Zaki and Radwan *Chem. Biol. Technol. Agric. (2022) 9:1*
https://doi.org/10.1186/s40538-021-00266-z

Chemical and Biological Technologies in Agriculture

RESEARCH

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Response of potato (*Solanum tuberosum* L.) cultivars to drought stress under in vitro and field conditions

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Abstract

Background: Potato (*Solanum tuberosum* L.), the world's third most important crop, is frequently thought to be sensitive to moderately sensitive to drought, and yield has fallen considerably over consecutive stress periods. Drought produces a wide range of responses in potato, from physiological alterations to variations in growth rates and yield. Knowledge about these responses is essential for getting a full understanding of drought-tolerance mechanism in potato plants which will help in the identification of drought-tolerant cultivars.

Results: A set of 21 commercial potato cultivars representing the genetic diversity in the Middle East countries market were screened for drought tolerance by measuring morpho-physiological traits and tuber production under in vitro and field trials. Cultivars were exposed to drought stress ranging from no drought to 0.1, 0.2 and 0.3 mol L^{-1} sorbitol in in vitro-based screening and 60, 40 and 20% soil moisture content in field-based screening. Drought stress adversely affected plant growth, yield and cultivars differed for their responses. Shoots and roots fresh weights, root length, surface area of root, no. of roots, no. of leaves, leaf area, plant water content %, K^+ content, under in vitro drought treatments and shoots fresh and dry weights, no. of tubers and tuber yield under field drought treatments were examined and all decreased due to drought. The stress tolerance index decreased with increasing drought in examined cultivars; nevertheless, it revealed a degree of tolerance in some of them. Grouping cultivars by cluster analysis for response to drought resulted in: (i) a tolerant group of five cultivars, (ii) a moderately tolerant group of 11 cultivars, and (iii) a sensitive group of five cultivars. Furthermore, stress-related genes, i.e., *DRO*, *ERECTA*, *ERF*, *DREB* and *StMYB* were up-regulated in the five cultivars of the tolerant group. Likewise, the stomatal conductance and transpiration explained high correlation with the tuber yield in this group of cultivars.

Conclusion: The diversity in germplasm indicated that potato cultivars can be developed for production under certain degrees of drought. Some cultivars are good candidates to be included in drought-tolerant breeding programs and recommended for cultivation in drought-stricken regions.

Keywords: Drought tolerance, Potato, Root traits, Tuber production, Stress tolerance index, Drought-related genes, Physiological traits

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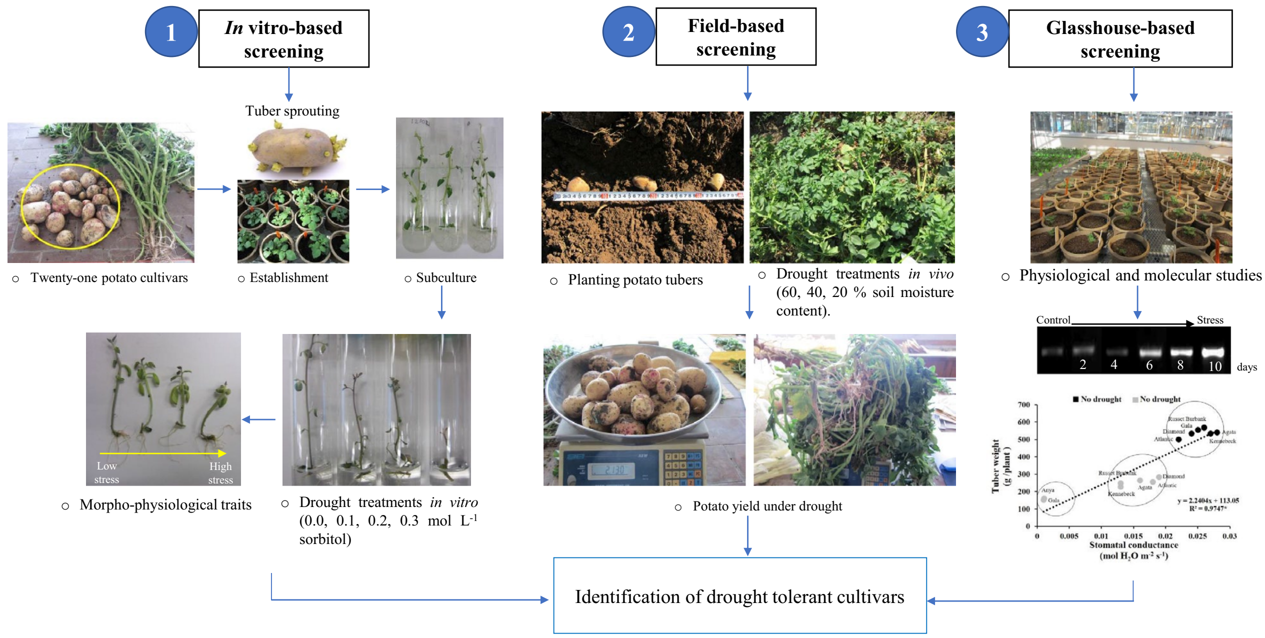
Graphical Abstract



Introduction

Plants are subjected to a wide range of stressors as a result of their environment. Abiotic stress is one of the most serious and prevalent agricultural problems, resulting in considerable crop yield losses and jeopardizing long-term crop production [1–4]. One of the primary problems for the coming decade will be to reduce the impact of abiotic stress on crop development, with a focus on maintaining agricultural production rates in the face of reduced water supply or drought [5].

Potato is one of the world's most important food crops, alongside wheat, rice and maize. Cultivated potatoes (*Solanum tuberosum* L.) are sensitive to moderately sensitive to drought, depending on the criteria used for classification [6, 7]. This sensitivity is related to the growth stage of the plant, being more sensitive to drought in the early growth and tuberization periods [8, 9]. Drought stress occurs when soil moisture content is low, relative humidity is low and temperature is high. If drought continues, plants will dry up and production will be adversely affected. In potatoes, drought stress delays emergence, slows plant development, and reduces plant mass weight [10–12] as well as dramatically reducing tuber number, size and yield [13–16].

Under open field conditions, environmental factors may vary from season to season, and a genotype that is successful at one season may fail in another season, although no extensive evaluation of the varieties has been reported [17, 18]. The identification and development of potato stress tolerant cultivars are currently needed as climate change is associated with an increase in global temperature and a decrease in precipitation [19, 20]. A solution to this issue may be the cultivation of cultivars that can withstand abiotic stress while retaining high productivity. The most promising solution for the drought problem is to develop drought-tolerant crops, although in the past this has not been a high priority [8]. Variations in flowering ability, leaf characteristics, plant maturity, and tuber production have all been documented in potatoes [1, 6, 8]. Growing asexual propagating crops on a wide scale creates possibilities for different genes and, as a consequence, selection for desired characteristics [2, 6, 7, 13]. Drought tolerance in plants can be improved through traditional breeding or genetic manipulation techniques. Traditional breeding for drought tolerance has been problematic, since it appears that drought tolerance is a complex trait [21, 22]. However, progress has been made in identifying candidate genes in recent years. The identification of genes involved in drought tolerance opens up new possibilities for identifying tolerant germplasm. Genes associated with drought tolerance, such as deeper rooting (*DRO*) in potato, LRR receptor-like serine/threonine-protein kinase ERECTA (*ERECTA*), ethylene response factor (*ERF*), dehydration responsive element binding (*DREB*) and *Solanum tuberosum* MYB (*StMYB*) have been identified [23–29].

Potato seed tubers are largely imported from the Netherlands, Ireland, and the United Kingdom into several

Middle East countries, including Egypt. This is practiced every summer season to avoid the buildup of viral infection caused by high temperature and high population of insects that spread potato viruses. Many of these countries are located in arid or semi-arid environments, therefore evaluating existing potato cultivars for drought tolerance can assist in sustaining the potato production. Several researchers have suggested in vitro-based screening for potato germplasm with drought tolerance [7, 20, 30, 31] but field-based screening is still required. Although field-based screening for drought-tolerant variations is limited and time demanding, the current study's main goal is to analyze 21 potato cultivars for drought tolerance in vitro and in the field. It is therefore very important to discuss the genotypic variability of drought tolerance in cultivated potatoes with regard to morpho-physiological parameters, molecular traits and tuber yield under in vitro, and field conditions. The detailed objectives of this study are to understand (1) the extent of genetic variability for drought tolerance among potato cultivars using in vitro studies; (2) the stability of drought tolerance of potato cultivars under field conditions; (3) the regulation of some drought-related genes and transcription factors that contribute to plant response to drought, and (4) the correlation between physiological traits and tuber production under drought stress.

Materials and methods

The present study was carried out at the experimental farm of the Departments of Horticulture and Plant Pathology, Faculty of Agriculture, Minia University, El-Minia, Egypt, laboratory of the Department of Applied Biotechnology, University of Technology and Applied Sciences-Sur, The Sultanate of Oman, and the laboratory of Plant Breeding, Faculty of Agriculture, Iwate University, Morioka, Iwate, Japan.

Plant materials

Twenty-one potato cultivars (*Solanum tuberosum* L.), Agata, Almond, Anya, Atlantic, Burren, Cara, Champion, Desiree, Diamond, Gala, Gazella, Kennebec, King Edward, Lady Balfour, Lady Rosetta, Marble, Marfona, Maritiema, Mizen, Russet Burbank and Spunta were used for in vitro and field drought response studies. Tuber seeds of cultivars were obtained from Agricultural research center (ARC), Egypt. These cultivars were chosen as they have a wide range of morphology and are widely grown in Middle East countries, including Egypt. The list of cultivars with place of origin, year, maturation, skin color, flesh color and tuber shape is shown in Table 1.

