agriculture

MDPI

Article

Response of Different Potato Genotypes to Drought Stress

Muhammad Waqar Nasir * and Zoltan Toth

Georgikon Campus Keszthely, Institute of Agronomy, Hungarian University of Agriculture and Life Sciences, 2100 Gödöllő, Hungary; Toth.zoltan@uni-mate.hu
* Correspondence: raow273@gmail.com; Tel.: +36-20-4398752

Abstract: A pot trial was established to evaluate the response of different potato genotypes to drought stress. Two potato genotypes (Demon and Hopehely) were exposed to two water levels (80% and 50% water holding capacity). The trial was replicated 16 times and 4 replications were harvested at 36 DAS, 54 DAS, 72 DAS, and 90 DAS. The results revealed that drought significantly reduced the growth and plant development of Demon (G1). Hopehely (G2) produced a higher yield in control as well as drought condition. Tuber yield positively correlated with tubers number, and root weight that was significantly higher in Hopehely under both experimental conditions. Hopehely produced a higher number of tubers (18) than Demon whereas Demon produced 11 tubers per plant. Moreover, under drought conditions, the relative water content of leaves and nitrogen content in foliage increased in Hopehely while decreased in Demon. Drought stress caused a 40% reduction in plant height and a 24.3% reduction in the number of leaves in Demon that was significantly higher than the 11% plant height reduction and 9.1% leaf count reduction in Hopehely. It was observed that the morphology of Hopehely (producing dwarf plants, fewer leaves, maintaining water content of leaves, producing more tubers) helped it to be a better drought-tolerant genotype compared to Demon.

Keywords: *Solanum tuberosum*; abiotic stress; relative water content; canopy development; nitrogen content; yield

Citation: Nasir, M.W.; Toth, Z. Response of Different Potato Genotypes to Drought Stress. *Agriculture* **2021**, *11*, 763. https://doi.org/10.3390/agriculture11080763

Academic Editor: Rachael Symonds

Received: 7 July 2021
Accepted: 9 August 2021
Published: 11 August 2021

1. Introduction

Potato (*Solanum tuberosum*) is the fifth most produced main crop in the world after sugar cane (*Saccharum officinarum*) wheat (*Triticum aestivum*), rice (*Oryza sativa*), and maize (*Zea mays*). Its production has increased from 314,208 thousand tonnes in 2007 to 388,191 thousand tonnes in 2017 [1]. Modern cultivars are successful in improving tuber yield [1], yet they are sensitive to drought. Drought is multidimensional stress as it affects physiology, morphology, ecology, biochemical and molecular traits of plants [2]. Potato has shallow roots that make it prone to drought resulting from limited water availability [3]. Several in vitro and field studies have been conducted to understand the effect of drought stress on potatoes [4–8]. Reduction in the number of shoots [5], plant height [5,6], leave numbers and area [9], stolons [10], root length, and expansion [5] have been reported in previous studies.

Plants have adopted various strategies to withstand drought stress through avoidance or tolerance [11]. However, it is very complicated to characterize drought tolerance in potato cultivars as the different yields of different cultivars are not related to specific physiological or morphological traits [8]. Different potato cultivars adapt to drought stress in different ways e.g., by higher assimilation portioning to tuber or by producing more tubers or by producing few but larger tubers [12]. Understanding the mechanism of potato response to drought stress is a challenge to enhance crop drought tolerance. Water scarcity enforces the need for potato genotypes identification that exhibits high tolerance to drought stress [4]. Widely used drought tolerance indicators in potatoes are leaf water content [13] and yield [14]. Leaves are involved in photosynthesis and account for most of the water loss via transpiration; therefore, better canopy development, such as leaf shape, leaf areas, number of leaves, and stem length indicates a drought tolerance in potatoes [6]. Under drought conditions leaf wilting is the most visual response to drought accompanied by a reduction in the number of leaves and stem length. Several agro-physiological parameters such as leaf area index, leaf area duration, chlorophyll content, and decrease in water loss have been established to be related to drought tolerance [15–17]. Moreover, root system development has important implications for plant development and survival under drought conditions, as they absorb water and dissolved nutrients. Potatoes having a shallow root system; therefore, drought tolerance partially depends on root development as well [18,19]. Potato cultivars with larger and more expanded root systems are more likely to be able to retrieve water from the soil; therefore, being less susceptible to periodic drought [20,21]. Measurement of the size and extent of the root system of different cultivars gives key information for breeding cultivars adapted to regions with frequent shortages of rainfall. That is why drought stress response of the genotypes can be observed by variation in several above ground and/or below ground plant development.

This study aimed to attempt to describe the differences between genotypes' responses to drought in terms of the agro-physiological parameters studied and to establish which characters were the most related to the yield and/or drought tolerance.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

To evaluate the effect of drought stress on potatoes a pot experiment was established in the greenhouse of Hungarian University of Agriculture and Life Sciences, Georgikon Campus Potato Research Centre, Keszthely, Hungary. For this purpose, soil and peat mixture (1:1 by weight) was used in 50 kg soil bearing pots (diameter at top = 41 cm; the height of pot = 40 cm) and a controlled environment (day/night temperature 25/21 °C, relative humidity 50%, and 18 h photoperiod) was maintained in the greenhouse. Two mid-late potato genotypes Demon (G1) and Hopehely (G2) were collected from Potato Research Centre, Keszthely, Hungary. Both genotypes are high-yielding and immune to potato Y and A virus, highly resistant to leaf drift virus. Both are moderately resistant to foliar phytophthora (*Phytophthora infestans*). Moreover, both are resistant to tuberculosis (*Mycobacterium tuberculosis*) and Ro1 and Ro4 potato nematode races.

2.2. Drought Stress Induction

Both genotypes were exposed to two water levels i.e., control (80% water holding capacity) and drought-stressed (50% water holding capacity). Drought stress was imposed at germination completion 18 days after sowing (DAS). Randomized complete block design (RCBD) was used with sixteen (16) replications. 5 kg pre-washed and dried gravel was used to line the pot base and was covered by a plastic net. A pipe was also embedded in the gravel for watering and aeration purposes. The remaining empty pot was filled with soil peat mixture (1:1 by weight). Soil from "A" horizon of a Eutric cambisol soil having a sandy clay loam texture was collected from the research farm area of the Hungarian University of Agriculture and Life Sciences, Georgikon Campus, and Baltic peat of low pH was brought from Latvia. Both soil and peat were sieved through a 10 mm sieve to obtain a finer and favorable growth medium. 10 kg of soil and 10 kg of peat were mixed using a cement mixer to obtain a homogenized mixture that was used as a growth medium in pots. The water holding capacity of the soil peat mixture was determined by the gravimetric method to quantify the amount of irrigation to be supplied to control and stressed pots. Pot weight was controlled weekly to ensure desired water level. 3 tubers per pot were sown. At germination completion (18 DAS) thinning was performed to maintain two plants per pot.

