Potato Research
https://doi.org/10.1007/s11540-024-09720-5

Soil Water Stress Effects on Potato Tuber Starch Quality Formation

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Received: 1 April 2023 / Accepted: 13 March 2024

Abstract

Soil water stress has a significant impact on crop physiology, however, the specific response of starch quality formation in potato tubers remains unreported. Here, two potato (*Solanum tuberosum* L.) varieties, one with high, and the other with low tuber starch content, were grown in pots under three different soil water stress treatments, maintaining 75, 50 and 25% of soil field capacity, respectively. Soil water stress restricted potato plant growth and development, and severe stress reduced tuber yield by 47.8% relative to the control. It also inhibited tuber starch biosynthesis, which declined by 62.4% (AGPase activity) relative to the control. Furthermore, water stress reduced tuber starch accumulation by 23.6% (total starch content) relative to the control, and finally, it shortened the tuber starch gelatinization process by 1.44% (pasting temperature) compared to the control. These results reflect the soil water stress regulation mechanism on starch formation and potato tuber quality. Moreover, the study provides a scientific basis for breeding of varieties with high starch content, for improving starch quality and high-efficiency cultivation in dryland potato production.

Keywords Photosynthesis · Starch synthesis key enzyme · Starch content · Starch gelatinization

Yong Zhen Ma and Nian Pan contributed equally to this work.

Key Points Soil water stress restricted the growth and development of potato plant.
Soil water stress inhibited the biosynthesis of tuber starch.
Soil water stress reduced the accumulation of tuber starch.
Soil water stress shortened the gelatinization process of tuber starch.

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Published online: 12 April 2024

Introduction

Potato is the fourth largest food crop globally, with 18.13 million hectares and 353.53 million tons produced in 2021 (FAO), which is only inferior to rice, wheat and corn. With climate warming, drought stress frequency has increased annually (Adesina & Thomas 2020), and poses a serious threat to the world's potato production and food security (Su & Wang 2019).

Currently, as the effects of climate change become more extreme, water availability is one of the main factors limiting potato production (Alvarez-Morezuelas et al. 2022); drought resistance studies mainly focus on evaluation of germplasm resources (Cabello et al. 2012; Stark et al. 2013), responses of the reactive oxygen system (Alhoshan et al. 2019; Boguszewska et al. 2010), transcriptome / metabolome / proteome analysis (Aliche et al. 2022; Boguszewska- Mańkowska et al. 2020; Evers et al. 2010; Zhang et al. 2014), functional identification of gene or transcription factors (Shin et al. 2011; Wang et al. 2017), yield and physiological indicator changes (Rudack et al. 2017; Wagg et al. 2021). Starch synthesis and accumulation research has mainly focused on identifying key enzyme gene functions in starch synthesis (Edwards et al. 1999; Fulton et al. 2002; Schwall et al. 2000; Tiessen et al. 2002), and exploring new genes or proteins involved in potato tuber starch biosynthesis (Albrecht et al. 2001; Davis et al. 2003).

Accordingly, most research reports describe physical and chemical methods, often used to change potato starch quality (Fornal et al. 2012; Tamaki et al. 1997), or potato starch as an additive to change wheat or other crop flour properties (Nemar et al. 2015; Zhang et al. 2011).

Therefore, by selecting potato varieties with high and low starch content, and setting different degrees of soil water stress, we investigated the formation mechanism of tuber starch quality under soil water stress by measuring growth and development, starch synthesis, starch accumulation, and starch quality indicators in potato tubers. Our study aims to provide a scientific basis for breeding potato varieties with high starch content and improved starch quality for highly efficient dryland potato farming.

Materials and Methods

Site Description

The experiment was conducted in Ershilipu Town, Chengbei District, Xining City, Qinghai Province, China (31.73° N, 101.75° E, altitude 2339 m), located in a continental semi-arid climate on the northeastern Tibetan Plateau. The region experiences an annual average of 1940 sunshine hours, 7.6 ℃ annual average temperature, and a 180-day frost-free period. Soil samples were taken from the 0–20 cm soil layer of the study area, and their chemical and physical properties were determined. Soil field capacity was 29.5% v/v, pH 8.3, organic matter 22.4

mg·kg^{-1}, hydrolytic N 117.0 mg·kg^{-1}, Olsen-P 63.4 mg·kg^{-1}, and available K was 393.0 mg·kg^{-1}.

Potato Varieties

Experimental potato varieties included Qingshu 9 (high starch variety, dry matter average 23.6%, P1) and Minshu 1 (low starch variety, dry matter average 17.8%, P2).

Design

The trial was conducted in pots under a rainout shelter and laid out as a randomized block design with three irrigation treatments: T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity). Each treatment was replicated 18 times, meaning the entire experiment consisted of a total of 108 pots. The bottom of each plastic flowerpot (diameter 36 cm, height 20 cm) was filled with a 2-cm layer of stones, two layers of gauze were placed on the stones as a filter layer, and then an obliquely placed PVC pipe (diameter 2 cm, length 23 cm) was inserted for ventilation. The lower part of the pipe was located in the middle of the pot, and the upper part against the edge of the pot (height 30 cm, width 42 cm). Eighteen kilograms of experimental soil was placed in each pot, and then 0.32 kg of diamine phosphate (containing 18% N, 46% P_2O_5, produced by Yunnan Yun Tian Hua Co., Ltd), 0.16 kg of potassium sulfate (containing 50% K_2O, produced by Qinghai Special Fertilizer Factory) and 0.22 kg of urea (containing 46% N, produced by Qinghai Yun Tian Hua International Fertilizer Co., Ltd) were evenly applied on top of the soil. The pots were then watered to field capacity. On May 16, seed potatoes were planted in each pot, and one plant was maintained after emergence. After planting, a normal water supply was provided to all treatments. From the beginning of the bud period, potatoes were subjected to water stress using the weighing method, until the potato matured. During the full potato flowering period, 0.1% potassium dihydrogen phosphate was sprayed on the plants twice to supplement the plant potassium level.

Table 1 Potato target gene and sequence of qRT-PCR primers

Gene name	Forward primer (5′-3′)	Reverse primer (5′-3′)
Tublin1	GTCAGTCTGGTGCTGGTAATAA	TCTCAGCCTCCTTCCTTACA
AGPase	TTCCTTCCACCAACCAAGATAG	CACTATGGAGTGTTCCACAGAA
GBSSI	CTTGCGTTTGCTGAGATGATAAA	CAGAAGCTCCTAAGCCCAATAG
SBEI	GCGAACATGTGTGGCTTATTAC	TCTCGTCACTCTCCTCGATATT
SBEII	CTCTGGATAGACCGTCAACATC	AGGTACCCTTCTCCTCCTAATC
SSII	CAACAGGACCTACTTCAACAGA	CTACCACTCCCACCATCATAAG
SSIII	GTCACCTGTTCGTGTATCATCT	CCACTCTCTTCCGATCTCTTTG

Sampling

At the potato flowering stage, 10 plants were selected and their height was measured. During first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), when 1/3 of the plant base was withered and yellow (S4), when 2/3 of the plant base was withered and yellow (S5) and all aboveground stems and leaves were withered and yellow (S6), the chlorophyll content and photosynthetic characteristics of five upper leaves were measured. Three plants with consistent growth were selected from each treatment, their tubers were harvested, and after washing, tuber length and width, and individual plant tuber yield were assessed.