Table 1 List of potato cultivars, their place of origin, year, maturation, skin and flesh color and tuber shape

Ser	Cultivar	Place of origin	Year	Maturation	Skin color	Flesh color	Tuber shape
1	Agata	Netherlands	1976	Early	Yellow	Yellow	Oval
2	Almond	Norway	Unknown	Early	Yellow	Yellow	Oval
3	Anya	Scotland	1996	Early	Pinkish beige	White waxy	Long knobby–oval
4	Atlantic	United States	1978	Early	Cream	Cream	Short-oval
5	Burren	Ireland	Unknown	Early maincrop	Cream	Medium yellow	Long-oval
6	Cara	Ireland	Unknown	Maincrop	Red parti	Cream	Short-oval
7	Champion	Scotland	1963	Maincrop	White	Yellow	Round
8	Desiree	Netherlands	1862	Maincrop	Red	Light yellow	Long-oval
9	Diamond	India	Unknown	Maincrop	Cream	Yellow	Short-oval
10	Gala	Germany	1992	Early maincrop	Red parti	Light yellow	Long-oval
11	Gazella	Scotland	1983	Maincrop	Cream	Yellow	Short-oval
12	Kennebec	United States	1941	Early maincrop	Cream	Cream	Oval
13	King Edward	Scotland	1902	Maincrop	Red parti	Cream	Long-oval
14	Lady Balfour	United Kingdom	1974	Maincrop	Red parti	White	Oval
15	Lady Rosetta	Netherlands	Unknown	Early maincrop	Red	Light yellow	Round
16	Marble	Netherlands	1995	Maincrop	Red	Yellow	Round
17	Marfona	Netherlands	1975	Early	Cream	Light yellow	Short-oval
18	Maritiema	United Kingdom	1993	Early maincrop	White yellow	Cream	Short-oval
19	Mizen	Ireland	1978	Maincrop	Creamy yellow	White	Long
20	Russet Burbank	United States	1902	Maincrop	Cream	White	Long
21	Spunta	Scotland	Unknown	Early	White	Light yellow	Long

In vitro experiment

Plant micropropagation

This experiment was carried out at the Applied Biotechnology Department of the University of Technology and Applied Sciences in Sur, Oman. A tissue culture technique was implemented for rapid propagation of the previously mentioned potato cultivars. To collect the explants, sprouted potato tubers were planted in greenhouse in 15 cm pots of ProMix with basic soil composition. In a sequential procedure, shoot tips were cut and washed roughly. Then shoot tips were surface sterilized in a solution of 0.5% (v:v) sodium hypochlorite for 5 min and they were rinsed thoroughly with sterile distilled water. Subsequently, the surface sterilized shoot tips were cultured on agar-solidified (8 g L^{-1}) and sucrose (30 g L^{-1}) Murashige and Skoog (MS) basic medium [32]. The pH was adjusted to 5.7 ± 0.1 before the addition of Agar and subsequent autoclaving at 121 °C and 15 psi for 20 min. Tissue excision, implantation and transfer procedure were performed under sterile conditions. The cultured shoot tips were incubated for four weeks in the incubation room at 16 h photoperiod, 25 ± 2 °C and white cool fluorescent bulbs providing approximately 90 μmol m^{-2} s^{-1} PPFD. Subcultures were done using shoot tip.

In vitro drought treatments

By using the plantlets of the same age, individual stem nodes were cultured in tubes containing 8 mL of MS growth medium, 30 g L^{-1} sucrose and 8 g L^{-1} agar supplemented with/without sorbitol of 0.0, 0.1, 0.2 or 0.3 mol L^{-1} at pH 5.7. The plantlets were allowed to grow for 30 days to test the cultivars drought tolerance or sensitivity. The experimental design was a factorial experiment with three replications in a split block design. Twenty plantlets were evaluated per cultivar per each of the four drought treatments and the experiment was repeated at approximately monthly intervals three times. All subcultures were maintained under 16 h photoperiod, 25 ± 2 °C and white cool fluorescent bulbs providing approximately 90 μmol m^{-2} s^{-1} PPFD.

In vitro propagation measurements

When subcultures were 30 days old (without subculturing) and fully grown with stout stems and broad leaves in the control treatment (i.e., MS medium without sorbitol), data were recorded for various morphological and physiological characteristics associated with drought stress treatments. Plantlets were removed from the tubes, and their fresh weight of roots and shoots, and number of leaves/plantlet were measured. The millimeter graph paper was used to estimate leaf area/plantlet. Furthermore root traits, i.e., total root length, surface area of root and number of roots were analyzed by WinRhizo Basic 2009 software (Regent Instruments Canada, Inc.). Meanwhile, plantlets water content (PWC%) was measured according to the previous study [33]. Ions of potassium (K^{+}) content were determined based on the described method [34].

Field experiment

Drought treatments under field conditions

The experiment was conducted at the experimental farms and labs of the Departments of Horticulture and Plant Pathology, Faculty of Agriculture, Minia University, El-Minia, Egypt. Potato seed tubers of the 21 cultivars were planted on September 10 and 15 during the 2016 and 2017 seasons, respectively. Sowing was performed on one side of the row in all plots, each plot consisted of five rows (0.70 m in width and 3.0 m in length) and the planting distance within the row was 20 cm interval. The area of each experimental plot was 10.5 m^2 to be considered (1/400 of feddan). Over the two seasons, physical and chemical analyses of soil samples from a depth of 0.0 to 30 cm were performed, and the average findings are shown in Additional file 1: Table S1. Three different drought regimes (60%, 40% and 20% soil moisture content) were examined compared to control (no drought). The drip irrigation system was patched up, and irrigation was undertaken on a daily basis to keep the three drought regimes in place. Soil water content was monitored daily by time domain transmission (Sidney, BC, Canada). Ten plants per plot per cultivar were evaluated for each of the drought regimes and the applied experimental design was randomized complete block design (RCBD) in a split plot with three replications which contained four levels of drought stress and 21 potato cultivars. The main plots concerned the four stress treatments, while the 21 potato cultivars were randomly distributed in the subplots. All other agricultural practices such as fertilization and control of pests and diseases were performed as recommended for the commercial production [35].

Field measurements

At 100–110 days after planting, tubers were harvested and the following horticultural traits were characterized: number of tubers/plant, weight of tubers (g/plant), shoot fresh and dry weights (g).

Drought tolerance analysis

Classification of potato cultivars as a drought tolerant or sensitive was performed using both in vitro and field measurements. The stress tolerance index (STI) for each cultivar was estimated according to the method [36]. STI was calculated as the ratio of the trait performance at 0.1, 0.2, or 0.3 mol L^{-1} to the trait performance at 0.0 mol L^{-1}

sorbitol for in vitro experiment or at 60%, 40% and 20% soil moisture content to the trait performance at no drought regime for field experiment as described in the following formula:

$$\mathrm{STI} = \frac{T_\mathrm{s}}{T_\mathrm{p}},$$

where T_s is the trait of cultivar under stress conditions and T_p is the trait of cultivar under normal conditions.

Glasshouse experiments

Expression profile of drought-related genes

The experiment was carried out at the laboratory of Plant Breeding, Faculty of Agriculture, Iwate University, Morioka, Iwate, Japan. Potato seed tubers of examined cultivars were planted pots until harvesting the roots for comparative genes expression experiment. All tubers were planted in commercial soil (Gattirikun N-120; Tokita Seed Co., Saitama, Japan) for two months in controlled climate chambers (Koito, Tokyo, Japan) at 25°/15 °C (day/night) temperatures. The number of plants was adjusted to 1 plant per pot (25 cm up diameter—22.5 cm base diameter—13.5 cm deep), with 10 pots for each cultivar. All other agricultural practices such as irrigation, fertilization and control of pests and diseases were performed as recommended for the commercial production [35]. 45-day-old plants were subjected to drought stress, with no water for 2 weeks. Roots were collected from normal irrigated plants (control) and drought exposed plants after 2, 4, 6, 8 and 10 days. Soil water content was monitored daily by time domain transmission (Sidney, BC, Canada). Poly $(A)^+$ RNA was isolated from the roots using a micro-FastTrack 2.0 mRNA isolation kit (Invitrogen, San Diego, CA, USA) as instructed by the manufacturer. cDNAs were synthesized from 1 µg of mRNA in a total volume of 20 µL containing 1 µL of oligo (dT) primer (0.5 µg μL^{-1}), 4 µL of first-strand buffer (5× concentrated), 2 µL of dithiothreitol (100 mM), 2 µL of dNTPs (10 mM) and 0.2 µL Superscript II (300 unit). The reaction was carried out at 30 °C for 10 min, 42 °C for 50 min, and 70 °C for 10 min. For this study, five distinct drought-related genes; deeper rooting (*DRO*) in potato, LRR receptor-like serine/threonine-protein kinase ERECTA (*ERECTA*), ethylene response factor (*ERF*), dehydration responsive element binding (*DREB*) and *Solanum tuberosum* MYB (*StMYB*) were selected. To evaluate the differential expression of the chosen genes in roots of potato cultivars with different tolerance reaction, RT-PCR was carried out using gene-specific primers (Additional file 1: Table S2). Conditions for the thermal cycling were 94 °C for 2 min; 28 cycles of 94 °C for 20 s, 55 °C for 20 s, and 72 °C for 40 s; and finally, 72 °C for 2 min. The reproducibility of the results was confirmed using samples from three independently grown plants.

Physiological measurements

The experiment was carried out at the laboratory of Plant Breeding, Faculty of Agriculture, Iwate University, Morioka, Iwate, Japan. Potato seed tubers were planted in pots (25 cm up diameter—22.5 cm base diameter—13.5 cm deep) in a controlled chamber at 25°/15 °C (day/night) temperatures. Drought stress (20% soil moisture content) was applied compared to control (no drought). Soil water content was monitored daily by time domain transmission (Sidney, BC, Canada). Ten plants per cultivar per treatment were evaluated and physiological characteristics were examined 60 days after planting. A portable photosynthesis system (LI6400 TX model, LI-COR, Lincoln, NE, USA) was used to determine the water stomatal conductance at night (8:00 pm). Total daily transpiration was measured by using a transparent plastic to cover the soil surface of the pots to avoid loss of evaporation. Total daily transpiration was measured in a period of 24 h by weight difference as previously defined [37] and 100–110 days after planting, tubers were weighed to have tubers fresh weight/plant and examine the correlation between the physiological traits and tuber yield. All experiments and strategy used to identify the drought-tolerant cultivars are shown in Fig. 1.