2.3. Sequential Harvesting

For growth analysis, 4 replications per treatment were harvested and sampled in 4 consecutive sampling times (S1–S4) during the experimental period on S1 (36 DAS), S2 (54 DAS), S3 (72 DAS), and S4 (90 DAS). Biomass was divided into leaves, stems, roots, and tubers. During 90 days experiment; data regarding plant height (cm), number of leaves per plant, -foliage fresh weight (g/plant), foliage dry matter (g), numbers of tuber per plant, tubers weight (g/plant), root length (cm), and root fresh weight (g/plant) were recorded manually at each harvesting (S1–S4).

Leaf area index (LAI) was measured at each harvesting by using the formula described by Watson, [22]

$$LAI = \frac{TOTAL\ LEAF\ AREA\ OF\ THE\ PLANT}{GROUND\ AREA\ OCCUPIED\ BY\ PLANT} \quad (1)$$

Leaf area duration (LAD) was measured at each harvesting by using the formula described by Power et al. [23]

$$LAD = \frac{LAI_1 + LAI_2}{2} \times (t_2 - t_1) \quad (2)$$

where t_1 and t_2 are the time of first and second sampling and LAI_1 and LAI_2 are leaf area index at t_1 and t_2 respectively.

2.4. Relative Water Content, Chlorophyll, and Nitrogen Contents Measurements

Relative water content (RWC) was measured at regular ten days intervals starting from first harvesting (36 DAS) up till senescence (76 DAS) by using the formula described by Barrs, [24]

$$RWC = \frac{FRESH\ LEAF\ WEIGHT\ (FW) - DRY\ LEAF\ WEIGHT\ (DW)}{TURGID\ LEAF\ WEIGHT\ (TW) - DRY\ LEAF\ WEIGHT\ (DW)} \times 100 \quad (3)$$

Chlorophyll content in leaves was determined weekly by using SPAD-502 with the method described by Li et al., [25]. SPAD values on the top leaflet, 1st side leaflets, and 2nd side leaflets of the 3rd, 4th, and 5th compound leaf from the apex, and at 3 points (top, middle and basal) within a leaflet were taken weekly after 45 DAS.

Nitrogen content (N%) in the foliage was also determined at each harvesting stage. To determine nitrogen content; foliage samples were sun-dried followed by oven drying. The dried samples were first ground using a Restch SN200 cutting mill and then further ground to dust-sized particles (10–50 µm) using Fritsch Analysette 3 Spartan Pulverisette 0. 100 mg ground samples were then placed in tin containers (8 mm × 55 mm) to deliver samples to Elementar Vario Macro Cube CHN analyzer (Germany) using 96 wells plates where N% was determined.

2.5. Measurement of Enzymatic Antioxidant Activity

For enzymatic antioxidant activity, leaf samples were collected at 72 DAS and stored at −52 °C. Enzymes were extracted by adapting the published method by Yasmeen et al. [26]. To extract the enzymes, 0.5 g leaf samples were homogenized in 5 mL of 50 mM phosphate buffer with pH 7.8. The homogenate was then centrifuged at 15,000× g at 4 °C for 20 min. The supernatant was used to measure the superoxide dismutase (SOD) activity and catalase (CAT) activity. SOD and CAT activity was determined by following the procedure described by Giannopolitis and Ries [27], and Chance and Maehly [28], respectively.

2.6. Statistical Analysis

SPSS/PASW Statistics for Windows, version 18 (SPSS Inc., Chicago, IL, USA) was used for statistical analysis. Experimental data were assessed for normality of distribution and homogeneity of variances. Analysis of variance (ANOVA) was performed to determine significant differences amongst treatments followed by Duncan's Multiple Range test to recognize specific differences amongst treatments. Pearson correlation was performed to determine the relationship between variables. A $p < 0.05$ was considered significant.

3. Results

Variance analysis showed that genotype, water availability, and their interaction significantly affect growth and yield contributing factors at the different developmental stages of potatoes. The most significant effects were observed at the tuber bulking stage (Table 1). Demon produced tallest plants but drought stress significantly reduced plant height in Demon while no significant effect was observed on plant height of Hopehely throughout the experiment. Thus, it suggests that under drought stress conditions plant height of Demon is reduced while Hopehely maintains its plant height. The number of leaves was also significantly affected by genotype and its interaction with water availability at each harvesting, however, drought stress showed a significant effect on leaves count only at the tuber bulking stage (72 DAS). Demon produced a significantly higher number of leaves under control as well as drought-stressed conditions. Drought stress significantly reduced leaf count in Demon at tuber bulking and senescence stage while Hopehely maintained its leaf count under stress conditions.

Table 1. Analysis of variance for growth and yield parameters of different potato genotypes under water stress conditions at different DAS (days after sowing).

		36 DAS			54 DAS			72 DAS			90 DAS		
		Mean Square	***F***	***p***	**Mean Square**	***F***	***p***	**Mean Square**	***F***	***p***	**Mean Square**	***F***	***p***
Plant Height	Genotype	1008.0	19.4	0.00	1056.2	12.0	0.00	992.2	6.1	0.02	637.5	3.9	0.06
	Water levels	324.0	6.2	0.02	576.0	6.5	0.02	2070.2	12.7	0.00	3108.0	19.3	0.00
	Genotype × Water levels	420.2	8.1	0.01	2500.0	28.5	0.00	4225.0	26.0	0.00	1425.0	8.8	0.01
No. of leaves per plant	Genotype	4128.0	53.1	0.00	6380.0	111.6	0.00	1225.0	22.5	0.00	3766.8	29.0	0.00
	Water levels	33.0	0.4	0.52	50.7	0.9	0.36	272.2	5.0	0.04	534.7	4.1	0.06
	Genotype × Water levels	25.0	0.3	0.58	13.1	0.2	0.64	264.0	4.8	0.04	244.1	1.8	0.19
Foliage fresh weight	Genotype	3048.4	2.1	0.16	626.4	0.3	0.59	13,343.1	13.7	0.00	349.2	0.1	0.69
	Water levels	138.3	0.1	0.75	356.4	0.1	0.68	20,934.5	21.5	0.00	36,945.6	16.8	0.00
	Genotype × Water levels	1407.1	0.9	0.33	11,357.7	5.5	0.03	19,164.9	19.7	0.00	5950.2	2.7	0.12
Foliage Dry Matter	Genotype	125.6	23.3	0.00	196.0	16.0	0.00	2.8	0.4	0.51	96.3	4.8	0.04
	Water levels	6.0	1.1	0.31	23.5	1.9	0.19	152.6	23.8	0.00	169.9	8.5	0.01
	Genotype × Water levels	1.0	0.2	0.66	1.0	0.1	0.77	147.2	22.9	0.00	43.2	2.1	0.16
No. of tubers per plant	Genotype	34.5	2.0	0.18	19.1	1.8	0.19	62.0	9.8	0.00	203.0	23.1	0.00
	Water levels	92.66	5.4	0.03	43.8	4.2	0.06	1.2	0.2	0.66	9.0	1.0	0.33
	Genotype × Water levels	70.1	4.1	0.06	87.8	8.5	0.01	0.1	0.02	0.88	1.0	0.1	0.74
Tuber yield	Genotype	18.9	1.9	0.18	424.9	0.3	0.58	53,113.0	35.3	0.00	159,251	10.6	0.00
	Water levels	25.0	2.6	0.13	6812.4	5.1	0.04	10,678.6	7.1	0.02	2977	0.2	0.66
	Genotype × Water levels	30.4	3.2	0.09	22,264.4	16.7	0.00	9450.3	6.3	0.02	35,245	2.4	0.15
Leaf Area Index	Genotype	11.5	7.0	0.02	13.9	4.8	0.04	0.01	0.0	0.96	0.2	0.07	0.80
	Water levels	0.1	0.1	0.80	1.1	0.4	0.53	8.5	0.9	0.34	38.1	13.1	0.00
	Genotype × Water levels	1.2	0.7	0.40	19.4	6.7	0.02	80.1	9.1	0.01	9.2	3.2	0.09

