflower (*Helianthus annuus*) showed that the values of Fv/Fm for non-stressed plants were 0.78–0.80 and decreased to 0.45-0.62 when the crop was subjected to abiotic stresses (drought and heavy metal) (Plesni˘ar et al., 1994; Azevedo et al., 2005; Yalcin et al., 2016). In this study, the Fv/Fm values for W1, W2, and W3, ranged from 0.846-0.850 at 40 DAT, 0.802-0.813 at 60 DAT, and 0.680-0.691 at 70 DAT. This revealed that there was no chronic damage occurring in the PSII of JA leaves during 40-60 DAT, and water stress did not impact the performance of this trait. While Fv'/Fm' is one of the indicators of plant photosynthetic performance reflecting the efficiency of excitation energy capture by open PSII reaction centers, this value exhibited the highest efficiency of PSII for the transfer of electrons to Q_A at the point of measurement, and its value varies with light intensity (Kalaji and Guo, 2008). A decrease in Fv'/Fm' may reflect light-induced non-photochemical quenching (Lu and Zhang, 1999). Our study noted that water stress had no effect on Fv'/Fm' values. The Fv'/Fm' values for W1, W2 and W3 ranged between 0.6244-0.633 for 40 DAT, 0.668-0.679 for 60 DAT, and 0.566-0.587 for 70 DAT.

According to the results, it is possible that this JA germplasm might have other drought-tolerant mechanisms, such as partially or nearly completely closing its stomata during a period of drought to prevent

damage to the photosynthetic system, especially during the daytime (Puangbut et al., 2017; 2022; Chaimala et al., 2021), expansion of the fibrous root system into the deeper soil layers to uptake soil water (Ruttanaprasert et al., 2015), decreasing the leaf area (Puangbut et al., 2017; 2022; Chaimala et al., 2021), or increasing the specific leaf area (Ruttanaprasert et al., 2015). It has been noted in previous studies that water stress normally resulted in a decrease in leaf transpiration, thereby resulting in an increase of leaf temperature due to stomatal closure. Increasing the thermostability of PSII in water-stressed treatments may thus help to improve the resistance of the photosynthesis mechanism to high temperatures and this may increase the resistance of the whole plant to high temperatures (Lu and Zhang, 1999). This may be explained why water stress had no effect on the chlorophyll fluorescence parameters in this study.

Drought also reduced the days required to reach maturity and there was a significant difference in days to reach maturity among genotypes (Janket et al. 2016). A parallel study showed that the fewest number of days to reach maturity was observed for W3 under the driest conditions, followed by W2, and W1, respectively. Since severe drought conditions (W3) accelerated leaf and crop senescence, this may explain why statistically significant correlations between chlorophyll fluorescence and STI, yield, and biomass, were not observed at 70 DAT under this condition. Principally, loss of chlorophyll molecules, degradation of proteins, leaf yellowing, and the disassembly of the photosynthetic system appear during leaf senescence (Domínguez and Cejudo, 2021).

As mentioned above, the evaluation of genetic diversity can be useful in breeding JA with drought tolerance by a selection of parental lines in a JA breeding program. In this study, the top-ten genotypes with the highest Fv/Fm and F'v/F'm across plant ages were CN52867, JA70, HEL257, JA125, and JA92. Yet only JA70 showed a consistently statistically significantly high F'v/F'm at all plant ages, whereas CN52867 showed the greatest values for Fv/Fm at all plant ages **(Table 5)**. It is interesting to note here that the genotypes that had high performance in this study, also performed well in other agronomic traits in the parallel studies. It was noted in parallel studies that CN52867 had consistently high tuber dry weight, whereas JA92 had a high tuber width and JA70 performed a high tuber length across water regimes and years (Ruttanaprasert et al. 2014; Janket et al., 2016).