Statistical analyses

The experimental design was a 21 × 4 (cultivars × drought treatments) in a factorial experiment with three replications in a split block design for in vitro-based screening. Randomized complete block design (RCBD) in a split plot with three replications was used for field-based screening and all obtained data were subjected to the analysis of variance using the combined data from the two seasons. Data obtained from this study were subjected to analysis using SAS, version 9.3 (Cary, NC). Differences among potato cultivars were tested by an analysis of variance (ANOVA), and mean significant differences were tested by the Least Significant Difference (LSD) test at the 0.05 level of significance. The interplay of the characteristics evaluated in vitro and in field conditions, as well as their contributions to heatmaps, was investigated using multivariate data. The traits of the 21 potato cultivars were recorded in the dataset under the studied drought stress levels or regimes. Meanwhile, Clustvis was used to determine the correlation coefficients between each trait.

Results

Several researchers advocated in vitro screening for drought-tolerant potato germplasm; however, few studies examined the relationship between in vitro and field

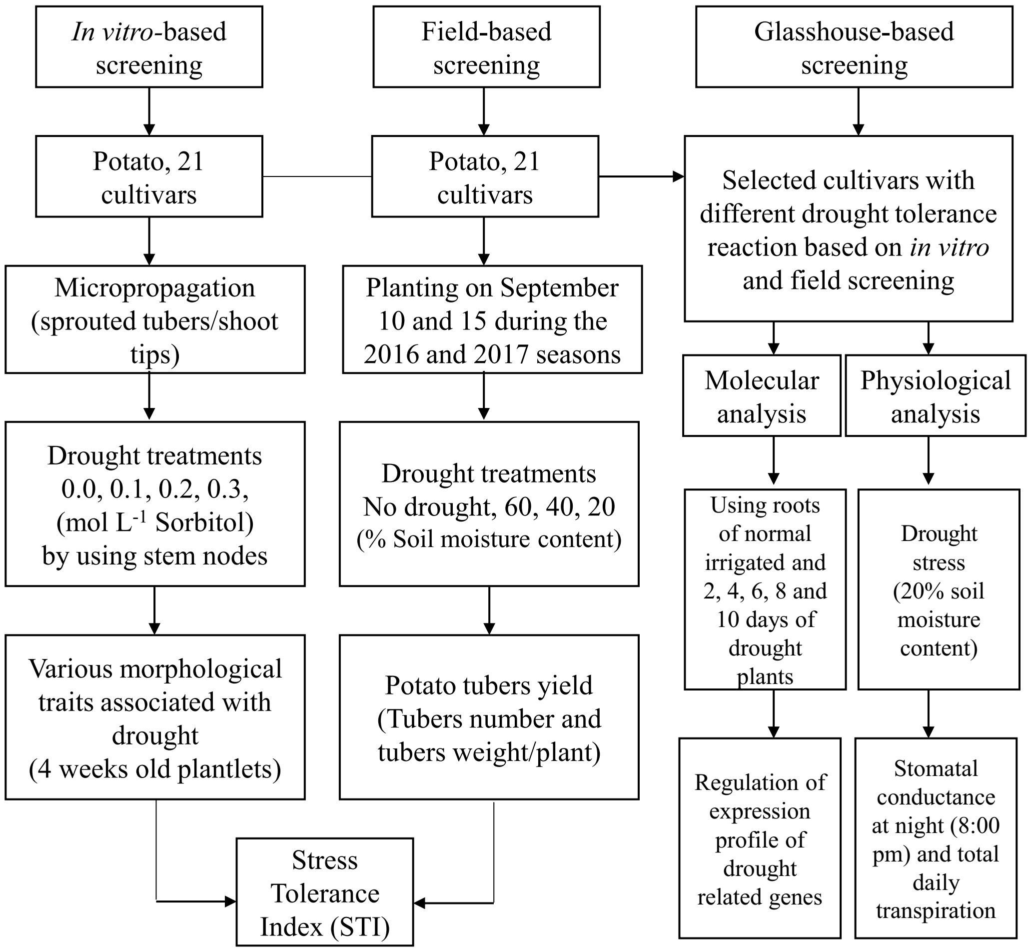


Fig. 1 Schematic diagram of the experiments conducted under current research to identify drought-tolerant potato genotype

(in vivo) screening. This study looked at the differences in morphological traits and tuber yield production in 21 potato cultivars under in vitro and field-based complementary drought assessment. Furthermore, a series of molecular and physiological experiments were carried out on potato plants grown in a glasshouse and subjected to drought stress. In the meantime, these cultivars have been chosen for this research as they exhibit a high degree of morphology diversity and many of them are also widely cultivated in Egyptian farms and other Middle East regions. Figure 1 shows a schematic diagram of the tests that were conducted.

In vitro experiment

Effects of drought on plantlets grown in vitro

The plantlets development of 21 different potato cultivars was studied in vitro under three different levels of drought stress. Sorbitol was utilized at three doses to alleviate drought: 0.1, 0.2, and 0.3 mol L^{-1}. The water potentials (MPa) of these concentrations of cultural media were − 1.11, − 1.51, and − 1.84, respectively. The drought treatments were compared to 0.0 mol L^{-1} sorbitol (no-drought), which yielded − 0.79 MPa.

Potato plantlets that were successfully grown in vitro onto MS medium showed significant differences after 30 days of culture. In general, shoots fresh weight (ranging from 0.21 to 1.51 g) and roots fresh weight (ranging from 0.05 to 1.29 g) greatly varied among the examined cultivars under the drought treatments (Table 2). Over the drought treatments, there were significant differences among cultivars for average shoots fresh weight and Burren cv. and Almond cv. gave the heaviest weight. With respect to roots fresh weight, most of the 21 cultivars tested showed sensitive reaction to drought stress treatments as the roots fresh weight significantly decreased however, five cultivars showed different degree of tolerance reaction and could develop roots in response to drought stress levels. Two of them namely, Diamond cv. and Russet Burbank cv., respectively gave higher roots fresh weight (1.11 and 0.84 g, respectively) under

Table 2 Shoots fresh weight, roots fresh weight, total root length, surface area of root and no. of roots of stem node derived in vitro plantlets of 21 potato (*Solanum tuberosum* L.) cultivars

Cultivar	Shoots fresh weight (g)				Roots fresh weight (g)				Total root length (mm)				Surface area of root (cm^2)				No. of roots/plantlet			
	0.0[a]	0.1	0.2	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2	0.3
Agata	0.70	0.65	0.63	0.56	0.85	0.82	0.79	0.68	113.32	112.0	105.0	99.35	1.14	1.10	0.94	0.89	8.45	7.51	7.40	7.11
Almond	1.20	0.98	0.88	0.67	0.52	0.15	0.11	0.09	71.21	25.51	14.51	5.210	0.75	0.27	0.22	0.13	7.45	4.50	3.25	2.14
Anya	0.95	0.85	0.61	0.52	0.38	0.11	0.08	0.05	68.51	40.21	30.24	20.11	0.55	0.32	0.29	0.31	6.51	4.61	2.51	2.01
Atlantic	1.11	0.93	0.80	0.41	0.54	0.51	0.48	0.21	66.21	57.51	50.21	39.58	0.79	0.75	0.71	0.66	6.21	6.48	6.31	5.99
Burren	1.31	1.16	0.89	0.65	0.51	0.33	0.21	0.15	85.51	41.25	31.54	15.27	0.89	0.56	0.25	0.13	7.95	5.51	2.24	1.91
Cara	1.00	0.86	0.74	0.68	0.42	0.35	0.22	0.15	64.62	38.50	30.10	20.14	0.65	0.42	0.21	0.15	6.35	3.51	2.11	1.84
Champion	1.06	0.82	0.78	0.64	0.51	0.35	0.24	0.11	63.62	28.51	21.25	14.25	0.55	0.40	0.14	0.12	7.14	3.62	1.51	1.12
Desiree	0.95	0.79	0.65	0.54	0.49	0.21	0.11	0.11	60.50	30.11	20.15	11.24	0.46	0.26	0.15	0.11	6.57	2.95	1.21	1.05
Diamond	1.12	0.92	0.61	0.45	1.29	1.24	1.18	1.11	91.61	89.08	82.36	72.00	1.11	1.07	1.06	1.04	8.67	9.56	8.91	8.51
Gala	0.71	0.54	0.34	0.21	0.61	0.21	0.10	0.08	98.65	25.61	19.57	11.36	0.96	0.25	0.15	0.10	8.45	3.51	1.11	1.01
Gazella	0.83	0.52	0.50	0.41	0.52	0.14	0.14	0.10	62.35	22.10	19.56	13.26	0.45	0.21	0.15	0.12	6.95	3.21	2.14	1.01
Kennebec	0.67	0.56	0.52	0.41	0.80	0.75	0.72	0.58	56.24	64.51	50.25	41.00	0.72	0.69	0.60	0.55	6.14	6.32	6.15	5.93
King Edward	0.87	0.74	0.65	0.61	0.56	0.32	0.11	0.12	69.80	44.42	30.00	21.00	0.46	0.34	0.21	0.20	7.54	3.14	2.55	1.32
Lady Balfour	1.51	0.78	0.65	0.51	0.41	0.20	0.16	0.08	53.25	25.16	20.10	14.21	0.27	0.21	0.20	0.11	5.12	2.15	1.11	1.00
Lady Rosetta	0.99	0.85	0.74	0.65	0.47	0.21	0.12	0.11	61.25	31.22	19.54	12.53	0.41	0.26	0.21	0.10	5.95	3.01	1.14	1.11
Marble	0.95	0.84	0.65	0.47	0.49	0.15	0.11	0.08	61.35	32.51	20.15	13.25	0.42	0.26	0.23	0.12	5.99	2.57	1.58	1.14
Marfona	0.97	0.62	0.55	0.47	0.45	0.21	0.21	0.11	60.52	29.54	18.65	11.23	0.41	0.21	0.14	0.11	5.14	2.35	2.21	1.10
Maritiema	1.25	0.89	0.65	0.55	0.30	0.25	0.14	0.07	51.25	24.61	19.51	14.62	0.26	0.22	0.20	0.14	5.01	2.31	1.56	0.90
Mizen	1.05	0.89	0.78	0.65	0.49	0.15	0.11	0.08	62.32	35.21	25.61	17.62	0.45	0.31	0.24	0.18	5.84	3.10	1.54	1.21
Russet Burbank	1.17	0.86	0.63	0.46	1.15	1.08	0.98	0.84	88.45	76.85	72.50	66.84	1.11	1.10	0.97	0.86	9.54	9.22	9.10	8.88
Spunta	0.79	0.52	0.42	0.40	0.55	0.33	0.22	0.11	71.24	41.56	31.25	22.54	0.55	0.27	0.29	0.11	7.55	3.51	1.51	1.12
LSD (0.05)	0.0550				0.0819				1.104				0.2701				0.225			

Explants were grown on media supplemented with three different levels of sorbitol (0.1, 0.2 or 0.3 mol L^{-1}) compared with the control (no sorbitol). The experiment was repeated three times ($n = 20$) and significant differences were calculated using LSD test

[a] Sorbitol mol L^{-1}

drought stress treatment (0.3 mol L^{-1} sorbitol) than the other cultivars. In Agata cv., Atlantic cv., and Kennebec cv. nevertheless, the roots fresh weight decreased with a rise in stress levels, but the reduction was non-significant under the low (0.1 mol L^{-1} sorbitol) and intermediate (0.2 mol L^{-1} sorbitol) drought stress treatments. On the other hand, Anya cv. was the most significantly affected cultivar and gave the lowest roots fresh weigh (0.05 g) at the highest stress level of drought (Table 2).