Table 1. *Cont.*

		36 DAS			54 DAS			72 DAS			90 DAS		
		Mean Square	***F***	***p***	**Mean Square**	***F***	***p***	**Mean Square**	***F***	***p***	**Mean Square**	***F***	***p***
Leaf Area Duration	Genotype	-	-	-	4132.2	14.0	0.00	1212.3	1.0	0.33	7.5	0.01	0.92
	Water levels	-	-	-	160.0	0.5	0.47	1296.9	1.1	0.31	6708.4	7.7	0.01
	Genotype × Water levels	-	-	-	2455.9	8.3	0.01	14,447.4	12.1	0.00	11,639.2	13.4	0.00
Root length	Genotype	9.0	0.8	0.38	6.2	1.0	0.33	52.5	3.2	0.09	132.2	2.9	0.11
	Water levels	2.2	0.2	0.66	9.0	1.4	0.25	33.0	2.0	0.18	1.0	0.02	0.88
	Genotype × Water levels	1.5	0.1	0.71	4.437×10^{-31}	0.0	1.00	0.5	0.03	0.85	6.2	0.1	0.71
Root fresh weight	Genotype	147.0	0.9	0.35	777.7	12.5	0.00	1611.0	109.7	0.00	643.8	30.5	0.00
	Water levels	1139.0	7.2	0.01	5.1	0.0	0.77	65.4	4.4	0.05	191.1	9.1	0.01
	Genotype × Water levels	50.7	0.3	0.58	40.1	0.6	0.43	0.2	0.01	0.91	16.0	0.7	0.40
Nitrogen content in foliage	Genotype	2.3	4.9	0.04	1.9	18.2	0.00	1.1	30.8	0.0	0.2	4.4	0.05
	Water levels	0.2	0.5	0.46	0.01	0.06	0.81	0.0	0.06	0.8	0.7	012.2	0.00
	Genotype × Water levels	1.3	2.8	0.11	0.1	1.6	0.22	0.1	3.4	0.08	0.1	2.27	0.15

Genotypes (Hopehely and Demon); Water levels (80% WHC and 50% WHC).

Genotype × water availability interaction significantly affected leaf area index (LAI) at each harvesting. At the early stage, variance in LAI was due to genotype while at senescence drought stress showed a significant effect on LAI. Drought stress significantly reduced the LAI of Demon while Hopehely maintained its LAI. Statistically equal LAI for genotypes at 3rd and 4th harvesting despite statistically different numbers of leaves suggests that Hopehely produced larger leaves to attain higher LAI. Hopehely reduced water loss under stress and maintained the highest relative water content (RWC) in leaves while in Demon; relative water content of leaves varied throughout the experiment and stressed plants showed the least RWC among all treatments (Figure 1). Similarly, higher and more uniform distribution of chlorophyll was also observed for Hopehely under control as well as stressed conditions (Figure 2). Moreover, significant differences were also observed for antioxidant activity (SOD and CAT). The highest SOD and CAT activity was recorded for drought-stressed Hopehely plants while the lowest antioxidant activity was observed for Demon under control conditions (Figure 3).

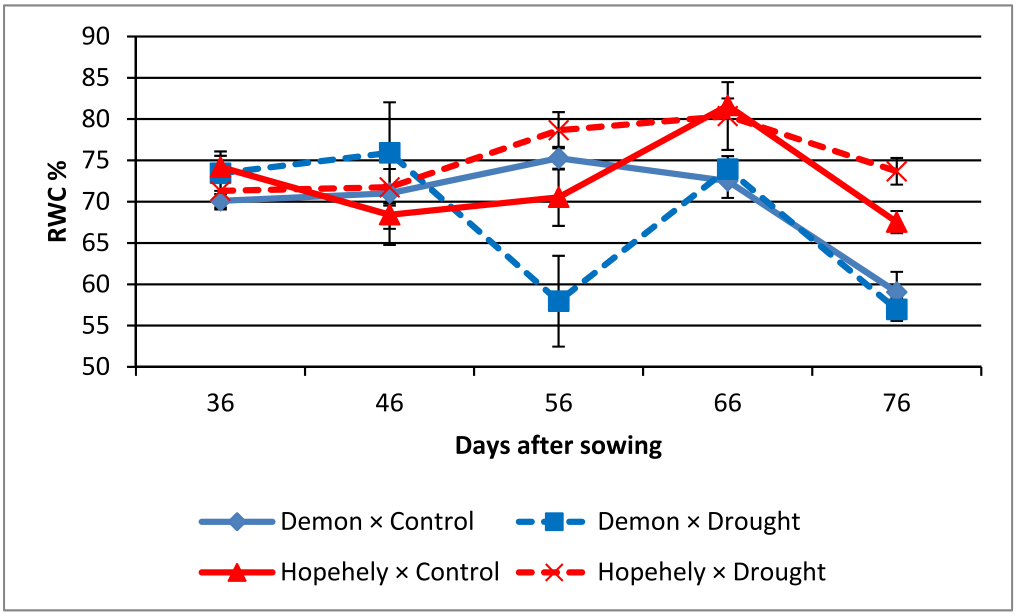

Figure 1. Relative water content of leaves in different potato genotypes observed under different water levels. Genotypes: Demon, Hopehely. Control: 80% Water holding capacity. Drought: 50% Water holding capacity. Relative Water Content (RWC) and error bars indicate the standard error.