In the laboratory, soil was removed from the tubers, and selected tubers of the same size, were cut into thin slices, and stored in a freezer (-80℃) for later determination of ADP-Glucose Pyrophosphorylase (AGPase), Granule Bound Starch Synthase (GBSS), Starch Branching Enzyme (SBE), Soluble Starch Synthase (SSS) activities, and *AGPase*, *GBSSI*, *SBEI*, *SBEII*, *SSII*, *SSIII* gene expressions. Tubers from three plants were cut and dried to determine total starch content, amylose content and amylose/amylopectin ratio. Starch from the remaining tubers was extracted by the natural sedimentation method, and starch granule morphology, particle size distribution and gelatinization characteristics determined.

Measurements

Plant height was measured with a tape, chlorophyll content was determined with a SPAD-502 plus Chlorophyll Meter (Konica Minolta, Japan), and photosynthetic characteristics, including photosynthetic rate *(Pn)*, stomatal conductance (*Gs)*, intercellular CO_2 concentration (*Ci)* and transpiration rate (*Tr*), were measured between 10:00 and 11:00 with a Li-6400 XT Portable Photosynthetic Measurement System (Li-COR, USA). Tuber length and width were measured with a vernier caliper.

Total RNA and genomic DNA were extracted from tuber samples (Huang et al. 2014), and first strand cDNA was synthesized by RNA reverse transcription using a PrimeScript RT Reagent Kit (Takara Bio, Inc., Japan). Primers for qRT-PCR were designed using Primer Premier 5.0 software based on gene sequence in NCBI (Table 1). Using *Tublin1* as an internal reference gene, qRT-PCR was carried out with a *Tag* SYBR®Green qPCR Kit (Bio-Rad Laboratories, Inc., USA) with first strand cDNA as a template. Each sample was analyzed three times, and target gene relative expression was calculated using the $2^{-\triangle\triangle Ct}$ method (Pfaffl 2001).

Table 2 Plant height (cm) of potato at the flowering stage under different soil water stress treatments for cultivars P1 and P2

Treatment	P1	P2
T1	59.08 ± 5.84 a	30.54 ± 3.99 a
T2	50.92 ± 4.23 b	27.15 ± 4.49 b
T3	47.23 ± 6.67 b	21.85 ± 1.99 c

Different lowercase letters indicate significant difference among treatments at p = 0.05 level

Table 3 Length and width of potato tubers under soil water stress treatments for cultivars P1 and P2 at different stages (cm)

Stage	Treatment	P1		P2	
		Length	Width	Length	Width
S1	T1	5.33 ± 0.66 a	3.43 ± 0.40 a	5.87 ± 0.26 a	3.69 ± 0.35 a
	T2	4.47 ± 0.57 b	2.91 ± 0.47 ab	4.79 ± 0.60 b	3.00 ± 0.45 b
	T3	3.80 ± 0.38 b	2.58 ± 0.43 b	3.92 ± 0.26 c	2.74 ± 0.15 b
S2	T1	6.07 ± 0.63 a	3.75 ± 0.28 a	5.96 ± 0.29 a	3.77 ± 0.19 a
	T2	5.17 ± 0.70 b	3.03 ± 0.33 b	4.85 ± 0.50 b	3.15 ± 0.40 b
	T3	4.28 ± 0.50 c	2.69 ± 0.39 b	4.24 ± 0.46 c	2.87 ± 0.23 b
S3	T1	6.62 ± 0.58 a	4.60 ± 0.38 a	6.08 ± 0.51 a	3.88 ± 0.11 a
	T2	6.05 ± 0.30 a	3.94 ± 0.16 b	5.22 ± 0.43 b	3.31 ± 0.32 b
	T3	4.55 ± 0.33 b	3.52 ± 0.08 c	4.84 ± 0.29 b	3.08 ± 0.37 b
S4	T1	7.04 ± 0.59 a	5.17 ± 0.23 a	6.22 ± 0.32 a	4.25 ± 0.31 a
	T2	6.46 ± 0.25 a	4.67 ± 0.20 b	5.45 ± 0.22 b	3.63 ± 0.13 b
	T3	4.86 ± 0.60 b	3.92 ± 0.34 c	4.43 ± 0.25 c	3.13 ± 0.19 c
S5	T1	7.48 ± 0.68 a	5.00 ± 0.39 a	8.22 ± 0.37 a	4.30 ± 0.17 a
	T2	6.63 ± 0.71 b	4.64 ± 1.07 a	5.86 ± 0.21 b	4.00 ± 0.19 ab
	T3	4.96 ± 0.32 c	3.09 ± 0.54 b	5.14 ± 0.36 c	3.54 ± 0.55 b
S6	T1	7.98 ± 1.03 a	4.41 ± 0.34 a	8.41 ± 0.80 a	4.12 ± 0.29 a
	T2	6.67 ± 0.91 b	3.75 ± 0.36 b	6.20 ± 1.09 b	3.60 ± 0.24 b
	T3	5.00 ± 0.56 c	2.81 ± 0.15 c	6.12 ± 0.41 b	2.76 ± 0.08 c

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base was withered and yellow (S4), 2/3 plant base was withered and yellow (S5) and all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity). Different lowercase letters indicate significant difference among treatments at $p = 0.05$ level

A 0.1-g tissue sample was weighed, 1 mL of extracted solution added, the sample homogenized in an ice bath, centrifuged at 10000 × g 4℃ for 10 min, and the supernatant was placed on ice as a crude enzyme solution for AGPase, SBE, SSS analysis. Then 1 mL of extracted solution in precipitation was added as crude enzyme solution for GBSS. AGPase, GBSS, SBE, and SSS activities were determined with a Starch Synthesis Enzyme Kit (Suzhou Keming Biotechnology Co., Ltd.). Each sample was analyzed three times.

Liquid N was added to a 0.01-g tissue sample in a mortar and the sample was ground. Then the sample total starch and amylose contents were determined with a Starch Content Kit (Suzhou Keming Biotechnology Co., Ltd.). Amylopectin content and the amylose/amylopectin ratio were then calculated. Each analysis was repeated three times.