Furthermore, other root characteristics such as total root length, root surface area and no. of roots under drought stress were examined using WinRhizo (Table 2). A reduction of 35 to 60% in root length, 42 to 69% in mean root surface area and 37 to 62% in no. of roots due to drought were observed. Drought stress significantly affected most cultivars to grow long roots; however, Agata, Diamond, Kennebec, Russet Burbank and Atlantic cvs, respectively, showed substantial differences with drought treatment (Table 2). Under drought stress (0.3 mol L^{-1} of sorbitol), Agata cv., had longer root length (99.35 mm) than the other cultivars however, Kennebec cv. gave longer roots (64.51 mm) under low drought treatment (0.1 mol L^{-1} of sorbitol) compared with 56.24 mm under no drought treatment (0.0 mol L^{-1} of sorbitol). On the other hand, Almond cv., Marfona cv., Desiree cv. and Gala cv. were significantly sensitive and produced short roots (5.21, 11.23, 11.24 and 11.36 mm, respectively) under drought stress (0.3 mol L^{-1} of sorbitol). Meanwhile, roots covered narrow surface area with drought stress levels in most cultivars under this investigation. Overall, mean surface area of roots among the cultivars ranged from 0.1 to 1.14 cm. While the root surface area decreased significantly in most of the cultivars, there was a non-significant reduction in Diamond cv., Agata cv., Russet Burbank cv., Atlantic cv. and Kennebec cv. (Table 2). There was also a decrease in the no. of roots from 9.54 to 1.0 due to drought stress. Most of cultivars had significant low no. of roots under stress while the reduction was not significant in Diamond, Atlantic and Kennebec cultivars. Interestingly, Diamond cv. Atlantic cv. and Kennebec cv. developed more roots (9.65, 6.48 and 6.32, respectively) under low drought treatment (0.1 mol L^{-1} of sorbitol) than the control treatment (8.67, 6.21 and 6.14, respectively). On the other hand, Lady Balfour cv., Maritiema cv., Gala cv. and Marfona cv. had the lowest average roots number in response to drought treatments.

Likewise, cultivars plantlets showed a decrease in the average no. of leaves (from 10.62 to 4.55) and leaf area (from 962.64 to 30.08) due to drought stress treatments; 0.1, 0.2 and 0.3 mol L^{-1} of sorbitol as shown in Table 3. The number of leaves significantly declined in all cultivars with great reduction in Gala cv., (1.5) although plantlets of Diamond cv. yielded a large number of leaves/plantlet (6.67) under 0.3 mol L^{-1} of sorbitol. At the same time, Anya, Gala and Almond cultivars had the lowest average leaf area, while Burren and Atlantic cultivars had the highest average leaf area over the drought treatments.

Effects of drought on plantlets water content %

The percentage of plantlet water content (PWC%) is one of the stress physiological indices primarily of drought. Variations in PWC % based on cultivar and degree of drought were observed, and it ranged from 20% under high stress level to 95% under no-drought treatment with an approximately fivefold difference (Table 3). PWC % of potato cultivars was low with increasing concentrations of sorbitol compared to control (no drought) but the decrease in PWC was more pronounced in Gala, Anya and Lady Balfour cultivars, respectively, with significant differences. On the other hand, data showed that Diamond, and Agata cultivars did not differ significantly in PWC % with increasing levels of drought stress when they gave the highest PWC % (87% and 84%, respectively) under the highest level of drought.

Effects of drought on the potassium content

Potassium (K^+) is a vital mineral that influences plant growth and metabolism through a variety of physiological and biochemical mechanisms. Root growth and K^+ diffusion rates towards the roots were both confined during drought stress, restricting K^+ acquisition. Plant tolerance to drought stress, as well as K^+ absorption, may be further negatively affected as a result of the lower K^+ concentrations. Plant drought tolerance depends on

Table 3 Number of leaves/plantlet, leaf area/plantlet, plantlet water content (PWC%), and potassium content (K^+) of stem node derived in vitro plantlets of 21 potato (*Solanum tuberosum* L.) cultivars

Cultivar	No. of leaves/plantlet				Leaf area/plantlet (mm^2)				PWC%				K^+ (mmol kg^{-1} FW)			
	0.0[a]	0.1	0.2	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2	0.3
Agata	11.10	8.21	7.45	6.21	896.3	455.6	366.3	268.2	91	88	85	84	82	81	42	30
Almond	11.56	9.55	6.32	3.25	1000.3	365.2	265.2	155.2	94	77	60	45	73	29	22	19
Anya	11.20	9.90	6.90	4.15	905.2	346.1	209.0	115.0	93	75	40	20	80	35	25	22
Atlantic	11.65	9.98	6.10	5.10	1105.2	921.0	895.0	150.1	93	84	79	75	82	81	42	30
Burren	11.00	9.00	5.60	4.67	1103.1	1151.0	507.0	406.0	91	72	56	41	73	36	23	20
Cara	10.20	8.90	5.50	4.64	1100.0	850.0	496.0	401.0	92	76	57	42	72	30	25	21
Champion	10.35	8.40	5.50	3.10	1100.5	816.0	506.0	319.0	95	75	55	41	73	36	23	20
Desiree	11.30	8.50	5.50	3.80	899.2	507.0	406.0	299.0	93	70	55	40	70	30	25	20
Diamond	12.67	9.00	8.21	6.67	1000.2	910.0	446.0	425.0	93	90	88	87	81	81	51	38
Gala	8.40	7.50	4.50	1.50	884.5	436.0	265.0	167.2	91	60	45	25	77	30	21	18
Gazella	9.70	7.44	6.54	4.10	878.5	516.0	496.0	407.0	94	73	55	40	73	35	25	20
Kennebec	11.50	10.67	8.57	7.21	984.1	855.3	516.0	406.0	94	87	82	76	85	84	50	32
King Edward	9.85	7.90	5.50	4.34	856.3	649.0	526.0	410.0	94	74	56	41	73	29	22	19
Lady Balfour	10.33	6.33	4.67	3.67	993.5	509.0	413.0	319.0	91	77	49	30	73	36	23	20
Lady Rosetta	11.40	8.70	5.60	3.50	847.5	607.0	316.0	246.0	90	71	56	41	76	30	22	18
Marble	10.25	8.44	5.74	3.11	888.9	507.0	330.0	269.0	94	72	55	42	70	28	26	19
Marfona	10.65	8.10	5.66	3.02	898.6	612.0	352.0	254.0	91	72	56	41	70	26	22	20
Maritiema	9.67	6.67	5.33	3.33	874.6	549.0	406.0	322.0	90	76	58	43	67	33	24	18
Mizen	10.10	7.10	4.10	3.21	996.3	649.0	316.0	253.0	92	77	48	34	75	32	22	16
Russet Burbank	10.24	8.45	7.50	6.54	1002.3	855.0	423.0	356.0	94	86	80	76	85	84	50	32
Spunta	9.87	7.01	6.54	4.58	1000.3	516.0	412.0	396.0	94	75	56	40	82	43	42	30
LSD (0.05)	0.2115				16.214				7.1641				6.021			

Explants were grown on media supplemented with three different levels of sorbitol (0.1, 0.2 or 0.3 mol L^{-1}) compared with the control (no sorbitol). The experiment was repeated three times ($n = 20$) and significant differences were calculated using LSD test

[a] Sorbitol mol L^{-1}

having sufficient plant K^+ levels. In Table 3, treatments with drought resulted in a significant reduction in K^+ content of the roots of all the 21 cultivars examined, although the K^+ decrease was greater for Mizen, Marfona, Maritiema, Lady Rosetta, Marble, King Edward and Almond cultivars. Overall, K^+ content among the cultivars ranged from 16 to 85 mmol kg^{-1} FW. Potassium was significantly reduced by drought stress in roots started from the treatment with the lowest concentration of 0.1 mol L^{-1} sorbitol. In Russet Burbank, Kennebec, Diamond, Atlantic and Agata cultivars, respectively, a reduction in K^+ was observed in the 0.1 mol L^{-1} sorbitol treatment, although the decrease was not statistically significant. At high stress level, Diamond cv. showed the highest K^+ content (38 mmol kg^{-1} FW) whereas Mizen cv. had the lowest content (16 mmol kg^{-1} FW).

Field experiment

Effects of drought on potato plants and yield under field conditions

The drought tolerance assessment in potatoes is usually based on a comparison of plant growth and tuber yield responses under non-drought and drought-growing conditions, whether in the lab or in the field. In addition to the in vitro experiment, this field experiment was assigned to determine the drought tolerance variations and stability of the same 21 potato cultivars. The screening was conducted under three drought regimes (60%, 40% and 20% soil moisture content) in comparison to the control (no drought). Field screening was carried out in two successive seasons, and the drought treatments used for the experiments found mild, moderate, and severe drought conditions.

The combined analysis of the effects of drought stress on the shoots fresh weight and shoots dry weight of plants grown under field conditions of the two growing seasons is shown in Table 4. At harvesting time, fresh and dry weights of shoots decreased as the drought regimes increased and the values ranged from 101.0 to 980.0 g and 15.96 to 77.5 g under 20% soil moisture content and no drought treatment, respectively. In general, the 21 studied potato cultivars showed more shoots fresh dry weights at the control level (no drought) than any of the three different drought regimes (60%, 40% and 20% soil moisture content), although Diamond, Russet Burbank and Agata cultivars outperformed other cultivars at 60% and 40% soil moisture content. The reduction was generally greater in 20% soil moisture content. Diamond cv. had the maximum shoots fresh weight (526.67 g) when Agata cv. had the highest shoots dry weight (41.17 g). Marfona cv., Gazella cv., Desiree cv. and Lady Rosetta cv. showed the greatest decrease in shoots fresh and dry weights when grown in field with elevated drought regimes (Table 4).