Our study also noted that there were negative and significant correlations between Fv/Fm at 60 DAT with tuber dry weight and biomass across all water regimes **(Table 6)**. This might be due to the fact that almost all JA genotypes showing high Fv/Fm in the JA germplasm often produced low biomass and low tuber dry weight, with smaller plants and a lower leaf area index. This reflects the importance of JA breeding by crossbreeding the genotypes with high yields and high photosynthetic capacity. The phenotypic and genotypic variations for these traits have previously been reported by Ruttanaprasert et al. 2014. However, a higher leaf area index indicates a higher capacity of plant canopy to produce total photosynthate (Fang and Liang, 2014), therefore, the combination of higher photosynthetic capacity, longer leaf duration, and appropriate leaf area index are the JA idiotypes, thereby contributing to higher yield potential (Puangbut et al., 2002). As positive and significant correlations between Fv/Fm at 60 DAT with STI for biomass and yield were observed, Fv/Fm could be possibly used as indirect selection traits with low selection intensity in JA for drought tolerance. Yet, the correlation coefficients were medium for most traits and plant ages, therefore, the use of other physiological traits with a higher correlation coefficient as indirect selection criteria in JA would be more effective.

Conclusion

There were significant genetic variations in chlorophyll fluorescence in this set of JA germplasm, and there was no significant interaction between genotypes and water regimes for these traits. CN52867, JA70, HEL257, JA125 and JA92 were identified as superior genotypes in terms of F'v/F'm values, with JA 70 performed well across water regimes. Whereas CN52867 was the best for Fv/Fm. This indicated JA70 had high adaptation to drought and CN52867 had high drought recovery. The findings of this study will enable JA breeders to choose superior genotype parents for future breeding programs. Yet, the evaluation of superior JA genotypes using this trait has a low selection intensity, therefore, the use of other physiological characteristics showing high selection intensity and significantly correlated with drought tolerance as selection criteria in JA would be more effective. This study used only four different sources of origin in a one-year experiment. Further studies through multiple years and sources of origin are necessary.

Acknowledgement

Acknowledgment is extended to Plant Gene Resources of Canada (PGRC) and The Leibniz Institute of Plant Genetic and Crop Plant Research (IPK) of Germany for their donation of Jerusalem artichoke germplasm. We would like to thank the Office of International Relations, Ubon Ratchathani University for language editing.

References

Azevedo, H., C.G. Glória Pinto, J. Fernandes, S. Loureiro, and C. Santos. 2005. Cadmium effects on sunflower growth and photosynthesis. Journal of Plant Nutrition. 28(12): 2211-2220.

Chaimala, A., S. Jogloy, N. Vorasoot, B. Toomsan, N. Jongrungklang, T. Kesmala, C.C. Holbrook, and C.K. Kvien. 2020. Responses of total biomass, shoot dry weight, yield and yield components of Jerusalem artichoke (*Helianthus tuberosus* L.) varieties under different terminal drought duration. Agriculture. 10(6): 198.

Chaimala, A., S. Jogloy, N. Vorasoot, C. Holbrook, C. K. Kvien, and S. Laohasiriwong. 2021. The variation of relative water content, SPAD chlorophyll meter reading, stomatal conductance, leaf area, and specific leaf area of Jerusalem artichoke genotypes under different durations of terminal drought in tropical region. Journal of Agronomy and Crop Science. https://doi.org/10.1111/jac.12561.

Cosgrove, D.R., E.A. Oelke, J.D. Doll, D.W. Doll, D.W. Daves, D.J. Undersander, and S.E. Springer. 2000. Jerusalem artichoke. Available: http://hort.purdue,edu/newcrop/afcm/jerisart.html. Accessed January 3, 2022.

Domínguez, F., and F.J. Cejudo. 2021. Chloroplast dismantling in leaf senescence. Journal of Experimental Botany. 72: 5905-5918.