Starch granule morphology was observed under a JSM-6610 LV Scanning Electron Microscope (JEOL Company, Japan), and starch granule size distribution determined using a Mastersize 2000 Laser Particle Sizer (Malvern Company, UK). Then, starch gelatinization properties were measured with an RVA-TecMaster Rapid

Table 4 Yield of potato under soil water stress treatments for cultivars P1 and P2 at different stages (g)

Stage	Treatment	P1	P2
S1	T1	165.9 ± 28.8 a	182.3 ± 45.1 a
	T2	115.1 ± 16.4 b	147.0 ± 25.8 a
	T3	80.6 ± 22.9 b	122.0 ± 14.5 a
S2	T1	260.0 ± 51.4 a	230.5 ± 57.5 a
	T2	190.5 ± 20.7 a	184.7 ± 25.7 a
	T3	107.9 ± 33.2 b	157.8 ± 37.0 a
S3	T1	377.2 ± 35.0 a	279.8 ± 63.8 a
	T2	252.7 ± 36.6 b	185.9 ± 19.2 b
	T3	147.3 ± 21.4 c	178.3 ± 8.0 b
S4	T1	403.0 ± 31.3 a	251.6 ± 21.8 a
	T2	303.3 ± 46.4 b	201.2 ± 47.6 a
	T3	162.0 ± 6.6 c	185.8 ± 46.4 a
S5	T1	639.0 ± 47.0 a	306.4 ± 23.7 a
	T2	434.3 ± 53.3 b	240.9 ± 24.1 b
	T3	183.5 ± 34.6 c	218.7 ± 18.1 b
S6	T1	807.1 ± 37.5 a	383.9 ± 43.0 a
	T2	483.6 ± 38.0 b	260.1 ± 44.8 b
	T3	204.5 ± 28.5 c	223.8 ± 5.1 b

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base was withered and yellow (S4), 2/3 plant base was withered and yellow (S5) and all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity). Different lowercase letters indicate significant difference among treatments at $p = 0.05$ level

Viscosity Analyzer (Perten Company, Sweden) (Liu et al. 2020). Each analysis was repeated three times.

Data Analyses

Microsoft Excel 2007 and SAS v8.0 were used for data processing and statistical analysis, respectively. Origin 7.5 was used for drawing the figures, and Duncan's Multiple Range Test for statistical comparisons.

Results

Growth and Development

Crop growth and development changed under adverse conditions. Potato plant height, leaf chlorophyll content, leaf photosynthetic capacity, tuber length and width,

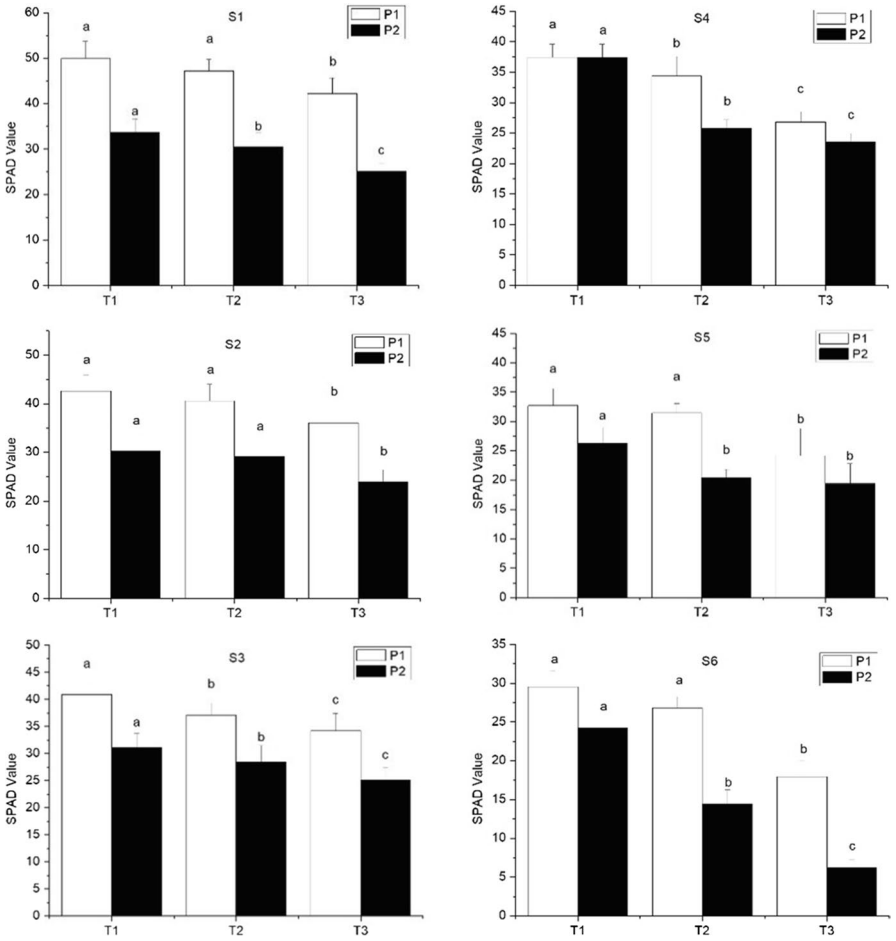

Fig. 1 Leaf chlorophyll content of potato under soil water stress treatments. Note: P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6). The different lowercase letters indicate significant differences among treatments at $p = 0.05$ level

and tuber yield under the soil water stress treatment were all significantly lower than under normal water supply (Table 2, 3 and 4 and Figs. 1 and 2). The higher the level of soil water stress, the lower the various potato growth and development indicators.

Compared to T1 under T2 and T3 treatments, during flowering, P1 and P2 plant height decreased by 13.8 and 20.1%, and 11.1 and 28.5%, respectively. During tuber development, leaf chlorophyll content decreased by 12.3 and 25.5%, and 9.0 and 26.0%, respectively; leaf *Pn* decreased by 24.0 and 55.8%, and 19.14 and 34.1%, respectively; leaf *Cond* decreased by 26.7 and 57.2%, and 29.8 and 60.5%, respectively; leaf *Ci* decreased by 15.0 and 72.8%, and 11.7 and 30.6%, respectively; leaf *Tr* decreased by 29.2 and 72.8%, and 10.3%, 52.4%, respectively; tuber