Potato yield was highly more variable due to drought regimes than the growth response as clear in Table 4. The number and the weight of tubers/plant were observed under the three drought regimes and compared to the control (no drought). Tuber's production declined as a result of drought stress in all studied 21 cultivars, and there were significant variations in the number and the weight of tubers/plant at the higher drought regime among the cultivars. The average number of tubers per plant ranged from 0.13 under high stress regime (20% soil moisture content) to 7.55 under no stress treatment. With the lowest drought level (60% soil moisture content), all cultivars formed tubers and the number was significantly different from the production under normal conditions (no drought) with the exception of Agata, Atlantic, Diamond, Kennebec, and Russet Burbank cultivars which showed no significant difference. When cultivars were subjected to the highest level of drought stress (20% soil moisture content), the number of tubers greatly declined in the most of cultivars, however, Diamond, Agata and Russet Burbank, gave higher number of tubers than the other cultivars (2.4, 2.1, 1.88, respectively). On the other hand, Gazella, King Edward, Gala, Marfona and Anya cultivars, respectively, formed the lowest average number of potato tubers over the stress treatments (Table 4). For tuber yield, in parallel statistical analysis of the combined data indicated that the tuber fresh weight/plant significantly affected by increasing drought regimes from 60 to 20%. The fresh weight of tubers ranged from 15 g/plant under high drought stress to 567.4 g/plant under no drought conditions. At the highest stress level, Diamond cv., Agata cv., Russet Burbank cv. and closely followed by Atlantic cv. and Kennebec cv. had the highest weight of tubers/plant (139.1, 130.3, 125.4, 115.1 and 105.01 g/plant, respectively) while Anya, Mizen, Almond, Marfona, Gazella and Gala cultivars gave the lowest fresh weight (Table 4).

Stress tolerance index (STI) and cluster analysis

In the STI, there was a control (no drought) for each experiment and drought stress levels in in vitro or field-based screening. Values for each cultivar and each drought treatment to that cultivar's no drought treatment were calculated to give the stress-tolerance index (STI) for root parameters, i.e., roots fresh weight, no. of roots, total root length and surface area of root studied under tissue culture conditions (in vitro) and tuber production, i.e., no. of tubers and tuber yield examined under field conditions (in vivo). Drought tolerance, as expressed by the stress tolerance index (STI) is shown in Table 5.

The STIs of roots fresh weight, no. of roots, total root length and root surface area revealed a degree of

Table 4 Shoots fresh weight, shoots dry weight, no. of tubers/plant, and weight of tubers/plant at harvesting time of 21 potato (*Solanum tuberosum* L.) cultivars

Cultivar	Shoots fresh weight (g)				Shoots dry weight (g)				No. of tubers/plant				Weight of tubers /plant (g)			
	No drought	60%[a]	40%	20%	No drought	60%	40%	20%	No drought	60%	40%	20%	No drought	60%	40%	20%
Agata	802.3	702.0	665.0	524.1	72.50	59.17	48.20	41.17	5.90	5.33	3.75	2.10	540.0	390.4	270.1	130.3
Almond	750.0	266.7	222.0	130.0	70.50	39.50	31.25	20.50	7.07	4.27	1.21	0.21	560.0	320.0	160.0	21.0
Anya	546.7	520.0	290.0	310.0	55.50	50.60	32.65	32.83	7.55	3.27	0.56	0.13	535.0	290.0	150.0	15.0
Atlantic	890.0	750.0	510.0	259.0	75.50	61.50	40.25	31.50	5.60	5.17	2.37	1.92	500.0	410.0	241.0	115.1
Burren	885.0	562.0	254.0	132.0	77.50	55.50	35.67	23.50	6.37	5.63	1.91	0.64	567.1	335.0	171.1	46.0
Cara	651.0	415.0	212.0	148.0	63.83	33.50	31.47	21.50	6.63	5.37	1.94	0.70	560.0	328.0	172.1	36.0
Champion	648.0	401.0	141.0	124.0	60.50	31.83	22.36	20.50	6.17	5.20	1.64	0.65	541.0	315.0	161.0	25.0
Desiree	658.0	255.0	154.0	110.0	64.50	22.50	23.65	18.50	6.33	4.73	1.78	0.49	544.0	315.0	176.0	31.0
Diamond	953.0	858.1	756.7	526.7	77.50	50.15	40.15	35.50	6.63	6.33	4.79	2.40	534.0	435.0	277.0	139.1
Gala	955.0	248.0	147.0	101.0	75.50	25.50	21.50	16.15	5.47	3.97	1.22	0.28	555.0	304.2	156.0	22.0
Gazella	647.0	214.0	145.0	124.0	64.24	23.10	20.36	18.54	5.47	3.63	1.10	0.30	545.0	301.0	154.0	21.0
Kennebec	621.0	587.0	501.0	152.0	61.58	42.36	38.47	20.10	5.70	5.11	1.91	1.20	570.0	346.0	230.0	105.01
King Edward	663.0	441.0	412.0	295.0	63.55	34.50	32.50	26.14	4.57	3.54	1.90	0.60	551.0	317.0	173.1	25.0
Lady Balfour	665.0	214.0	197.0	114.0	64.21	23.44	19.70	17.54	7.30	5.40	1.74	0.64	567.0	325.1	171.2	24.0
Lady Rosetta	612.0	256.0	214.0	101.0	60.14	24.15	23.44	15.96	6.60	5.67	1.78	0.58	555.0	325.0	171.2	35.0
Marble	615.0	263.0	231.0	121.0	61.47	27.44	25.00	17.54	6.27	3.63	1.37	0.60	554.0	312.0	170.6	31.0
Marfona	611.0	211.0	141.0	111.0	60.50	22.36	19.57	17.41	5.50	3.46	1.43	0.59	551.0	309.0	165.0	21.0
Maritiema	663.0	223.0	204.0	142.0	64.65	25.65	21.40	19.57	6.90	5.30	1.56	0.66	541.0	315.0	174.0	25.0
Mizen	647.0	314.0	241.0	184.0	63.25	31.50	26.50	21.20	6.63	3.64	1.10	0.31	556.0	308.3	156.0	20.0
Russet Burbank	980.0	866.7	633.3	386.7	76.38	69.58	46.57	32.54	5.47	4.93	2.92	1.88	567.4	371.0	245.0	125.4
Spunta	646.7	266.7	190.0	110.0	64.20	29.50	21.10	17.54	6.40	5.30	1.79	0.91	570.0	341.0	173.5	26.0
LSD (0.05)	25.0421				9.3321				0.621				25.1312			

Plants were grown in field under three different regimes of drought (60%, 40% or 20% of moisture content) compared with the control (no drought). Values are means ($n = 10$) of three replicates of the combined analysis of the first and second season and significant differences were calculated using LSD test

[a] Soil moisture content

Table 5 Drought tolerance as expressed by the stress tolerance index (STI) of roots fresh weight, no. of roots, total root length and surface area of root of stem node derived in vitro plantlets grown under three different levels of sorbitol 0.1, 0.2 or 0.3 mol L^{-1}, and no. of tubers, and weight of tubers of plants grown in field under three different regimes of drought 60%, 40% or 20% of moisture content of 21 potato (*Solanum tuberosum* L.) cultivars

Cultivar	Stress tolerance index (STI)																	
	Roots fresh weight			No. of roots			Total root length			Surface area of root			No. of tubers			Weight of tubers		
	0.1[a]	0.2	0.3	0.1	0.2	0.3	0.1	0.2	0.3	0.1	0.2	0.3	60%[b]	40%	20%	60%	40%	20%
Agata	0.96	0.93	0.80	0.89	0.88	0.84	0.99	0.93	0.88	0.96	0.83	0.78	0.90	0.64	0.36	0.72	0.50	0.24
Almond	0.28	0.21	0.17	0.60	0.44	0.29	0.36	0.20	0.07	0.36	0.30	0.17	0.60	0.17	0.03	0.57	0.29	0.04
Anya	0.29	0.21	0.13	0.71	0.39	0.31	0.59	0.44	0.29	0.59	0.53	0.57	0.43	0.07	0.02	0.54	0.28	0.03
Atlantic	0.95	0.87	0.39	1.04	1.02	0.96	0.87	0.76	0.60	0.95	0.90	0.83	0.92	0.42	0.34	0.82	0.48	0.23
Burren	0.65	0.42	0.29	0.69	0.28	0.24	0.48	0.37	0.18	0.64	0.29	0.15	0.88	0.30	0.10	0.59	0.30	0.08
Cara	0.85	0.53	0.37	0.55	0.33	0.29	0.60	0.47	0.31	0.64	0.33	0.23	0.81	0.29	0.11	0.59	0.31	0.06
Champion	0.68	0.47	0.22	0.51	0.21	0.16	0.45	0.33	0.22	0.73	0.26	0.23	0.84	0.27	0.11	0.58	0.30	0.05
Desiree	0.44	0.23	0.23	0.45	0.18	0.16	0.50	0.33	0.19	0.56	0.34	0.24	0.75	0.28	0.08	0.58	0.32	0.06
Diamond	0.96	0.91	0.86	1.10	1.03	1.00	0.97	0.90	0.79	0.96	0.95	0.94	0.95	0.72	0.36	0.81	0.52	0.26
Gala	0.34	0.16	0.13	0.42	0.13	0.12	0.26	0.20	0.12	0.26	0.15	0.11	0.73	0.22	0.05	0.55	0.28	0.04
Gazella	0.27	0.27	0.19	0.46	0.31	0.15	0.35	0.31	0.21	0.48	0.32	0.28	0.66	0.20	0.06	0.55	0.28	0.04
Kennebec	0.93	0.90	0.72	1.03	1.00	0.97	1.15	0.89	0.73	0.95	0.83	0.77	0.90	0.34	0.21	0.61	0.40	0.18
King Edward	0.58	0.20	0.22	0.42	0.34	0.18	0.64	0.43	0.30	0.74	0.46	0.42	0.78	0.42	0.13	0.58	0.31	0.05
Lady Balfour	0.93	0.74	0.37	0.42	0.22	0.20	0.47	0.38	0.27	0.81	0.74	0.43	0.74	0.24	0.09	0.57	0.30	0.04
Lady Rosetta	0.46	0.25	0.25	0.51	0.19	0.19	0.51	0.32	0.20	0.62	0.52	0.25	0.86	0.27	0.09	0.59	0.31	0.06
Marble	0.32	0.23	0.16	0.43	0.26	0.19	0.53	0.33	0.22	0.63	0.56	0.29	0.58	0.22	0.10	0.56	0.31	0.06
Marfona	0.48	0.48	0.25	0.46	0.43	0.21	0.49	0.31	0.19	0.51	0.34	0.27	0.63	0.26	0.11	0.56	0.30	0.04
Maritiema	0.82	0.47	0.23	0.46	0.31	0.18	0.48	0.38	0.29	0.85	0.78	0.54	0.77	0.23	0.10	0.58	0.32	0.05
Mizen	0.32	0.23	0.16	0.53	0.26	0.21	0.56	0.41	0.28	0.70	0.54	0.41	0.55	0.17	0.05	0.55	0.28	0.04
Russet Burbank	0.94	0.85	0.73	0.97	0.95	0.93	0.87	0.82	0.76	0.99	0.87	0.77	0.90	0.53	0.34	0.65	0.43	0.22
Spunta	0.61	0.41	0.20	0.46	0.20	0.15	0.58	0.44	0.32	0.49	0.53	0.20	0.83	0.28	0.14	0.60	0.30	0.05