Dinh, H.T., W. Kaewpradit, S. Jogloy, N. Vorasoot, and A. Patanothai. 2014. Nutrient uptake of peanut genotypes with different levels of drought tolerance under midseason drought. Turkish Journal of Agriculture and Forestry. 38(4): 495-505.

Doorenbos, J., and W.O. Pruitt. 1992. Calculation of crop water requirements. p.1–66. Crop Water Requirements. FAO of The United Nation, Rome.

Fang, H., and S. Liang. 2014. Leaf area index models, Reference module in earth systems and environmental sciences. Encyclopedia of Ecology. 2139-2148. https://doi.org/10.1016/B978-0-12-409548-9.09076-X.

Gomez, K.A., and A.A. Gomez. 1984. Statistical Procedures for Agricultural Research. 2nd Edition. John Wiley & Sons, New York.

Guidi, L., E. Lo Piccolo, and M. Landi. 2019. Chlorophyll fluorescence, photoinhibition and abiotic stress: does it make any difference the fact to be a C3 or C4 species? Frontiers in Plant Science. 10: 174.

Hank, R.J., J. Keller, V.P. Rasmussen, and G.D. Wilson. 1976. Line source sprinkler for continuous variable-crop production studies. Soil Science Society of America Journal. 40: 426–429.

Hooshmandi, B. 2019. Evaluation of tolerance to drought stress in wheat genotypes. Idesia. 37: 37-43.

Janket, A., S. Jogloy, N. Vorasoot, T. Kesmala, C.C. Holbrook, and A. Patanothai. 2013. Genetic diversity of water use efficiency in Jerusalem artichoke (*Helianthus tuberosus* L.) germplasm. Australian Journal of Crop Science. 7(11): 1670-1681.

Janket, A., N. Vorasoot, R. Ruttanaprasert, T. Kesmala, and S. Jogloy. 2016. Genotypic variability of yield components and crop maturity in Jerusalem artichoke germplasm. SABRAO Journal of Breeding & Genetics. 48(4): 474-490.

Kalaji, M.H., and P. Guo. 2008. Chlorophyll fluorescence: A useful tool in barley plant breeding programs. Photochemistry Research Progress. 29: 439-463.

Kays, S.J., and S.F. Nottingham. 2008. Biology and Chemistry of Jerusalem artichoke (*Helianthus tuberosus* L.). 1st Edition. CRC Press, Florida.

Kramer, P.J. 1980. Drought, stress and the origin of adaptation. p.11. In: Turner N.C. and P.J. Kramer (eds) Adaptation of plant to water and high temperature stress. John Wiley and Sons, New York.

Lebot, V. 2009. Tropical Root and Tuber Crop: Cassava, Sweet potato, Yams and Aroids. CABI, UK.

Lu, C., and J. Zhang. 1999. Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. Journal of Experimental Botany. 50(336): 1199-1206.

Murchie, E.H., and T. Lawson. 2013. Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. Journal of Experimental Botany. 64(13): 3983-3998.

Onsoy, T., P. Thanonkeo, S. Thanonkeo, and M. Yamada. 2007. Ethanol production from Jerusalem artichoke by *Zymomonas mobilis* in batch fermentation. KMITL Science and Technology Journal. 71: 55-60.

Plesni˘ar, M., R. Kastori, N. Petrović, and D. Panković. 1994. Photosynthesis and chlorophyll fluorescence in sunflower (*Helianthus annuus* L.) leaves as affected by phosphorus nutrition. Journal of Experimental Botany. 45(7): 919-924.

Puangbut, D., S. Jogloy, N. Vorasoot, S. Srijaranai, C.C. Holbrook, and A. Patanothai. 2015. Variation of inulin content, inulin yield and water use efficiency for inulin yield in Jerusalem artichoke genotypes under different water regimes. Agricultural Water Management. 152: 142–150.

Puangbut, D., S. Jogloy, and N. Vorasoot. 2017. Association of photosynthetic traits with water use efficiency and SPAD chlorophyll meter reading of Jerusalem artichoke under drought conditions. Agricultural Water Management. 188: 29-35.