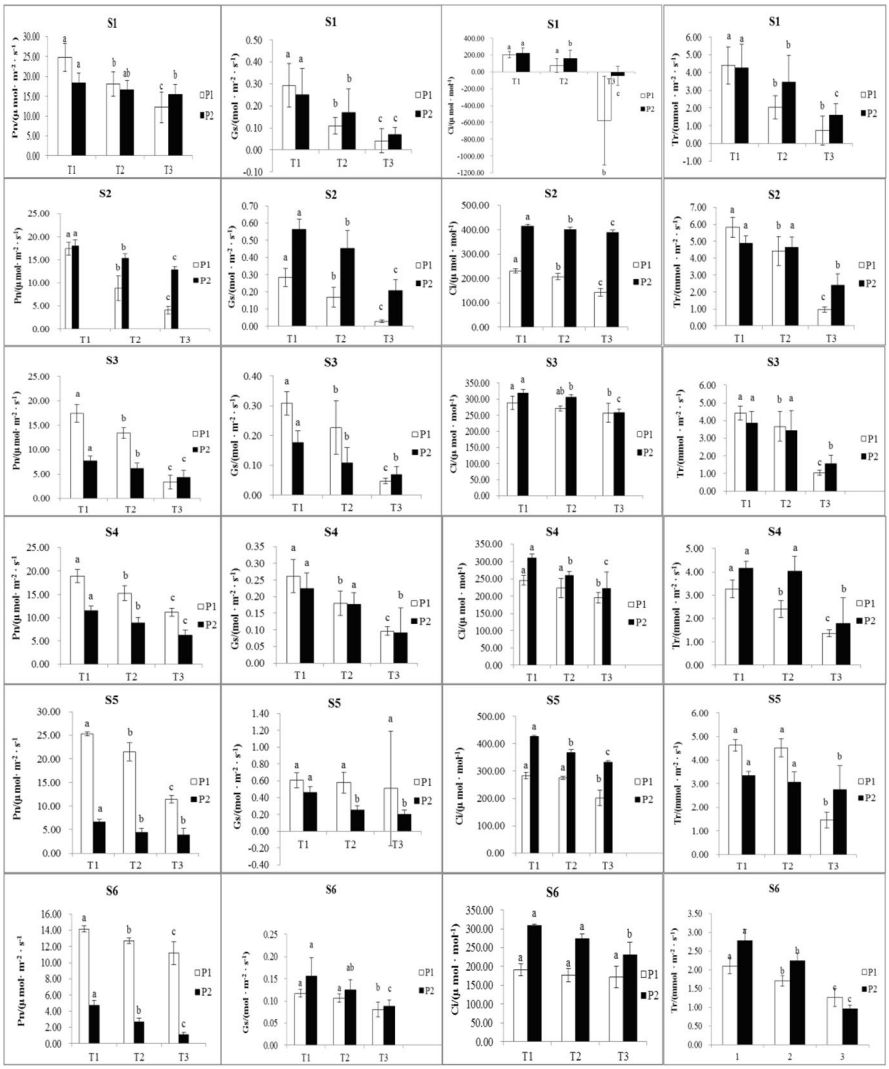

Fig. 2 *Pn*, *Gs*, *Ci* and *Tr* of potato leaf under soil water stress treatments. Note: P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6). Different lowercase letters indicate significant differences among treatments at p = 0.05 level

length decreased by 12.5 and 32.2%, and 20.6 and 29.6%, respectively; tuber width decreased by 13.0 and 29.4%, and 13.8 and 24.6%, respectively; and tuber yield decreased by 31.2 and 62.8% and 24.4 and 32.9%, respectively. Overall, soil water stress significantly restricted potato growth and development.

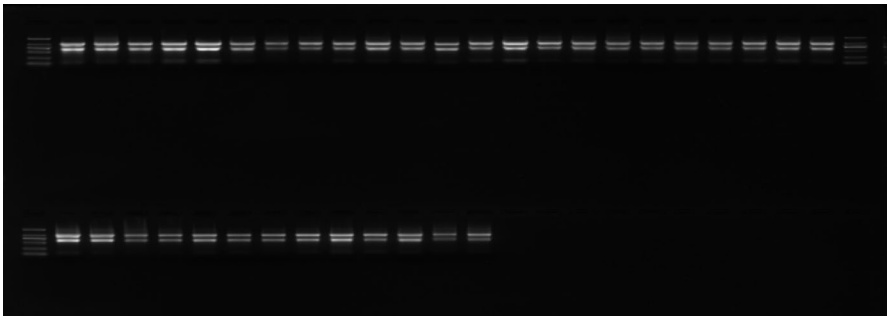

Fig. 3 RNA bands of potato tubers. Note: 1% agar gel was used to verify the quality of RNA

Transcriptional Expression of Starch Synthesis Genes and Enzyme Activity Related to Starch Synthesis

RNA did not degrade and maintained good integrity (Fig. 3). During tuber development, soil water stress significantly enhanced the expression of starch synthesis genes (Fig. 4). However, with increasing soil water stress in P1, gene expressions of *AGPase* and *GBSSI* were down-regulated, and gene expressions of *SSII*, *SSIII*, *SBEI* and *SBEII* were up-regulated. Gene expressions of *SSIII* was down-regulated in P2, while gene expressions of *AGPase*, *GBSSI*, *SSII*, *SBEI* and *SBEII* were up-regulated.

Stress can change enzyme activity. During tuber development, soil water stress significantly reduced AGPase, GBSS, SSS, and SBE enzyme activities (Table 5). However, with increasing soil water stress, AGPase and SSS enzyme activities increased in P1, but GBSS and SBE declined. AGPase, GBSS, SSS and SBE enzyme activities all decreased in P2. Overall, soil water stress significantly inhibited potato tuber starch biosynthesis.

Tuber Starch Accumulation

During tuber development, soil water stress significantly reduced starch accumulation in potato tubers (Table 6). With increased soil water stress, potato tuber total starch content slightly increased, while amylose content and the amylose/amylopectin ratio decreased. Overall, soil water stress significantly reduced starch accumulation in potato tubers.

Starch Quality

There was no significant difference in starch particle morphology between P1 and P2, and both were irregular ellipsoids that were not affected by soil water stress (Fig. 5). Crop starch quality is easily affected by stress. During tuber development, soil water stress significantly increased the granule dispersion, peak