[a] Sorbitol mol L^{-1}

[b] Soil moisture content

tolerance to drought stress in some of the cultivars compared to others based on the level of drought and/or trait. The STIs decreased with increasing drought in all examined cultivars. Agata cv. showed the highest STI of roots fresh weight when the plants were subjected to slightly or moderately drought conditions (0.1 and 0.2 mol L^{-1} sorbitol) however, Diamond cv. had better STI with the highest level of drought (0.3 mol L^{-1} sorbitol). On the other hand, Diamond, Atlantic, Kennebec, Russet Burbank and Agata cultivars showed remarkable STI of number of roots across all drought levels. For STI of root length, Agata cv. was more tolerant than any other cultivars under intermediate and high drought conditions, when Kennebec cv. had higher STI under the low level of drought stress. When the plants were treated with low drought condition (0.1 mol L^{-1} sorbitol), Russet Burbank cv. exhibited the largest STI of surface area of root; nevertheless, Diamond cv. exhibited great tolerance with the higher levels of drought (0.2 and 0.3 mol L^{-1} sorbitol).

Variations in the STIs of number of potato tubers and tubers fresh weight among cultivars were noticed from low to high drought; however, the STI decreased with increasing drought stress under field-based screening (60%, 40% and 20% soil moisture content). Diamond cv. and Agata cv. were more tolerant and had higher STI of tuber numbers across high drought regime. Atlantic cv. preferred slightly drought conditions to give higher STI of tubers weight. But under the moderate and high drought environment Diamond cv. followed by Agata cv. had better STI. Thus, based on the results obtained from both in vitro-based screening and field-based screening, some cultivars were rated as drought-tolerant.

Based on the variations of the previous examined growth, physiology and yield traits, clustering for response to drought resulted in three distinct groups: (1) drought-tolerant group consisting of cultivars Russet Burbank, Diamond, Agata, Kennebec, Atlantic; (2) a moderately tolerant group consisting of cultivars

Maritiema, Lady Balfour, Mizen, Marfona, Lady Rosetta, Marble, Desiree, Champion, Cara, Burren, and Almond, and (3) a sensitive group consisting of cultivars Anya, Gala, Spunta, King Edward, and Gazella (Fig. 2).

Glasshouse experiments

Effect of drought on the expression profile of stress-related genes

The main objective of this experiment was to study the regulation of genes and transcription factors that are involved in the response of plant to drought for example; deeper rooting (*DRO*) potato, LRR receptor-like serine/threonine-protein kinase ERECTA (*ERECTA*), ethylene response factor (*ERF*), dehydration responsive element binding (DREB) and *Solanum tuberosum* MYB (*StMYB*). Therefore, drought-related genes were chosen and examined in some of the potato cultivars that differed in their response to drought on the in vitro and field-based screening for example; Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. which showed higher STI, and Anya cv. and Gala cv. which showed lower STI. In this experiment, drought stress was applied

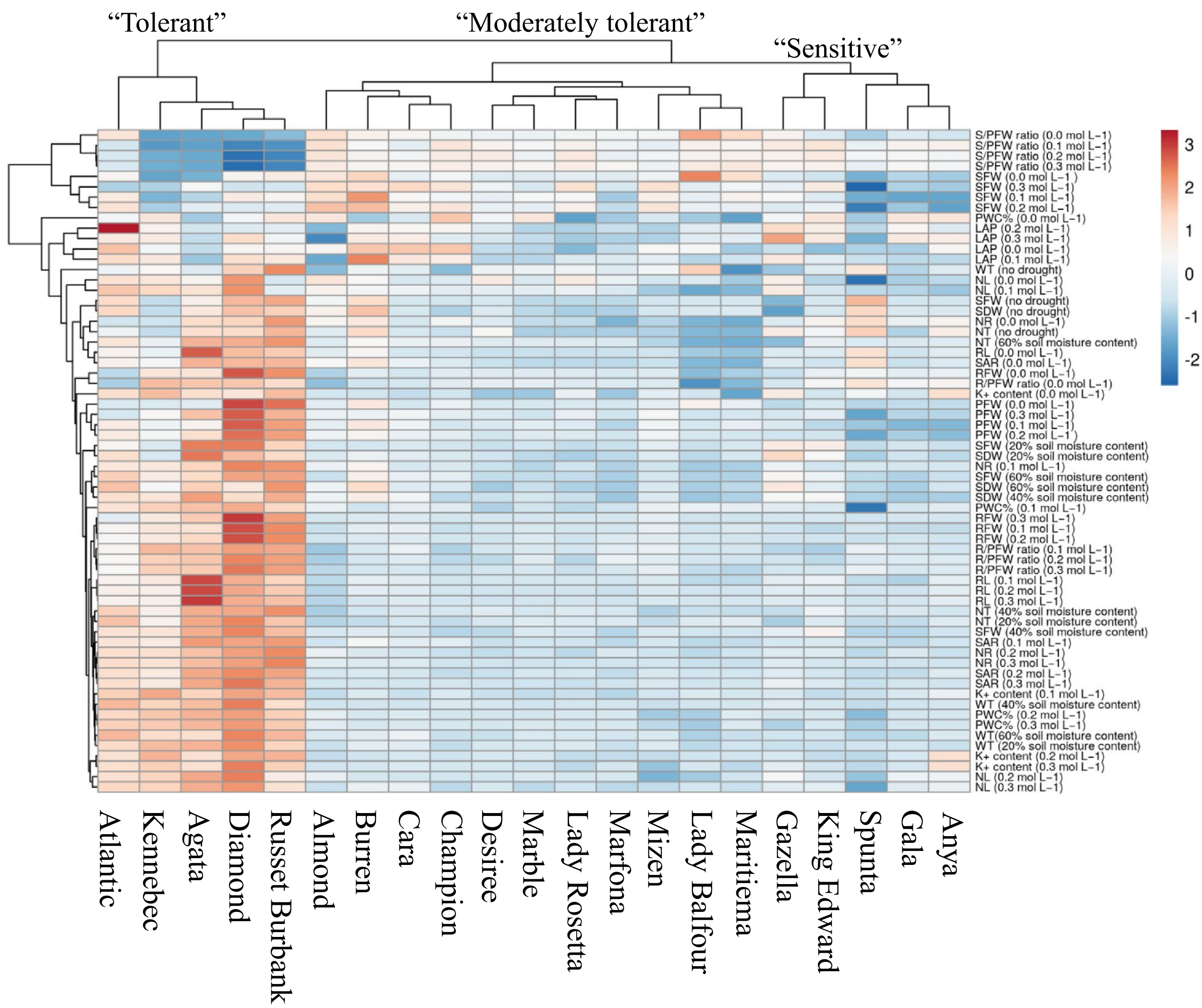


Fig. 2 Two-way hierarchal clusters associated with the morphological, physiological traits and tuber yield measured per plantlet/plant of combined data on 21 cultivars under different drought stress treatments in vitro and field conditions. Both in vitro and field experiments were conducted, and traits were recorded under drought conditions; 0.0, 0.1, 0.2 or 0.3 mol L^{-1} sorbitol for in vitro and 60%, 40% or 20% of moisture content for field studies. *PFW* plantlet fresh weight, *SFW* shoots fresh weight, *RFW* roots fresh weight, *R/PFW* roots/plantlet fresh weight, *S/PFW* shoots/plantlet fresh weight, *RL* root length, *SAR* surface area of root, *NR* no. of roots, *NL* no. of leaves, *LAP* leaf area/plantlet, *PWC* plantlet water content%, K^+ potassium content in roots, *SFW-F* shoot fresh weight under field trial, *SDW-F* shoot dry weight under field trial, *NT* no. of tubers/plant, *WT* weight of tubers/plant

to 45-day-old plants by withholding water for 2 weeks, and plant roots were tested at 2, 4, 6, 8, and 10 days. Roots from plants that were routinely watered were utilized as a control. RT-PCR analysis was done to identify the expression profile of the *DRO*, *ERECTA*, *ERF*, *DREB* and *StMYB* during this drought experiment using mRNA isolated from roots derived from plants of the seven cultivars (Fig. 3). mRNA accumulation of the studied genes was observable beginning early or late after exposed to drought stress of all cultivars examined. In general, the genes mRNA accumulated to a much greater degree in Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. which produced high plant growth, and yield under stress conditions than in Anya cv. and Gala cv. which produced low plant growth, and yield under stress conditions.