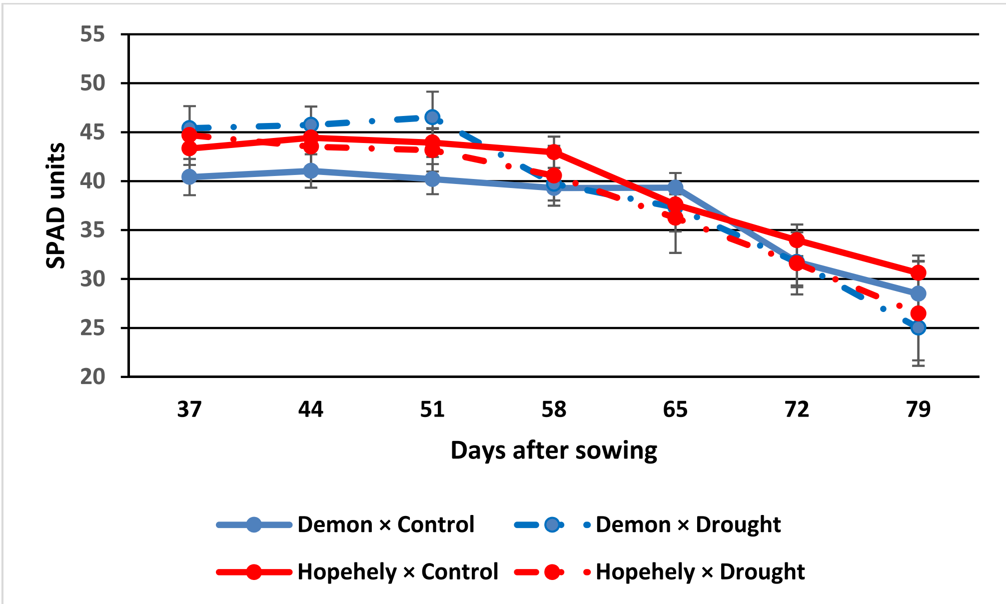

Figure 2. Chlorophyll concentration measured in SPAD units using SPAD-502 in different potato genotypes observed under different water levels. Genotypes: Demon, Hopehely. Control: 80% Water holding capacity. Drought: 50% Water holding capacity and error bars indicate the standard error.

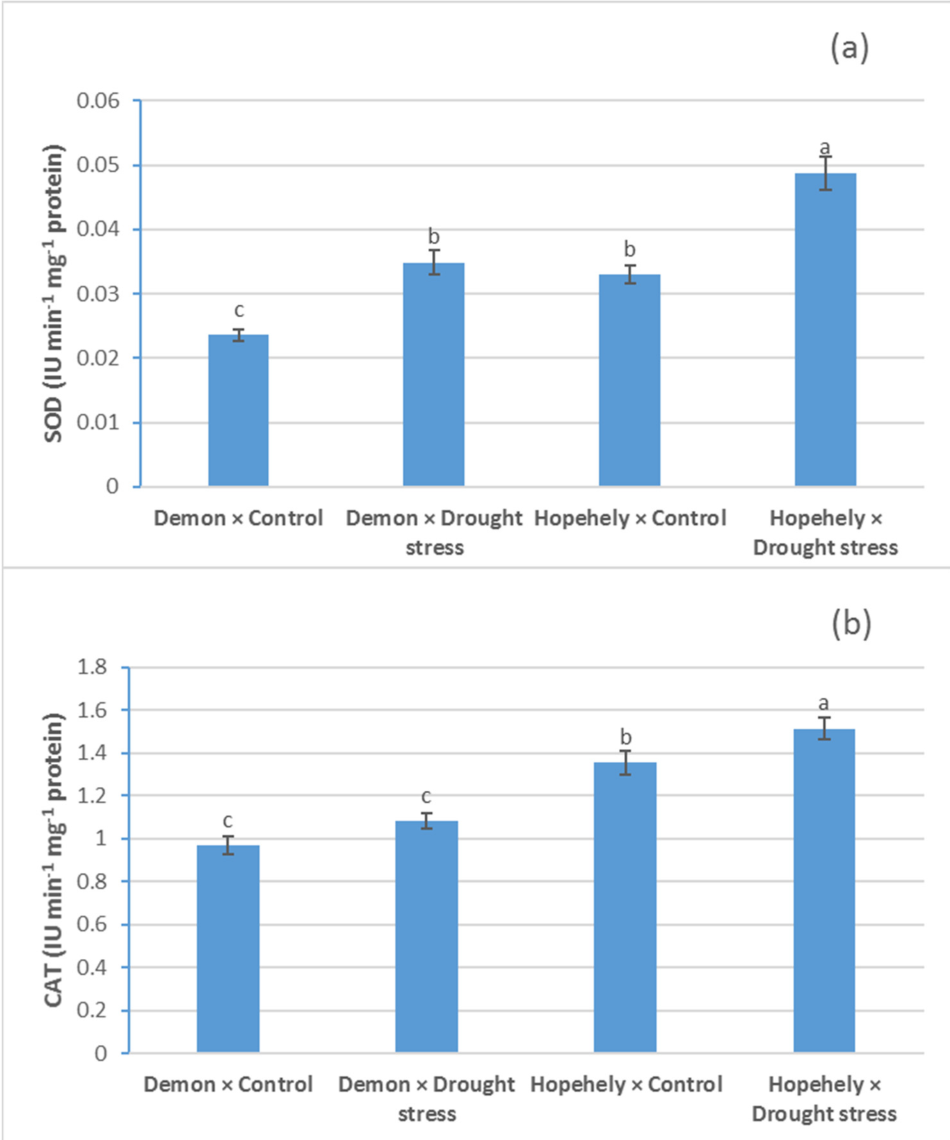

Figure 3. Antioxidant activity (SOD (**a**) and CAT (**b**) in the leaves of different potato genotypes grown under different water levels. a, b, and c indicate significant variation among means at a 5% probability level.

Above-ground biomass consisting of leaves and shoot started significantly decreasing for Demon under drought stress after flowering while no difference was observed for Hopehely. A significant effect of drought stress on foliage dry matter (FDM) was also observed after flowering, while at the early growth stage genotype showed a more significant effect on FDM. At the tuber bulking stage and senescence Demon produced the highest FDM and drought stress significantly reduced FDM of Demon while FDM produced by Hopehely under control and stress condition was statistically at par. This suggests that the difference in plant growth of above-ground parts was due to genotypic differences at the early stage while drought stress was more problematic after the tuber initiation stage. Moreover, the vegetative growth of Demon was reduced by drought stress while Hopehely was more resistant to drought stress (Tables 2 and 3).

Table 2. Meancomparison of growth and yield parameters of different potato genotypes at different water levels at 36 and 54 DAS (days after sowing).