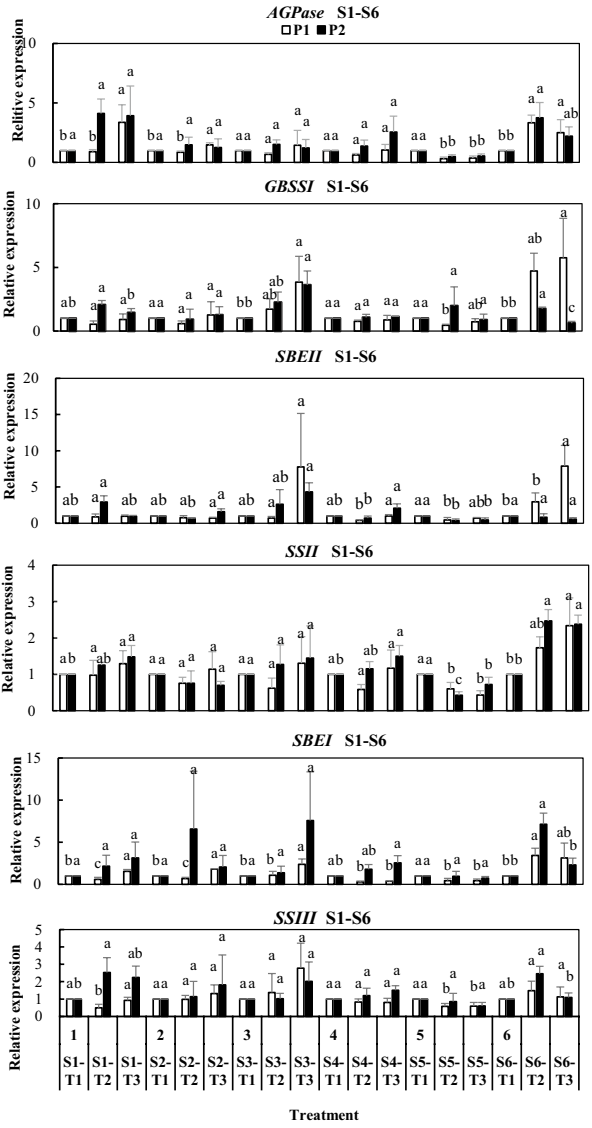

Fig. 4 Transcriptional expression of genes related to starch synthesis during the development of potato tuber under soil water stress treatment. Note: P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity). Different lowercase letters indicate significant difference among treatments at p = 0.05 level

viscosity and breakdown value of tuber starch (Table 7 and 8). With increased soil water stress, peak viscosity and breakdown value and granule dispersion increased in P1, while in P2 they decreased. An increase in soil water stress resulted in significant reductions in particle size, viscosity, final viscosity, setback value and pasting temperature of tuber starch ($P < 0.05$). Overall, soil water stress significantly improved potato tuber starch quality.

Table 5 Key enzymes activity of starch synthesis during the development of potato tuber under soil water stress treatments at different stages and for cultivars P1 and P2

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
AGPase (nmol/min/g fresh weight)							
P1	T1	679.81 ± 10.01 a	6357.38 ± 56.26 a	7587.29 ± 54.14 a	426.21 ± 29.53 c	388.46 ± 23.20 b	2395.31 ± 14.76 a
	T2	646.99 ± 28.13 a	2207.12 ± 21.64 c	156.28 ± 13.53 c	664.18 ± 13.53 b	2250.40 ± 28.13 a	2335.64 ± 78.13 a
	T3	383.59 ± 25.57 b	5106.02 ± 29.53 b	5907.30 ± 20.51 b	5110.28 ± 40.60 a	25.57 ± 3.26 c	454.41 ± 29.67 b
P2	T1	421.95 ± 28.13 b	273.49 ± 27.07 c	5890.25 ± 39.06 a	6887.59 ± 29.53 a	5149.35 ± 35.81 b	5148.64 ± 53.23 a
	T2	937.67 ± 30.69 a	4976.33 ± 76.07 b	3588.7 ± 64.36 b	5847.63 ± 120.85 b	6469.90 ± 40.56 a	4697.71 ± 28.13 b
	T3	281.30 ± 84.39 c	5123.07 ± 73.82 a	215.66 ± 16.24 c	2803.62 ± 70.79 c	476.65 ± 48.80 c	778.26 ± 58.56 c
GBSS (nmol/min/g fresh weight)							
P1	T1	45.85 ± 8.08 b	118.14 ± 6.11 a	121.67 ± 5.29 b	31.74 ± 5.29 b	56.43 ± 3.05 a	68.77 ± 9.16 a
	T2	40.56 ± 11.01 b	14.11 ± 3.05 c	209.84 ± 3.05 a	84.64 ± 5.29 a	49.37 ± 3.05 b	40.56 ± 3.05 c
	T3	179.86 ± 8.15 a	81.11 ± 6.11 b	28.21 ± 3.05 c	15.87 ± 9.16 c	15.87 ± 5.29 c	54.66 ± 6.11 b
P2	T1	183.39 ± 3.05 a	44.08 ± 3.05 c	162.23 ± 6.11 a	209.84 ± 12.22 b	208.07 ± 33.05 a	14.11 ± 3.05 c
	T2	77.59 ± 6.11 c	96.98 ± 6.11 a	75.82 ± 6.11 c	236.29 ± 3.05 a	199.26 ± 3.05 b	59.95 ± 3.05 a
	T3	148.12 ± 5.29 b	58.19 ± 5.29 b	96.98 ± 8.08 b	209.84 ± 3.05 b	56.43 ± 3.05 c	29.98 ± 8.08 b
SBE (U/g fresh weight)							
P1	T1	463.12 ± 17.18 b	205.46 ± 7.40 a	127.45 ± 8.49 b	257.03 ± 6.97 c	223.29 ± 7.61 a	601.45 ± 6.28 a
	T2	651.74 ± 3.91 a	188.61 ± 0.64 b	60.05 ± 7.02 c	585.71 ± 5.67 a	215.28 ± 12.03 a	251.17 ± 15.15 c
	T3	484.04 ± 10.53 b	96.97 ± 10.50 c	274.42 ± 8.21 a	316.46 ± 6.98 b	133.60 ± 13.84 b	574.30 ± 6.96 b
P2	T1	489.49 ± 3.57 c	238.99 ± 6.40 b	149.38 ± 1.07 c	264.67 ± 9.62 b	679.30 ± 4.48 a	255.60 ± 14.39 a
	T2	503.99 ± 4.57 b	614.20 ± 5.35 a	286.71 ± 8.07 b	97.56 ± 7.89 c	523.33 ± 1.83 b	172.04 ± 9.31 b
	T3	618.98 ± 2.71 a	216.04 ± 6.79 c	472.30 ± 3.97 a	293.58 ± 18.69 a	74.93 ± 14.48 c	122.38 ± 14.35 c
SSS (nmol/min/g fresh weight)							

Table 5 (continued)

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
P1	T1	47.61 ± 5.29 b	95.22 ± 5.29 a	96.98 ± 8.08 a	5.29 ± 0.97 b	45.85 ± 3.05 a	7.05 ± 3.05 c
	T2	54.66 ± 8.08 b	35.27 ± 3.05 b	35.27 ± 3.05 c	47.61 ± 5.29 a	38.79 ± 3.05 a	28.21 ± 6.11 b
	T3	75.82 ± 6.11 a	14.11 ± 6.11 c	77.59 ± 3.05 b	52.90 ± 8.63 a	14.11 ± 6.11 b	158.70 ± 10.11 a
P2	T1	590.72 ± 3.05 a	109.33 ± 6.11 b	52.90 ± 5.29 c	21.26 ± 5.29 b	14.11 ± 3.05 c	12.34 ± 3.05 b
	T2	275.08 ± 10.65 b	135.78 ± 6.11 a	81.11 ± 6.11 b	104.04 ± 3.05 a	38.79 ± 3.05 b	201.02 ± 10.58 a
	T3	123.43 ± 3.05 c	77.59 ± 3.05 c	303.29 ± 3.05 a	28.21 ± 3.05 b	84.64 ± 5.29 a	24.59 ± 3.05 b