DOR potato had the highest expression at drought day 10. It up-regulated over the drought period of time, however in Diamond cv. and Agata cv. *DOR* potato started to up-regulate directly after exposed to drought day 2. The *ERECTA* expression level increased in Atlantic and Agata plants and achieved the highest expression at day 10. Again, in Diamond plants, the expression of *ERECTA* increased early at the drought day 4. On the other hand, *ERECTA* had a high level of expression at 6 and 8 days in Kennebec cv. and at 10 days in Russet Burbank cv. *ERF* expressed abundantly in Atlantic cv., Agata cv., Diamond cv. however, the level of expression was low in Kennebec cv., Russet Burbank cv. and slightly increased over the drought days. In *StMYB*, the level of expression was higher at 6 days of drought in all cultivars which previously showed higher STI although it showed low level of expression at 10 days. *DREP* exhibited the highest expression at day 6 among Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv., and then, the expression decreased at day 8 in Agata cv., Diamond cv. and Kennebec cv. with slight increase at day 10. On the same time, the *DREP* level of expression was high early at 2 day of drought in Diamond cv. and Russet Burbank cv. In contrary, in Anya cv. and Gala cv. which showed lower STI, the *DOR* potato, *ERECTA*, *ERF*, *StMYB* and *DREP* level of expression was relatively stable or continually decreased over the time of drought (Fig. 3).

Effect of drought on stomatal conductance and transpiration

In this experiment, physiological characteristics, i.e., stomatal conductance and transpiration were examined using 60-day-old plants which subjected to drought stress (20% soil moisture content). Seven potato cultivars that differed in their stress tolerance index were studied, Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. which showed greater STI, and Anya cv. and Gala cv. which showed lower STI. Significant variations were identified for stomatal conductance and transpiration among examined cultivars and drought stress (Fig. 4A, B). Overall, Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. had higher stomatal conductance and transpiration than Anya cv. and Gala cv. The highest values were observed in Agata cv. under no drought conditions (0.028 mol H_2O m^{-2} s^{-1} and 211.1 g H_2O $plant^{-1}$, respectively) however, Diamond cv. had the highest value under the drought stress (0.019 mol H_2O m^{-2} s^{-1} and 121.32 g H_2O $plant^{-1}$, respectively). In comparison, Anya cv. and Gala cv. under drought conditions, both stomatal conductance and transpiration values showed a substantial decrease. For the correlation between tuber yield and physiological traits under drought conditions, linear function was fitted as clear in Fig. 4C, D. Likewise, the stomatal conductance and transpiration explained high correlation with the tuber yield in the seven studied cultivars under drought and no drought conditions.

Discussion

Potato is one of the world's most significant crops [7, 38, 39]. In Egypt, there are two primary growth seasons for potatoes: summer and fall. Every year, potato tuber seeds are imported from cold climate countries such as the Netherlands, Ireland, and the United Kingdom to be grown in Egypt during the summer season. Eventually, the tubers produced from the summer season will be stored for 3 months at 4 °C to be grown in the fall season, then the fall season production will be available for consumption. Egypt is located in a dry climate; yet, finding drought-tolerant cultivars is one approach for mitigating the negative consequences of drought stress [17, 18, 20]. There are significant variations in potato sensitivity, and individual cultivars' drought tolerance vary greatly [2, 7, 10]. Consequently, it is very important, in order to assign cultivars that can be grown in high drought regions or integrate drought-tolerant ones in breeding programs, to screen the available potato cultivars for their tolerance to drought [13–15]. Several researchers [7, 20, 40] have utilized in vitro assay to identify potato germplasm with drought tolerance; however, no thorough in vitro and field combined assessment of cultivars has been reported. In this study, in vitro and field experiments were used to assess the tolerance of potato cultivars (*Solanum tuberosum* L.) to distinct degrees of drought stress. The current study included the screening of 21 different potato cultivars which are commonly cultivated in the Middle East, including Egypt.

Significant differences were observed among cultivars for morphological and physiological parameters [41, 42]. A strong link was found in potato cultivars between growth and total plant production under drought

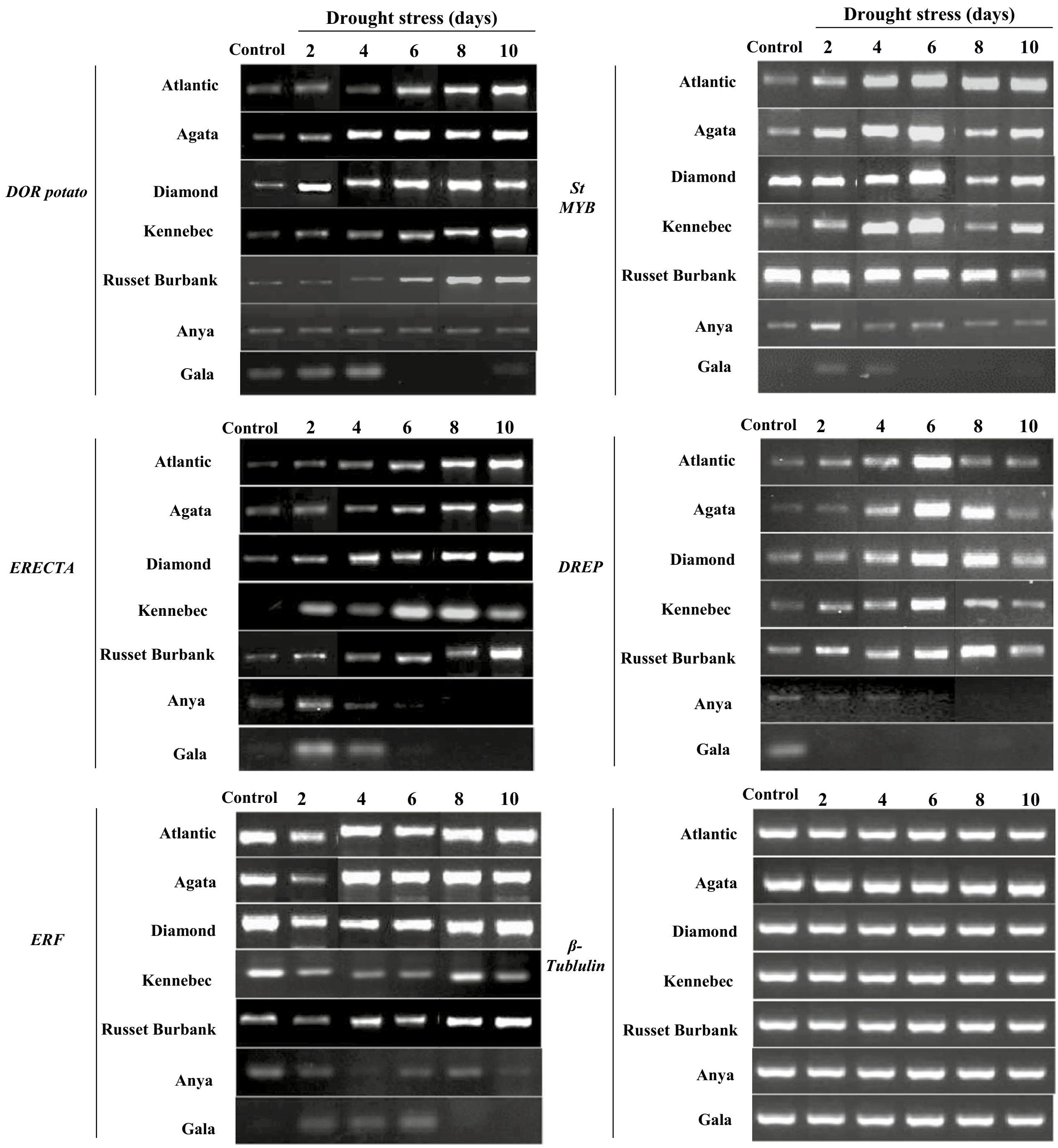


Fig. 3 Expression profile analysis of the drought-related genes or transcription regulators by RT-PCR. 45-day-old plants were subjected to drought stress, with no water for 2 weeks. mRNA was extracted from roots of normal irrigated plants (Control) and drought exposed plants after 2, 4, 6, 8 and 10 days. Deeper rooting (*DRO*) potato, LRR receptor-like serine/threonine-protein kinase ERECTA (*ERECTA*), ethylene response factor (*ERF*), dehydration responsive element binding (*DREB*) and *StMYB* were examined in Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. and Anya cv. and Gala cv. plants. The findings were verified to be reproducible using samples from three independently grown plants. PCR products were analyzed on a 2% agarose gel