Puangbut, D., S. Jogloy, N. Vorasoot, and K. Craig. 2018. Root distribution pattern and their contribution in photosynthesis and biomass in Jerusalem artichoke under drought conditions. Pakistan Journal of Botany. 50(3): 879-886.

Puangbut, D., S. Jogloy, N. Vorasoot, and P. Songsri. 2022. Photosynthetic and physiological responses to drought of Jerusalem artichoke genotypes differing in drought resistance. Agricultural Water Management. 259: 107252.

Roberfroid, M.B. 2000. Prebiotics and probiotics: are they functional food? The American Journal of Clinical Nutrition. 71: 1682–1687.

Roberfroid, M.B. 2005. Introducing inulin-type fructans. British Journal of Nutrition. 93: 13-25.

Ruttanaprasert, R., P. Banterng, S. Jogloy, N. Vorasoot, T. Kesmala, R.S. Kanwar, C.C. Holbrook, and A. Patanothai. 2014. Genotypic variability for tuber yield, biomass and drought tolerance in Jerusalem artichoke germplasm. Turkish Journal of Agriculture and Forestry. 38: 570–580.

Ruttanaprasert, R., S. Jogloy, N. Vorasoot, T. Kesmala, R. S. Kanwar, C.C. Holbrook, and A. Patanothai. 2015. Root responses of Jerusalem artichoke genotypes to different water regimes. Biomass and Bioenergy. 81: 369–377.

Ruttanaprasert, R., S. Jogloy, N. Vorasoot, T. Kesmala, S. K. Rameshwar, C.C. Holbrook, and A. Patanothaia. 2016a. Effects of water stress on total biomass, tuber yield, harvest index and water use efficiency in Jerusalem artichoke. Agricultural Water Management. 166: 130–138.

Ruttanaprasert, R., P. Banterng, S. Jogloy, N. Vorasoot, T. Kesmala, and A. Patanothai. 2016b. Diversity of physiological traits in Jerusalem artichoke genotypes under non-stress and drought stress. Pakistan Journal of Botany. 48(1): 11-20.

Santanoo, S., K. Vongcharoen, P. Banterng, N. Vorasoot, S. Jogloy, S. Roytrakul, and P. Theerakulpisut. 2019. Seasonal variation in diurnal photosynthesis and chlorophyll fluorescence of four genotypes of cassava (*Manihot esculenta* Crantz) under irrigation conditions in a tropical savanna climate. Agronomy. 9(4): 206.

Sawatraksa, N., P. Banterng, S. Jogloy, V. Vorasoot, and G. Hoogenboom. 2018. Chlorophyll fluorescence and biomass of four cassava genotypes grown under rain-fed upper paddy field conditions in the tropics. Journal of Agronomy and Crop Science. 204(6): 554-565.

Schittenhelm, M.S. 1999. Agronomic performance of root chicory, Jerusalem artichoke and sugar beet in stress and non-stress environment. Crop Science. 39: 1815–1823.

Sinclair, T.R., and M.M. Ludlow. 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Functional Plant Biology. 13(3): 329-341.

Summart, S., J. Khajarean, S. Khajarean, and T. Mingsakul. 2021. Effects of dietary supplementation of Jerusalem artichoke (*Helianthus tuberosus* L.) on performance of weaning pigs and manure ammonia nitrogen concentration. Khon Kaen Agriculture Journal. 34(2): 195-198.

Yalcin, K.A.Y.A., A.S.B. Nalcaiyi, S.Ç. Erdal, O. Arslan, N. Cicek, V. Pekcan, and Y. Ekmekçi. 2016. Evaluation of male inbred lines of sunflower (*Helianthus annuus* L.) for resistance to drought via chlorophyll fluorescence. Turkish Journal of Field Crops. 21(2): 162-173.