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base was withered and yellow (S4), 2/3 plant base was withered and yellow (S5) and all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity)

Table 6 Starch accumulation during the development of potato tuber under soil water stress treatments at different stages and for cultivars P1 and P2

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
Total starch content/%							
P1	T1	5.99 ± 0.01 b	2.75 ± 0.01 b	6.63 ± 0.01 b	5.18 ± 0.03 c	5.95 ± 0.02 a	5.87 ± 0.02 b
	T2	2.52 ± 0.01 c	1.92 ± 0.01 c	6.20 ± 0.01 c	5.49 ± 0.01 b	5.49 ± 0.01 b	6.35 ± 0.03 a
	T3	5.86 ± 0.02 a	4.62 ± 0.01 a	7.22 ± 0.03 a	6.26 ± 0.01 a	5.85 ± 0.02 a	5.71 ± 0.05 c
P2	T1	7.54 ± 0.02 a	5.52 ± 0.02 b	6.31 ± 0.02 a	4.33 ± 0.02 b	6.39 ± 0.08 b	5.69 ± 0.07 b
	T2	7.40 ± 0.02 b	5.85 ± 0.01 a	2.98 ± 0.02 b	2.16 ± 0.02 c	2.68 ± 0.04 c	7.42 ± 0.04 a
	T3	6.81 ± 0.01 c	2.35 ± 0.02 c	2.04 ± 0.01 c	6.27 ± 0.02 a	7.92 ± 0.03 a	5.78 ± 0.04 b
Amylose content/%							
P1	T1	11.54 ± 0.03 c	12.89 ± 0.03 b	2.06 ± 0.03 c	10.23 ± 0.03 a	1.39 ± 0.03 c	13.40 ± 0.03 a
	T2	11.73 ± 0.02 b	13.48 ± 0.03 a	5.27 ± 0.03 a	4.13 ± 0.03 b	4.68 ± 0.03 b	10.53 ± 0.01 b
	T3	12.11 ± 0.03 a	8.63 ± 0.03 c	4.85 ± 0.03 b	1.83 ± 0.03 c	5.27 ± 0.03 a	3.26 ± 0.03 c
P2	T1	7.49 ± 0.03 a	13.16 ± 0.01 a	7.38 ± 0.03 c	5.92 ± 0.01 c	9.66 ± 0.03 a	10.93 ± 0.01 a
	T2	5.02 ± 0.03 b	11.20 ± 0.03 c	14.37 ± 0.03 a	12.21 ± 0.03 a	4.78 ± 0.01 b	8.56 ± 0.03 b
	T3	0.8 ± 0.032 c	12.72 ± 0.03 b	10.25 ± 0.03 b	10.80 ± 0.03 b	4.53 ± 0.03 c	3.33 ± 0.03 c
Amylose/amylopectin ratio							
P1	T1	0.44 ± 0.03 c	0.49 ± 0.01 b	0.16 ± 0.01 c	0.40 ± 0.01 a	0.15 ± 0.03 c	0.51 ± 0.02 a
	T2	0.45 ± 0.01 b	0.52 ± 0.01 a	0.24 ± 0.01 a	0.21 ± 0.02 b	0.23 ± 0.01 b	0.41 ± 0.02 b
	T3	0.46 ± 0.01 a	0.34 ± 0.01 c	0.23 ± 0.01 b	0.16 ± 0.01 c	0.24 ± 0.01 a	0.19 ± 0.01 c
P2	T1	0.31 ± 0.02 a	0.50 ± 0.03 a	0.30 ± 0.03 c	0.26 ± 0.05 c	0.38 ± 0.01 a	0.42 ± 0.03 a
	T2	0.24 ± 0.01 b	0.43 ± 0.01 c	0.55 ± 0.01 a	0.47 ± 0.01 a	0.23 ± 0.03 b	0.34 ± 0.01 b
	T3	0.13 ± 0.02 c	0.49 ± 0.01 b	0.41 ± 0.01 b	0.42 ± 0.03 b	0.22 ± 0.01 c	0.19 ± 0.03 c

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity)

Discussion

Soil water deficit reduces nutrients and water supplied by the roots to aboveground plant parts, weakening leaf chlorophyll synthesis and photosynthetic capacity, inhibiting organic matter generation, and reduced organic matter transport to below ground plant parts, thus resulting in smaller tubers and lower potato yields. We provided systematic data for the whole potato growth period, and demonstrated that soil water stress inhibited aboveground plant growth and underground tuber development, thus compensating for shortcomings of previous research (Lahlou & Ledent 2005; Onder et al. 2005; Wagg et al. 2021).

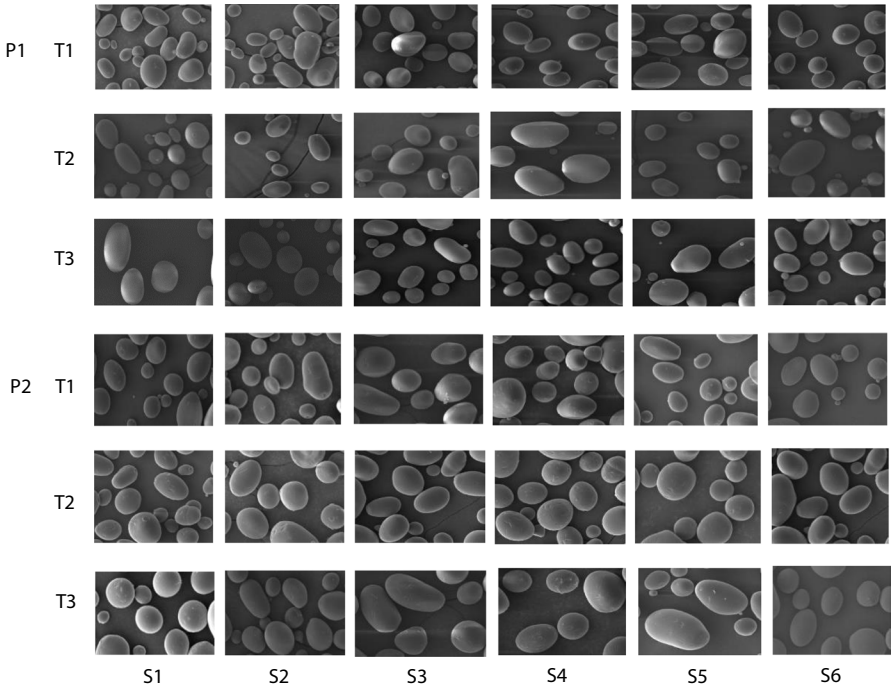

Fig. 5 Starch granule morphology during the development of potato tuber under different soil water stress treatments. Note: P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6). T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity)

Currently, soil water stress effects on starch synthesis have been primarily studied in rice (Prathap & Aruna 2020), wheat (Lu et al. 2019) and other crops (He et al. 2012), where starch biosynthesis is controlled by gene expression and enzyme activity. Our results for potato tubers indicated that soil water stress significantly increased gene expression of key enzymes for starch synthesis. This could be viewed as a potato survival strategy for adaptation to adverse circumstances, where potato produces more enzymes for starch synthesis by up-regulating gene expression. However, starch accumulation is more positively correlated with amylase activity, whereas enzyme activity (i.e. catalytic efficiency), is mainly regulated by cellular environmental conditions such as pH and temperature. However, we showed that soil water stress significantly reduced amylase activity, thereby limiting starch accumulation (Rudack et al. 2017). We suggest that soil water stress alters intracellular pH through signal transduction, thus reducing amylase activity, but further research is needed to confirm this.