	Plant Height (cm)	No. of Leaves	Foliage Fresh Weight (g)	Foliage Dry Matter (g)	Leaf Area Index	Root Length (cm)	Root Fresh Weight (g)	Number of Tubers	Tuber Fresh Weight (g)	Foliage Nitrogen Content (%)
					Tuber Initiation Stage (36 DAS)					
G1 [1]	78.375 a	69.938 a	307.13 a	21.796 a	7.2186 a	29.438 a	80.969 a	9.3750 a	4.2938 a	4.49 b
G2 [2]	62.500 b	37.813 b	279.52 a	16.192 b	5.5163 b	27.938 a	87.031 a	6.4375 a	2.1175 a	5.26 a
W1 [3]	74.938 a	55.313 a	296.27 a	18.380 a	6.4500 a	29.063 a	92.438 a	5.500 b	4.4562 a	5.0 a
W2 [4]	65.938 b	52.438 a	290.39 a	19.609 a	6.2849 a	28.313 a	75.563 b	10.313 a	1.9550 a	4.74 a
G1W1	88.000 a	72.625 a	319.45 a	20.927 a	7.5764 a	29.500 a	87.625 ab	4.875 b	1.6625 b	4.91 ab
G1W2	68.750 b	67.250 a	294.81 a	22.665 a	6.8608 ab	29.375 a	74.313 b	13.875 a	6.9250 a	4.06 b
G2W1	61.875 b	38.000 b	273.09 a	15.832 b	5.3237 b	28.625 a	97.250 a	6.125 b	2.2475 ab	5.09 ab
G2W2	63.125 b	37.625 b	285.96 a	16.552 b	5.709 ab	27.250 a	76.813 b	6.750 b	1.9875 b	5.42 a
					Flowering Stage (54 DAS)					
G1	99.000 a	87.813 a	355.94 a	32.015 a	9.5286 a	30.500 a	39.169 a	15.000 a	242.81 a	2.94 b
G2	82.750 b	47.875 b	343.43 a	25.015 b	7.6595 b	29.250 a	25.225 b	17.188 a	253.12 a	3.64 a
W1	96.875 a	69.625 a	344.96 a	27.301 a	8.8629 a	30.625 a	32.763 a	14.438 a	227.33 b	3.27 a
W2	84.875 b	66.063 a	354.40 a	29.729 a	8.3252 a	29.125 a	31.631 a	17.750 a	268.60 a	3.31 a
G1W1	117.50 a	90.500 a	377.86 a	30.550 ab	10.899 a	31.250 a	27.375 bc	11.000 b	184.88 c	3.03 bc
G1W2	80.50 b	85.125 a	334.01 a	33.480 a	8.158 b	29.750 a	23.075 c	19.000 a	300.75 a	2.86 c
G2W1	76.25 b	48.750 b	312.06 a	24.052 c	6.827 b	30.000 a	38.150 ab	19.000 a	269.79 ab	3.51 ab
G2W2	89.25 b	47.000 b	374.79 a	25.977 bc	8.492 ab	28.500 a	40.188 a	16.500 a	236.45 bc	3.76 a

Means followed by different letters in the same column are significantly different at a 5% probability level. Genotypes: [1] Demon (G1). [2] Hopehely (G2). [3] 80% Water holding capacity (W1). [4] 50% Water holding capacity (W2).

Table 3. Mean comparison of growth and yield parameters of different potato genotypes at different water levels at 72. and 90 DAS (days after sowing).

	Plant Height (cm)	No. of Leaves	Foliage Fresh Weight (g)	Foliage Dry Matter (g)	Leaf Area Index	Root Length (cm)	Root Fresh Weight (g)	Number of Tubers	Tuber Fresh Weight (g)	Foliage Nitrogen Content (%)
					Tuber Bulking Stage (72 DAS)					
G1 [1]	99.63 a	66.68 a	302.73 b	28.00 a	10.51 a	26.50 a	15.88 b	12.69 b	378.43 b	2.44 b
G2 [2]	83.88 b	49.18 b	360.49 a	27.16 a	10.44 a	30.12 a	35.95 a	16.62 a	493.66 a	2.97 a
W1 [3]	103.13 a	62.06 a	367.78 a	30.67 a	11.21 a	26.87 a	27.94 a	14.94 a	461.88 a	2.73 a
W2 [4]	80.38 b	53.81 b	295.44 b	24.49 b	9.74 a	29.75 a	23.90 a	14.38 a	410.21 b	2.70 a
G1W1	127.25 a	74.87 a	373.51 a	34.13 a	13.48 a	25.25 b	17.80 b	12.87 b	379.96 c	2.54 b
G1W2	72.00 b	58.50 b	231.95 b	21.88 c	7.54 b	27.75 ab	13.97 b	12.50 b	376.90 c	2.34 b
G2W1	79.00 b	49.25 b	362.05 a	27.21 b	8.94 ab	28.50 ab	38.08 a	17.00 a	543.80 a	2.89 a
G2W2	88.75 b	49.12 b	358.93 a	27.10 b	11.95 ab	31.75 a	33.82 a	16.25 ab	443.53 b	3.05 a
					Senescence (90 DAS)					
G1	95.13 a	70.31 a	215.99 a	26.12 a	5.588 a	32.37 a	17.39 b	11.75 b	497.82 b	1.40 a
G2	82.50 a	39.62 b	206.64 a	21.22 b	5.806 a	26.62 a	30.08 a	18.87 a	631.54 a	1.65 a
W1	102.75 a	60.75 a	259.37 a	26.93 a	7.241 a	29.75 a	27.19 a	14.56 a	583.95 a	1.73 a
W2	74.88 b	49.18 a	163.26 b	20.41 b	4.154 b	29.25 a	20.28 b	16.06 a	545.42 a	1.32 b
G1W1	118.50 a	80.00 a	283.32 a	31.03 a	7.892 a	33.25 a	19.85 bc	11.25 b	503.06 b	1.70 a
G1W2	71.75 b	60.62 b	148.65 c	21.22 b	3.286 c	31.50 a	14.94 c	12.25 b	492.59 b	1.11 b
G2W1	87.00 b	41.50 c	235.41 ab	22.83 b	6.590 ab	26.25 a	34.54 a	17.87 a	664.84 a	1.77 a
G2W2	78.00 b	37.75 c	177.88 bc	19.60 b	5.022 bc	27.00 a	25.62 b	19.88 a	598.25 ab	1.54 a

Means followed by different letters in the same column are significantly different at a 5% probability level. Genotypes: [1] Demon (G1). [2] Hopehely (G2). [3] 80% Water holding capacity (W1). [4] 50% Water holding capacity (W2).

Genotype and its interaction with water availability significantly affected tuber yield at different harvesting stages. Under well-watered as well as drought stress conditions, maximum tuber yield was observed for Hopehely, while lowest tuber yield was observed for Demon under drought stress conditions. The number of tubers produced was also significantly higher in Hopehely, however, the maximum number of tubers were produced by Hopehely under drought stress conditions followed by well-watered Hopehely. The demon under well-watered conditions produced the least number of tubers. Thus, it seems that tuber yield is reduced under drought stress, but plants try to cope with it by producing a greater number of tubers and vary significantly in the potential to produce the number of tubers thus tuber yield. No significant difference was observed for root length at any harvesting; however, root weight was significantly affected by genotype, water availability, and their interaction particularly at senescence. Hopehely produced significantly heavier roots than Demon at the tuber bulking and senescence stage. Drought stress significantly affected root fresh weight of Hopehely only, at first and last harvesting (Tables 2 and 3). Correlation showed that utilization of photosynthates in above-ground biomass production reduces tuber yield. Above-ground biomass positively correlated with plant height, number of leaves, leaf area index, and foliage dry matter. Tuber yield significantly increased with an increase in the number of tubers, root weight, and nitrogen content in foliage (Table 4).

Table 4. Pearson correlation among growth and yield contributing parameters at different DAS (days after sowing).