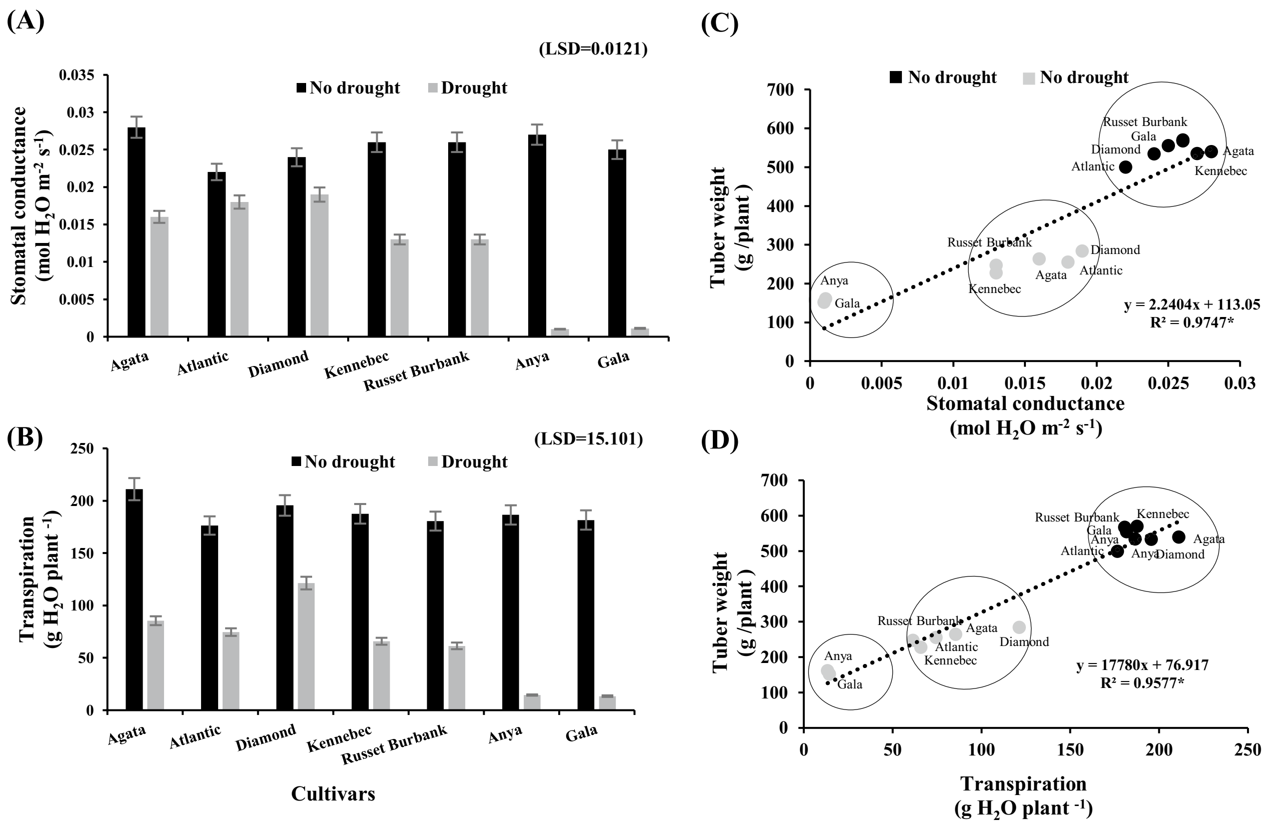


Fig. 4 Stomatal conductance (**A**), transpiration (**B**), linear function of stomatal conductance and tuber fresh weight (**C**) and linear function of transpiration and tuber fresh weight (**D**) under no drought and drought conditions in Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. and Anya cv. and Gala cv. plants. Stomatal conductance was measured at night (8:00 pm) while, total day transpiration was measured in a period of 24 h. Values are means ± SE, ($n = 10$) and the experiment was repeated three times and significant differences were calculated using LSD test

conditions. Discussions will therefore be summarized over experiments. In vitro-based screening with stem node culture may be a great way to check and select tolerance for drought [7, 20, 40]. The current study involved different levels of drought stress; no drought, 0.1, 0.2 and 0.3 mol L^{-1} sorbitol. Root traits were the first morphological traits that were significantly affected by stress. Such findings are not consistent with other studies that the reduction in leaf numbers was the first consequence of drought [7, 43]. On the other hand, the results are consistent with other studies reported for salt tolerance in potato and tomato plants [2, 4].

Under drought stress, five cultivars, Agata, Atlantic, Diamond, Kennebec, and Russet Burbank, produced more root growth than other cultivars. The results were greatly clarified when the five cultivars had the highest root traits at 0.3 mol L^{-1} of sorbitol under in vitro-based screening, suggesting that there is considerable variation in drought tolerance among cultivars. These findings are in agreement with previous studies [44, 45] which reported that developmental plant response to drought stress is manifested by increased root growth. Similarly, drought stress disrupted cell expansion and elongation, leading to a reduction in the leaf area and plant water content. The morphological consequence of drought was a reduction in leaf size, resulting in reduced photosynthesis and reduced accumulation of dry matter in tubers [7, 10, 14, 43]. At the same time, higher levels of drought contributed to a substantial reduction in the level of K^+ roots [46].

Screening in vitro may result in a loss of tolerance of plants or a different reaction under field conditions [17, 47]. To obtain full information, it is necessary to evaluate the tolerance of drought under field conditions. Several studies documented the effects of drought stress on tuberization [47–50]. In this study, the number and weight of tubers significantly declined in many of the evaluated cultivars. Russet Burbank, Agata, Diamond, Atlantic and Kennebec cultivars gave higher number of tubers than the other cultivars while, Diamond, Atlantic and Agata showed more tolerance and had the highest weight of tubers/plant under the drought regimes. These results confirm that the cultivars with higher stress tolerance index (STI) in tissue culture assay showed similar performance under field trial.

Significant developments in drought tolerance studies have addressed a range of primary genes and expression regulators that manipulate different growth or yield traits [24, 26, 27]. Root morphology and stomata growth genes play a crucial role in soil moisture extraction and preservation, and thus expression profile of some of these genes were analyzed under drought scheme [2, 24, 25, 33]. Any cultivars may be useful contributors in drought tolerance breeding programs if tissue culture and field findings are taken into account [16, 18]. Under drought stress of the current study, Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. displayed higher growth traits and yield than other cultivars and, for example, Anya cv. and Gala cv. had a responsive reaction. Meanwhile, based on the physiological and molecular investigations, these cultivars were chosen to emphasize the distinctions between drought-tolerant and drought-sensitive cultivars. Discussion of these findings found that five genes had variations in expression to which up or down-regulation of gene expression was observed in a drought-tolerant cultivars relative to a drought-sensitive cultivar in drought days. *DOR*, *ERECTA* and *StMYB* demonstrated a similar degree of expression on day 0 then highly up-regulated in drought-tolerant cultivars. *ERF and DREP* showed differential expression on day 0 but they also up-regulated in drought-tolerant cultivars. On the other hands, all genes exhibited low level of expression starting from day 0 to day 10 of drought stress in Anya cv. and Gala cv., the drought-sensitive cultivars. Surprisingly, these genes began to up-regulate early in Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. right after being subjected to stress. Taken together by roots morphological traits and tuber production which conducted in vitro and field, this might clarify why these cultivars response to drought was higher than that of other cultivars. These findings are consistent with those recognized by *DRO* and *ERECTA* as a stimulator of drought tolerance through root trait regulation and transpiration efficiency. *DRO* was classified as the root system architecture controller by modifying the root growth angle for rice. The profound rooting was seen as benefiting in rice not only for a tolerance to drought, but also for improved yield, nitrogen absorption and cytokinin fluxes from root to shoot in grain [25]. *ERECTA* is one of the transcription efficiency regulated genes which boost the biomass provided by the unit of water transpired and also connected to the deep root system [23]. *ERF*, *DREB* and *MYB* were reported as both positive and negative regulators of drought reactions in wheat, rice, maize and Arabidopsis [25–28, 33]. Over the last two decades, researchers have taken important steps in our understanding of the mechanisms involved in adaptation and tolerance to drought stress in some plants such as wheat and rice. Wheat cultivars adapted various drought-tolerance mechanisms, such as deeper root formation, higher biomass accumulation, enhanced stomatal control over transpiration [51], betterment of osmoprotective and antioxidant response [52, 53], and, most importantly, improved coordination of positive and negative gene expression. In rice the mechanisms included increasing chlorophyll content, harvest index, stomatal density and conductance, root thickness and length, waxy or thick leaf coverings, as well as decreasing osmotic potential, transpiration rates, and leaf weight and size [25, 33, 54, 55].

Stomatal closing leads to reduced water potential for leaves, reduced carbon assimilation, oxidation and increased canopy in response to stress [56]. Sustaining improved stomata regulation of transpiration is essential to the battle against inhibition of photosynthesis under drought stress [57]. Additionally, physiological traits, i.e., stomatal conductance and transpiration were performed under drought and normal irrigation. In general, cultivars that withstand drought, i.e., Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. had a higher stomatal activity and transpiration than in a drought-sensitive ones, i.e., Anya cv. and Gala cv. and the stomatal conductance and transpiration were highly correlated with the tuber production. Meanwhile, these cultivars, i.e., Atlantic cv., Agata cv., Diamond cv., Kennebec cv., Russet Burbank cv. were the best suited to drought stress conditions and may be recommended for cultivation or as parenting materials for breeding programs to develop higher yielding cultivars. In order to further understand the underlying mechanisms of drought interference with potato growth and yield, an intermediate experiment with interim tuber development and production assessments may be more insightful and a dedicated more molecular, cellular and physiological analysis is suggested.

Conclusion

The study's main aim is to assess drought tolerance in 21 potato cultivars in vitro and in the field. Drought stress induced by various concentrations of sorbitol (0.1, 0.2, and 0.3 mol L^{-1}) in vitro and different regimes of soil moisture content (60, 40, and 20%) under field conditions exhibited fairly comparable impacts on the parameters studied. The interactions between the factors examined revealed that: potato cultivars differed significantly in their response to drought stress under in vitro and field conditions. In general, some cultivars were considerably more tolerant to drought stress treatments than others. Plant growth, physiological traits, potato tuber yield were all reduced by stress, and the reduction was much greater at the highest drought stress level (0.3 mol L^{-1} sorbitol in vitro and 20% soil moisture content under field conditions). There was a high association between in vitro and field trials for plant growth and tuber yield. The regulation of drought-related genes was different among the cultivars which have high and low stress tolerance index. Diamond, Kennebec, Russet Burbank, Atlantic and Agata cultivars are good candidates for inclusion in breeding programs for drought tolerance. Choosing the appropriate cultivar(s) is essential for achieving high quality and economic returns under stress. Because potato is a drought-sensitive adapted species, the best approaches to incorporating its drought-tolerance would be to (1) identify more genes involved in drought-tolerance mechanism, or (2) intercross drought-tolerant cultivars with drought-sensitive adapted germplasm and screen for drought tolerance and/or genes involved in drought tolerance. Research on both fronts is being pursued in our laboratory.

Abbreviations

STI: Stress tolerance index; DRO: Deeper rooting in potato; ERECTA: LRR receptor-like serine/threonine-protein kinase ERECTA; ERF: Ethylene response factor; DREB: Dehydration responsive element binding; StMYB: *Solanum tuberosum* MYB.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40538-021-00266-z.

Additional file 1: Table S1. Distribution of particle size and chemical properties of the experimental site soil. **Table S2.** List of primers of the selected genes used for RT-PCR.

Acknowledgements

Dr. Zaki is thankful to the Cultural Affairs & Missions, Ministry of Higher Education, Egypt, for the award of Post-doctoral Fellowship, and to the Laboratory of Plant Breeding, Faculty of Agriculture, Iwate University, Morioka, Iwate, Japan, for the invitation as Visiting Scientist.

Authors' contributions

HEMZ: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, supervision, validation, visualization, writing—original draft, writing—review and editing. KSAR: data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing. Both authors read and approved the final manuscript.

Funding

Not applicable.

Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

This manuscript is an original paper and has not been published in other journals. The authors agreed to keep the copyright rule.

Consent for publication

The authors agreed to the publication of the manuscript in CBTA journal.

Competing interests

The authors declare that they have no conflict of interest.

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Received: 9 July 2021 Accepted: 16 October 2021
Published online: 11 January 2022

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