Previous studies on soil water stress regulation of starch quality mainly focused on corn (Huo & Yang 2022), cassava (Santisopasri et al. 2001), barley

Table 7 Starch granule distribution during the development of potato tuber under soil water stress treatments at different stages and for cultivars P1 and P2

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
Particle size / μm							
P1	T1	26.48 ± 0.09 b	28.23 ± 0.04 a	32.45 ± 0.08 a	34.43 ± 0.75 a	35.43 ± 0.12 a	34.76 ± 0.22 a
	T2	27.95 ± 0.14 a	25.62 ± 0.09 b	31.67 ± 0.05 b	31.52 ± 0.04 b	30.18 ± 0.02 c	32.58 ± 0.06 b
	T3	21.29 ± 0.05 c	25.61 ± 0.02 b	29.94 ± 0.17 c	30.52 ± 0.14 c	30.98 ± 0.03 b	28.22 ± 0.08 c
P2	T1	27.25 ± 0.02 a	28.66 ± 0.02 a	28.24 ± 0.03 a	28.38 ± 0.02 b	28.29 ± 0.10 b	28.77 ± 0.16 a
	T2	25.60 ± 0.04 c	27.00 ± 0.04 b	28.46 ± 0.07 a	29.59 ± 0.27 a	31.87 ± 0.16 a	27.97 ± 0.07 b
	T3	26.21 ± 0.08 b	27.04 ± 0.03 b	27.99 ± 0.45 a	28.70 ± 0.13 b	26.22 ± 0.05 c	27.31 ± 0.03 c
Granule dispersion							
P1	T1	16.46 ± 1.34 b	3.65 ± 0.18 b	15.45 ± 1.23 a	11.39 ± 7.21 a	2.53 ± 0.61 b	16.55 ± 1.40 a
	T2	15.50 ± 1.22 b	16.21 ± 0.05 a	15.06 ± 0.02 a	2.68 ± 0.89 b	14.44 ± 1.18 a	2.75 ± 0.23 b
	T3	20.48 ± 1.65 a	16.22 ± 0.02 a	15.24 ± 1.12 a	15.63 ± 0.07 a	14.73 ± 1.15 a	15.44 ± 1.29 a
P2	T1	3.29 ± 0.25 c	12.13 ± 7.80 ab	3.65 ± 0.12 b	2.74 ± 0.15 c	3.17 ± 0.01 b	7.22 ± 6.32 b
	T2	16.22 ± 0.02 a	16.14 ± 1.32 a	15.31 ± 1.29 a	19.43 ± 1.49 a	15.84 ± 1.36 a	17.06 ± 0.04 a
	T3	15.84 ± 0.05 b	3.31 ± 0.11 b	2.92 ± 0.29 b	15.90 ± 1.19 b	15.84 ± 0.03 a	15.96 ± 1.32 a

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) all aboveground stems and leaves withered and yellow (S6).T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity)

(Gous et al. 2013) and other crops, and there are few reports on potato. Starch gelatinization characteristics are closely related to its subsequent processing and utilization. We showed that soil water stress significantly reduced tuber starch average particle size and pasting temperature, thereby shortening the tuber starch gelatinization process. Compared with cereal crop starch, potato starch has a lower pasting temperature, higher transparency and larger expansion, making it unique in the processing of pasta, aquatic animal products, granular powder, and chemical starch. We believe that improving potato starch quality by shortening the gelatinization process will enhance its application in the aforementioned fields.

Conclusion

We investigated soil water stress regulation of potato tuber starch quality formation. Soil water stress restricted potato plant growth and development, inhibited tuber starch biosynthesis, and reduced tuber starch accumulation, thereby shortening the tuber starch gelatinization process.

Table 8 Starch gelatinization properties during the development of potato tuber under different soil water stress treatments at different stages and for cultivars P1 and P2

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
Peak viscosity / cp							
P1	T1	6446.33 ± 110.21 a	6108.00 ± 147.37 a	6405.00 ± 139.37 a	5925.33 ± 236.19 a	6210.67 ± 323.49 a	6357.33 ± 79.85 a
	T2	6551.33 ± 85.65 a	6083.50 ± 54.45 a	6000.67 ± 2068.40 a	5501.33 ± 16.07 b	6526.60 ± 84.10 a	6151.00 ± 120.17 b
	T3	6524.50 ± 137.24 a	6276.00 ± 34.12 a	6290.33 ± 85.66 a	5646.67 ± 85.38 ab	6561.33 ± 181.36 a	6330.67 ± 105.25 ab
P2	T1	6738.67 ± 98.52 a	6176.67 ± 396.90 a	6268.33 ± 113.78 a	6713.00 ± 136.44 a	4183.33 ± 1936.16 a	6803.33 ± 209.29 a
	T2	6676.00 ± 116.73 a	6544.33 ± 194.10 a	5497.67 ± 1162.79 a	6446.33 ± 61.61 b	6605.33 ± 109.44 a	6592.33 ± 143.14 ab
	T3	6665.33 ± 103.73 a	6272.67 ± 91.66 a	6366.67 ± 65.61 a	6400.67 ± 60.04 b	6466.67 ± 105.72 a	6383.67 ± 73.28 b
Trough viscosity / cp							
P1	T1	4887.33 ± 91.22 a	4573.00 ± 268.42a	5056.00 ± 80.52 a	3881.67 ± 145.21 a	4583.33 ± 298.01 a	4845.33 ± 87.65 a
	T2	4751.00 ± 63.21 a	4515.00 ± 97.58 a	4158.33 ± 575.44 b	3762.00 ± 27.84 a	4350.67 ± 30.01 ab	4392.33 ± 96.57 b
	T3	4612.00 ± 75.88 a	4594.67 ± 28.29 a	4561.00 ± 143.04 ab	3503.33 ± 30.99 b	4153.33 ± 186.78 b	4193.00 ± 78.33 c
P2	T1	4408.33 ± 82.32 b	4406.67 ± 175.85 b	4168.67 ± 106.92 a	4454.00 ± 163.50 a	3104.33 ± 890.00 b	3648.00 ± 63.27 b
	T2	4791.00 ± 56.24 a	3988.33 ± 84.36 a	3874.00 ± 560.67 a	4579.33 ± 17.62 a	4302.67 ± 62.01a	3907.00 ± 156.12 a
	T3	4109.67 ± 23.00 b	3820.33 ± 78.68 a	4012.33 ± 114.81 a	3435.00 ± 56.72 b	3820.33 ± 152.13 ab	3752.67 ± 92.80 ab
Breakdown value / cp							
P1	T1	1559.00 ± 58.81 b	1535.00 ± 121.31 a	1349.00 ± 77.38 a	2043.67 ± 210.86 a	1627.33 ± 71.60 c	1662.33 ± 76.83 b
	T2	1800.33 ± 37.55 ab	1568.50 ± 43.13 a	1842.33 ± 1584.22 a	1739.33 ± 42.52 b	2176.00 ± 91.41 b	1959.67 ± 55.65 a
	T3	1912.50 ± 62.47 a	1681.33 ± 17.95 a	1729.33 ± 157.79 a	2143.33 ± 85.59 a	2540.00 ± 240.33 a	2158.00 ± 42.18 a
P2	T1	2330.33 ± 46.76 b	1770.00 ± 228.81 b	2099.67 ± 184.37 a	2259.00 ± 165.76 b	1079.00 ± 1046.16 b	3155.33 ± 258.64 a
	T2	1885.00 ± 57.12 c	2556.00 ± 133.79 a	1623.67 ± 604.79 a	1867.00 ± 52.05 c	2302.67 ± 53.08 ab	2685.33 ± 108.52 b
	T3	2555.67 ± 100.01 a	2452.33 ± 68.48 a	2354.33 ± 49.22 a	2965.67 ± 91.82 a	2646.33 ± 254.46 a	2631.00 ± 21.93 b
Final viscosity / cp							