	Tuber Yield				**Above-Ground Biomass**			
	36 DAS	**54 DAS**	**72 DAS**	**90 DAS**	**36 DAS**	**54 DAS**	**72 DAS**	**90 DAS**
Tuber yield	1	1	1	1	−0.337	−0.563 *	0.482	0.191
Plant height	−0.231	−0.738 **	−0.365	−0.1	0.523 *	0.759 **	0.548 *	0.836 **
Number of leaves per plant	0.337	−0.196	−0.341	−0.411	0.528 *	0.302	0.151	0.566 *
Number of tubers per plant	0.897 **	0.603 *	0.508 *	0.606 *	−0.239	−0.14	0.229	0.023
Leaf area index	−0.308	−0.774 **	−0.241	0.362	0.765 **	0.729 **	0.509 *	0.962 **
Above-ground dry matter	0.338	−0.072	0.118	−0.078	0.683 **	0.514 *	0.833 **	0.908 **
Root length	0.295	0.006	0.09	−0.433	−0.05	0.161	−0.144	0.041
Root fresh weight	−0.431	−0.124	0.838 **	0.695 **	0.014	0.269	0.566 *	0.331
Foliage N %	−0.499 *	−0.173	0.508 *	0.328	0.124	0.005	0.500 *	0.174

* significantly different at $p \leq 0.05$. ** significantly different at $p \leq 0.01$.

4. Discussion

Drought tolerance in plants is a complex mechanism based on several factors. However, several phenological parameters have been discussed in previous studies [16,17,29] to determine the drought tolerance ability of a plant. Potato genotypes vary in phenotypic response to drought stress that can help them in tolerating drought stress leading to a better-sustained yield. This study was conducted in an attempt to describe which agro-physiological characters were the most related to yield and drought tolerance.

Reduction in plant height and leaf area is the first morphological symptom of drought stress in potatoes [30], followed by lesser canopy expansion and earlier senescence [31–33]. These results were confirmed in the present study where drought stress significantly reduced plant height, the number of leaves per plant, and leaf area index. Early senescence under drought stress was also observed in Demon that can be justified by the reduction in leaf area duration. Leaf size and retention account for LAI and LAD respectively, that directly affect tuber yield [34] and foliage dry matter [35] respectively. Moreover, LAI and LAD are more affected in later cultivars than earlier cultivars and have been reported as a major determinant of potato yield in previous studies [36–38]. Therefore, drought stress exhibited an inhibitory effect on the yield of potato genotypes by affecting growth and yield-related factors [12].

Between genotypes, Demon and Hopehely completely differed in plant establishment. Most of the above-ground characteristics i.e., plant height, number of leaves per plant, FDM, LAD were significantly better developed in Demon. Taller plants, higher number of leaves, and leaf area index directly contributed towards biomass production that in turn enhanced above-ground biomass of Demon, which on drying produced higher foliage dry matter

(FDM) content. The increase in leaf number in Demon was likely associated with the taller plant that provided with internodes elongation allowing more leaves from the apex of the plant to be exposed [39]. Leaf size was another reason for the high leaf number in Demon due to the size/number trade-off as smaller leaves are found on species that produce more of them. Westoby & Wright [40] also reported a negative relationship between the number of leaves per shoot and individual leaf area. Relatively small leaves, because of higher heat exchange capacity, are considered to be advantageous in hot, dry, high light, and low nutrient environments [41–43]. It can be the reason for significantly higher leaf area duration in Demon. These results are in line with [44] who showed genotypic differences in the ability to maintain leaf expansion with increasing soil moisture deficit. FDM being positively correlated with plant height and the number of leaves was also higher in Demon [45]. The least tuber yield was observed for Demon. It can be due to lower RWC, N%, and chlorophyll concentration that shows the inefficiency of Demon plants to produce higher assimilates. No correlation (R^2 = 0.399) was observed between above-ground parts and tuber yield that also justifies lower yield of Demon despite significantly better vegetative growth. It showed that assimilates produced during vegetative growth were may be utilized to produce biological yield (foliage) instead of tuber yield. On the other hand, underground parts i.e., root fresh weight, number of tubers per plant, tubers weight per plant were significantly higher in Hopehely. Hopehely developed a dense root system at the early stage of plant development that helped in better uptake and utilization of water and nutrients. Because of limited space available for root growth; no significant difference was observed for root length of the 2 genotypes but a significant difference was observed for root fresh weight that shows better uptake of water and nitrogen leading to better relative water content and nitrogen % in the foliage under both control and drought conditions. A greater and deeper root system is more drought-tolerant [18]. Zarzyńska et al. [46] reported that root density and LAI are determinant for yield. Besides a better and more developed root system; fewer and thicker leaves were also the reason for the high relative leaf water content in Hopehely as the large leaf has fitness benefits derived from a greater boundary layer thickness for heat exchange, thus maximizing photosynthetic activity [47]. A thick waxing layer on larger leaves reduces water losses thus maintaining higher leaf relative water content which is a drought tolerance characteristic [48–50]. Higher chlorophyll concentration and N% in the foliage were also observed which shows a higher photosynthetic activity in Hopehely. Drought adaptation strategy in potatoes includes but is not limited to higher assimilate partitioning to tubers, producing larger tubers, or more tubers [12]. Hopehely produced heavier tubers indicating a high assimilate partitioning to tubers. However, under drought conditions, Hopehely produced more tubers to ensure a better yield. These results are in line with another drought adapting strategy in potatoes where potatoes produce larger tubers or more tubers to sustain the yield [15]. Besides higher RWC and better-developed root system, an increase in SOD and CAT activity in Hopehely also suggests a strong defense mechanism that can help in drought tolerance leading to higher yield [51,52]. Yang and Poovaiah [53] also reported that SOD and CAT scavenge reactive oxygen species produced under stress conditions that help the plant to tolerate stress.

5. Conclusions

The present study provided insights on the phenological response of *Solanum tuberosum* to drought stress using two genotypes, 'Demon and Hopehely', common in Hungary. Although drought stress showed an inhibitory effect on the growth of both genotypes, yet all plants tolerated drought stress throughout their growth period starting from germination completion. Morphological development of understudy genotypes varied significantly. The drought tolerance mechanism of Demon involved reduction in plant height and the number of leaves to minimize water loss by transpiration and reducing the growth period (i.e., early senescence) but it also affected yield and yield-related parameters. On the other hand, the drought tolerance mechanism of Hopehely involved the production of a denser root system to ensure better uptake of water, producing fewer leaves and maintaining higher relative water content, and increase in the number of tubers produced per plant under drought stress to ensure a sustainable yield. Moreover, significantly higher enzymatic antioxidant activity in leaves of Hopehely also suggests better drought tolerance. Therefore, it can be concluded that cultivars with a better-developed root system and thicker, and fewer leaves are the most related agro-physiological characters to the yield and drought tolerance in potatoes. Moreover, the results also supported the idea of Hopehely being morphologically more drought tolerant than Demon. Although, drought tolerance is a complex mechanism that cannot be described by phenological response only, yet, this study provides the basis to continue the project for a transcriptomic investigation to analyze understudy genotypes for differential gene expression.

Author Contributions: Conceptualization, M.W.N. and Z.T.; methodology, M.W.N.; software, M.W.N.; validation, M.W.N. and Z.T.; formal analysis, Z.T.; investigation, M.W.N.; resources, Z.T.; data curation, M.W.N.; writing—original draft preparation, M.W.N.; writing—review and editing, Z.T.; visualization, M.W.N. and Z.T.; supervision, Z.T.; project administration, Z.T.; funding acquisition, Z.T. Both authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the Hungarian Government and the European Union, with the co-funding of the European Regional Development Fund in the frame of the Széchenyi 2020 Programme GINOP-2.3.2-15-2016-00054 project.

Institutional Review Board Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest. Moreover, the funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

References

1. FAO. *World Food and Agriculture—Statistical Pocketbook*; FAO: Rome, Italy, 2018.
2. Salehi-Lisar, S.Y.; Bakhshayeshan-Agdam, H. Drought stress in plants: Causes, consequences, and tolerance. In *Drought Stress Tolerance in Plants*; Springer: Berlin/Heidelberg, Germany, 2016; Volume 1, pp. 1–16.
3. Watkinson, J.I.; Hendricks, L.; Sioson, A.; Heath, L.S.; Bohnert, H.J.; Grene, R. Tuber development phenotypes in adapted and acclimated, drought-stressed Solanum tuberosum ssp. andigena have distinct expression profiles of genes associated with carbon metabolism. *Plant Physiol. Biochem.* **2008**, *46*, 34–45. [CrossRef]
4. Drought Tolerance in Potato (S. tuberosum, L.): Can We Learn from Drought Tolerance Research in Cereals? ScienceDirect. Available online: https://www.sciencedirect.com/science/article/pii/S0168945213000204?casa_token=WKsm3FB6g3wAAAAA:jE_YSQ1lHmD3A7LclzFENQ3kUqj252_V4MQMXOKSVji-YVfOd0vmHm68ypjcTO4SeProJNzLWiM (accessed on 6 November 2020).
5. Albiski, F.; Najla, S.; Sanoubar, R.; Alkabani, N.; Murshed, R. In vitro screening of potato lines for drought tolerance. *Physiol. Mol. Biol. Plants* **2012**, *18*, 315–321. [CrossRef]
6. Schittenhelm, S.; Sourell, H.; Löpmeier, F.-J. Drought resistance of potato cultivars with contrasting canopy architecture. *Eur. J. Agron.* **2006**, *24*, 193–202. [CrossRef]
7. Hassanpanah, D. Evaluation of potato cultivars for resistance against water deficit stress under in vivo conditions. *Potato Res.* **2010**, *53*, 383–392. [CrossRef]
8. Stark, J.C.; Love, S.L.; King, B.A.; Marshall, J.M.; Bohl, W.H.; Salaiz, T. Potato cultivar response to seasonal drought patterns. *Am. J. Potato Res.* **2013**, *90*, 207–216. [CrossRef]
9. Jefferies, R.; MacKerron, D. Radiation interception and growth of irrigated and droughted potato (Solanum tuberosum). *Field Crop. Res.* **1989**, *22*, 101–112. [CrossRef]
10. Haverkort, A.J.; Van De Waart, M.; Bodlaender, K.B.A. The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions. *Potato Res.* **1990**, *33*, 89–96. [CrossRef]
11. Yue, B.; Xue, W.; Xiong, L.; Yu, X.; Luo, L.; Cui, K.; Jin, D.; Xing, Y.; Zhang, Q. Genetic basis of drought resistance at reproductive stage in rice: Separation of drought tolerance from drought avoidance. *Genetics* **2006**, *172*, 1213–1228. [CrossRef] [PubMed]
12. Deblonde, P.; Ledent, J. Effects of moderate drought conditions on green leaf number, stem height, leaf length and tuber yield of potato cultivars. *Eur. J. Agron.* **2001**, *14*, 31–41. [CrossRef]
13. Omae, H.; Kumar, A.; Egawa, Y.; Kashiwaba, K.; Shono, M. Midday drop of leaf water content related to drought tolerance in snap bean (Phaseolus vulgaris L.). *Plant Prod. Sci.* **2005**, *8*, 465–467. [CrossRef]
14. Farshadfar, E.; Elyasi, P. Screening quantitative indicators of drought tolerance in bread wheat (Triticum aestivum, L.) landraces. *Eur. J. Experiment. Biol.* **2012**, *2*, 577–584.