Table 8 (continued)

Variety	Treatment	Tuber formation period					
		S1	S2	S3	S4	S5	S6
P1	T1	7742.00 ± 84.16 b	7492.67 ± 102.58 a	7401.67 ± 57.06 a	5835.00 ± 30.00 b	6144.67 ± 205.12 a	6126.67 ± 79.26 a
	T2	8099.00 ± 63.74 a	7499.50 ± 68.59 a	6142.67 ± 917.94 b	6632.33 ± 44.79 a	5359.00 ± 87.11 b	5626.33 ± 45.83 b
	T3	7460.00 ± 49.13 c	7258.33 ± 2.08 b	6361.67 ± 80.35 ab	5570.33 ± 25.17 c	5291.67 ± 137.76 b	5256.67 ± 72.51 c
P2	T1	5090.33 ± 88.57 b	5623.67 ± 41.79 a	5335.00 ± 63.27 a	5478.67 ± 98.44 b	4218.00 ± 1096.96 a	4169.33 ± 60.45 c
	T2	6325.67 ± 68.21 a	4928.00 ± 83.50 b	5488.67 ± 499.19 a	5660.00 ± 49.67 a	4802.33 ± 65.28 a	4676.67 ± 45.06 a
	T3	4169.00 ± 148.95 c	4317.33 ± 221.46 c	4987.67 ± 60.21 a	4137.67 ± 22.01 c	4514.00 ± 71.46 a	4474.67 ± 91.78 b
Setback value / cp							
P1	T1	2836.67 ± 29.16 b	2919.67 ± 176.17 ab	2345.67 ± 42.91 a	1953.33 ± 120.36 b	1561.33 ± 451.93 a	1302.67 ± 121.65 a
	T2	3348.00 ± 35.61 a	2984.50 ± 28.99 a	1984.33 ± 651.52 a	2870.33 ± 71.28 a	1008.33 ± 71.49 a	1010.33 ± 79.90 b
	T3	2848.00 ± 47.12 b	2663.67 ± 30.37 b	1800.67 ± 180.03 a	2067.00 ± 40.58 b	1138.33 ± 187.02 a	985.00 ± 107.52 b
P2	T1	682.00 ± 57.29 b	1217.00 ± 148.31 a	1166.33 ± 48.22 b	1024.67 ± 67.55 a	1113.67 ± 214.90 a	521.33 ± 40.28 a
	T2	1534.67 ± 77.32 a	939.67 ± 35.81 b	1614.67 ± 61.99 a	1080.67 ± 59.37 a	499.67 ± 13.50 b	769.67 ± 192.93 a
	T3	59.33 ± 28.47 c	497.00 ± 170.21 c	975.33 ± 61.60 c	702.67 ± 65.73 b	693.67 ± 89.31b	722.00 ± 100.18 a
Pasting temperature /℃							
P1	T1	71.83 ± 0.45 a	71.30 ± 0.39 a	70.83 ± 0.03 a	68.90 ± 0.44 a	67.98 ± 0.73 a	67.28 ± 0.97 a
	T2	71.10 ± 0.27 a	70.43 ± 0.53 a	70.38 ± 0.41 a	68.92 ± 0.42 a	67.28 ± 0.03 a	67.19 ± 0.45 a
	T3	71.58 ± 0.56 a	70.32 ± 0.42 a	69.20 ± 0.43 b	69.42 ± 0.03 a	67.02 ± 0.45 a	67.06 ± 0.09 b
P2	T1	67.68 ± 0.37 a	69.85 ± 0.35 a	69.20 ± 0.39 ab	68.92 ± 0.38 b	68.92 ± 0.88 ab	67.25 ± 1.34 b
	T2	69.65 ± 0.66 a	68.68 ± 0.10 b	69.67 ± 0.46 a	69.90 ± 0.48 a	69.17 ± 0.45 a	68.95 ± 0.39 a
	T3	67.93 ± 0.03 a	68.23 ± 0.45 b	68.45 ± 0.40 b	67.50 ± 0.44 c	67.73 ± 0.38 b	67.97 ± 0.03 ab

P1 is Qingshu 9 Hao and P2 Mingshu 1 Hao experimental potato varieties; first inflorescence (S1), flowering stage (S2), stem and leaf senescence (S3), 1/3 plant base withered and yellow (S4), 2/3 plant base withered and yellow (S5) and all aboveground stems and leaves withered and yellow (S6). T1, normal water supply (irrigated to 75% of soil field capacity) T2, moderate water stress (refilled to 50% of soil field capacity); and T3, severe water stress (refilled to 25% of soil field capacity)

Acknowledgements This work was jointly supported by China Agriculture Research System of MOF and MARA (CARS-9), and Innovation Platform Construction Project of Qinghai Province (2021-ZJ-Y09).

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Data Availability The datasets used or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have declared that no competing interests exist.

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