15. Deblonde, P.; Haverkort, A.; Ledent, J. Responses of early and late potato cultivars to moderate drought conditions: Agronomic parameters and carbon isotope discrimination. *Eur. J. Agron.* **1999**, *11*, 91–105. [CrossRef]
16. Khan, M.A.; Saravia, D.; Munive, S.; Lozano, F.; Farfan, E.; Eyzaguirre, R.; Bonierbale, M. Multiple QTLs Linked to agro-morphological and physiological traits related to drought tolerance in potato. *Plant Mol. Biol. Rep.* **2014**, *33*, 1286–1298. [CrossRef]
17. Lahlou, O.; Ouattar, S. The effect of drought and cultivar on growth parameters, yield and yield components of potato. *Agronomy* **2003**, *23*, 257–268. [CrossRef]
18. Iwama, K. Physiology of the Potato: New insights into root system and repercussions for crop management. *Potato Res.* **2008**, *51*, 333–353. [CrossRef]
19. Joshi, M.; Fogelman, E.; Belausov, E.; Ginzberg, I. Potato root system development and factors that determine its architecture. *J. Plant Physiol.* **2016**, *205*, 113–123. [CrossRef] [PubMed]
20. Wishart, J.; George, T.S.; Brown, L.K.; Ramsay, G.; Bradshaw, J.E.; White, P.J.; Gregory, P.J. Measuring variation in potato roots in both field and glasshouse: The search for useful yield predictors and a simple screen for root traits. *Plant Soil* **2012**, *368*, 231–249. [CrossRef]
21. Villordon, A.Q.; Ginzberg, I.; Firon, N. Root architecture and root and tuber crop productivity. *Trends Plant Sci.* **2014**, *19*, 419–425. [CrossRef] [PubMed]
22. Watson, D.J. Comparative physiological studies on the growth of field crops: I. variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot.* **1947**, *11*, 41–76. [CrossRef]
23. Power, J.F.; Willis, W.O.; Grunes, D.L.; Reichman, G.A. Effect of soil temperature, phosphorus, and plant age on growth analysis of barley 1. *Agron. J.* **1967**, *59*, 231–234. [CrossRef]
24. Barrs, H.D. Determination of water deficits in plant tissues. *Water Defic. Plant Growth* **1968**, *1*, 235–368.
25. Li, L.; Qin, Y.; Liu, Y.; Hu, Y.; Fan, M. Leaf positions of potato suitable for determination of nitrogen content with a SPAD meter. *Plant Prod. Sci.* **2012**, *15*, 317–322. [CrossRef]
26. Yasmeen, A.; Nouman, W.; Basra, S.M.A.; Wahid, A.; Rehman, H.U.; Hussain, N.; Afzal, I. Morphological and physiological response of tomato (Solanum lycopersicum L.) to natural and synthetic cytokinin sources: A comparative study. *Acta Physiol. Plant* **2014**, *36*, 3147–3155. [CrossRef]
27. Giannopolitis, C.N.; Ries, S.K. Superoxide dismutases: I. occurrence in higher plants. *Plant Physiol.* **1977**, *59*, 309–314. [CrossRef]
28. Chance, B.; Maehly, A. Assay of catalases and peroxidases. *Methods Enzym.* **1955**, *2*, 764–775. [CrossRef]
29. Sprenger, H.; Kurowsky, C.; Horn, R.; Erban, A.; Seddig, S.; Rudack, K.; Fischer, A.; Walther, D.; Zuther, E.; Köhl, K.; et al. The drought response of potato reference cultivars with contrasting tolerance. *Plant Cell Environ.* **2016**, *39*, 2370–2389. [CrossRef]
30. Fleisher, D.H.; Timlin, D.; Reddy, V. Elevated carbon dioxide and water stress effects on potato canopy gas exchange, water use, and productivity. *Agric. For. Meteorol.* **2008**, *148*, 1109–1122. [CrossRef]
31. Ahmadi, S.H.; Andersen, M.N.; Plauborg, F.; Poulsen, R.T.; Jensen, C.R.; Sepaskhah, A.R.; Hansen, S. Effects of irrigation strategies and soils on field grown potatoes: Yield and water productivity. *Agric. Water Manag.* **2010**, *97*, 1923–1930. [CrossRef]
32. De Oliveira, J.S.; Brown, H.E.; Gash, A.; Moot, D.J. An explanation of yield differences in three potato cultivars. *Agron. J.* **2016**, *108*, 1434–1446. [CrossRef]
33. Obidiegwu, J.E.; Bryan, G.J.; Jones, H.G.; Eprashar, A. Coping with drought: Stress and adaptive responses in potato and perspectives for improvement. *Front. Plant Sci.* **2015**, *6*, 542. [CrossRef]
34. Najm, A.; Haj Seyed Hadi, M.; Fazeli, F.; Darzi, M.; Shamorady, R. Effect of Utilization of organic and inorganic nitrogen source on the potato shoots dry matter, leaf area index and plant height, during middle stage of growth. *World Acad. Sci. Eng. Technol.* **2010**, *47*, 900–903.
35. Chang, D.C.; Jin, Y.I.; Nam, J.H.; Cheon, C.G.; Cho, J.H.; Kim, S.J.; Yu, H.-S. Early drought effect on canopy development and tuber growth of potato cultivars with different maturities. *Field Crop. Res.* **2018**, *215*, 156–162. [CrossRef]
36. Gaur, D.; Singh, S.P.; Sharma, K.; Sharma, S.K.; Dhakad, H.; Dangi, R.S.; Patidar, R.; Sharma, R.; Dixit, J.P.; Rawat, G.S. Effect of different phosphorus levels on growth attributes physiological parameter and grading of tuber in potato crop (Solanum tuberosum, L.). *Int. J. Chem. Stud.* **2017**, *5*, 215–219.
37. Salavati, S.; Valadabadi, S.A.; Parvizi, K.H.; Sayfzadeh, S.; Hadidi Masouleh, E. The effect of super-absorbent polymer and sowing depth on growth and yield indices of potato (Solanum tuberosum L.) in hamedan province, Iran. *Appl. Ecol. Environ. Res.* **2018**, *16*, 7063–7078. [CrossRef]
38. Pourasadollahi, A.; Siosemardeh, A.; Hosseinpanahi, F.; Sohrabi, Y. Physiological and Agro-Morphological Response of Potato to Drought Stress and Hormone Application. *J. Plant Physiol. Breed.* **2019**, *9*, 47–61.
39. Tadesse, M.; Lommen, W.; van der Putten, P.; Struik, P. Development of leaf area and leaf number of micropropagated potato plants. *NJAS Wagening J. Life Sci.* **2001**, *49*, 15–32. [CrossRef]
40. Westoby, M.; Wright, I. The leaf size—Twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia* **2003**, *135*, 621–628. [CrossRef]
41. Ackerly, D.; Knight, C.; Weiss, S.; Barton, K.; Starmer, K. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: Contrasting patterns in species level and community level analyses. *Oecologia* **2002**, *130*, 449–457. [CrossRef] [PubMed]
42. Bragg, J.G.; Westoby, M. Leaf size and foraging for light in a sclerophyll woodland. *Funct. Ecol.* **2002**, *16*, 633–639. [CrossRef]

43. McDonald, P.G.; Fonseca, C.R.; Overton, J.M.; Westoby, M. Leaf-size divergence along rainfall and soil-nutrient gradients: Is the method of size reduction common among clades? *Funct. Ecol.* **2003**, *17*, 50–57. [CrossRef]
44. Kebede, Z.; Mekbib, F.; Abebe, T.; Asfaw, A. Evaluation of leaf-water relation traits, as selection criterion for developing drought resistant potato (Solanum tuberosum, L.) genotypes. *Rev. Plant Stud.* **2019**, *6*, 1–10. [CrossRef]
45. Masarirambi, M.T.; Mandisodza, F.C.; Mashingaidze, A.B.; Bhebhe, E. Influence of plant population and seed tuber size on growth and yield components of potato (Solanum tuberosum). *Int. J. Agric. Biol.* **2012**, *14*, 7.
46. Zarzyńska, K.; Boguszewska-Mańkowska, D.; Nosalewicz, A. Differences in size and architecture of the potato cultivars root system and their tolerance to drought stress. *Plant Soil Environ.* **2017**, *63*, 159–164.
47. Banik, P.; Zeng, W.; Tai, H.; Bizimungu, B.; Tanino, K. Effects of drought acclimation on drought stress resistance in potato (Solanum tuberosum L.) genotypes. *Environ. Exp. Bot.* **2016**, *126*, 76–89. [CrossRef]
48. Anithakumari, A.M.; Dolstra, O.; Vosman, B.; Visser, R.G.F.; van der Linden, C.G. In vitro screening and QTL analysis for drought tolerance in diploid potato. *Euphytica* **2011**, *181*, 357–369. [CrossRef]
49. Anithakumari, A.M.; Nataraja, K.N.; Visser, R.G.F.; Van Der Linden, C.G. Genetic dissection of drought tolerance and recovery potential by quantitative trait locus mapping of a diploid potato population. *Mol. Breed.* **2012**, *30*, 1413–1429. [CrossRef]
50. Vasquez-Robinet, C.; Mane, S.; Ulanov, A.V.; Watkinson, J.I.; Stromberg, V.K.; De Koeyer, D.; Schafleitner, R.; Willmot, D.B.; Bonierbale, M.; Bohnert, H.J.; et al. Physiological and molecular adaptations to drought in Andean potato genotypes. *J. Exp. Bot.* **2008**, *59*, 2109–2123. [CrossRef]
51. Mittler, R. Oxidative stress, antioxidants and stress tolerance. *Trend Plant Sci.* **2002**, *7*, 405–410. [CrossRef]
52. Yasmeen, A.; Basra, S.M.A.; Farooq, M.; Rehman, H.U.; Hussain, N.; Athar, H. Exogenous application of moringa leaf extract modulates the antioxidant enzyme system to improve wheat performance under saline conditions. *Plant Growth Regul.* **2012**, *69*, 225–233. [CrossRef]
53. Yang, T.; Poovaiah, B.W. An early ethylene up-regulated gene encoding a calmodulin-binding protein involved in plant senescence and death. *J. Biol. Chem.* **2000**, *275*, 38467–38473. [CrossRef]