Promotion of potato yield under moderate water deficiency at the seedling stage by modifying sink-source relationship

Ligu Jia, Lan Wu#, Qiqige Suyala, Xiaohua Shi, Yonglin Qin and Mingshou Fan
College of Agronomy, Inner Mongolia Agricultural University, Hohhot, China

ABSTRACT
Water deficiency is the main bottleneck in potato production in many regions worldwide. The generation of higher tuber yields per unit of water is a key goal for both agronomists and potato growers. In this study, we found that under moderate deficit irrigation (DI; 50% relative water content (RWC)) at the seedling stage of potato growth, the leaf area index (LAI) and dry matter accumulation were lower than control; however, they caught up with and surpassed the control at later developmental stages with a normal water supply, and a higher yield was ultimately achieved. The LAI and total dry weight under severe water stress (35% RWC) also surpassed the control at harvest; however, the final yield remained low, due to the low distribution of dry matter into the tubers. Abscisic acid (ABA) increased under DI conditions at the seedling stage, while gibberellin (GA1 and GA3) levels decreased. Moreover, endogenous ABA increased as plant development proceeded from seedling stage to tuber initiation stage, regardless of water stress. Exogenous ABA application promoted dry matter accumulation and distribution into the tubers. Therefore, it may be that ABA, as a major signaling molecule, mediates water stress to regulate tuber sink capacity at early development period. Through a feedback regulation stronger source capacity was stimulated by sink enhancement mediated by moderate water stress at the seedling stage, reached a higher tuber yield finally by reestablishment of sink-source relationship.

ARTICLE HISTORY
Received 19 January 2021
Revised 25 May 2021
Accepted 16 July 2021

KEYWORDS
ABA; deficit irrigation; potato; sink; source

Graphical Abstract

Introduction
Potato (Solanum tuberosum L.) is the fourth most important food crop globally (FAO (Food and Agriculture Organization of the United Nations), 2012). It plays an important role in food security, particularly in developing regions, owing to its high carbohydrate and caloric content (Romero et al., 2017). However, low tuber yields are a constant problem due to limited water resources and under-developed water management strategies. It is possible, however, to exploit the yield potential by developing water-saving irrigation techniques during potato production (Du et al., 2015; Haverkort et al., 2015).

The strategy of using less water to produce greater crop yield has been investigated for several crops (Kang & Zhang, 2004). Deficit irrigation (DI) and controlled alternate partial root-zone irrigation (PRI) are two promising water-saving techniques (Xie et al., 2012; Yactayo et al., 2013). Moderate water DI using these techniques has improved the quality and maintained yield of many crops, and increased yield in some crops with approximately half the amount of normal irrigation (Du et al., 2014; Kang & Zhang, 2004). A study by Onder et al.
observed several reported different (Cheng tuberization sink under bundles photosynthetic accumulation Rodriguez-Falcon mone 2005 2010). The process is regulated by the phytohormone abscisic acid (ABA) originating from the root (Zhang et al., 1987). A similar mechanism has been observed in potato (Liu et al., 2005, 2006; Plauborg et al., 2010). ABA played an essential regulatory role in restricting leaf area expansion and stomatal conductance in potato, by which DI and PRI saved water more than 20–30% on the field experiment (Liu et al., 2006; Rodriguez-Falcon et al., 2006).

ABA is also instrumental in promoting dry matter accumulation in storing organs (Yang et al., 2001), and in increasing growth, by attenuating temporal water stress (Sansberro et al., 2004). The application of exogenous ABA to field-grown maize was shown to increase photosynthetic pigment and carbohydrate remobilization to the grain, by increasing the number of vascular bundles and the phloem area in the peduncle and thereby facilitating increased maize yield at harvest (Travaglia et al., 2012). Therefore, ABA may affect crop production by regulating source-sink relationships under water stress. A recent study showed that water supply mainly influenced source capacity via the net photosynthetic rate, total leaf area and leaf life span, affected yield finally in potato (Li et al., 2016). However, there are few reports on ABA regulation of the source-sink relationship during potato production.

It has been shown that exogenous ABA-promoted tuberization counteracts gibberellin (GA) activity (Cheng et al., 2017; Ševčiková et al., 2017). It is possible that the function of GAs in tuberization is regulated by ABA, because ABA works to inhibit GA activity (Vreugdenhil, 2007). Furthermore, auxin and cytokinin are also instrumental in tuber initiation and bulking (Roumeliotis et al., 2012, 2013; Vreugdenhil, 2007). The relationship between ABA and other hormones during the tuberization process remains poorly understood, but it was nonetheless the first hormonal response to water stress to be verified by multiple studies.

The sensitivity of yield response to water stress at different developmental stages varies in potato. Previous studies indicated that the most sensitive period was the early developmental stage (i.e. the 30-day period after sowing), while the stage least affected by water stress was the mature stage (Iqbal et al., 1999). Levy (1985) considered the yield to be most vulnerable to water stress in later developmental stages, and less sensitive in earlier stages (i.e. when tuber diameter < 20 mm). Deployment of DI at the most sensitive stage will result in significant yield reduction. We found that tuber initiation and bulking stages were sensitive to water deficiency (Jia et al., 2018). Determination of yield response and its regulation under DI condition at the seedling stage requires further study. Moreover, the relationship between phytohormone regulation under water deficit conditions applied during seedling development and yield formation remained poorly understood, but is a key issue in water management for potato production and will thus be investigated in this study.

**Materials and methods**

**Field experiment in rainproof shelters**

The experiments were conducted in rainproof shelters in China’s Chayouzhong County, Inner Mongolia (41°27’ N, 112°63’ E) in 2013 and 2014. The field soil was chestnut soil (Chinese classification) (Cui et al., 1990), with 15.6 g/kg organic matter, 0.72 g/kg total N, and available P (Olsen-P) and K (exchangeable K) levels of 38.5 and 193.7 mg/kg, respectively, in a 0–40 cm soil layer; the pH was 8.1. The soil was sandy loam and the bulk density was 1.47, 1.50, and 1.58 g/cm³ in 0–20, 20–40, and 40–60 cm soil layers, with maximum field water capacities of 23.9%, 18.9%, and 13.2%, respectively.

Two very popular local, virus-free seed potato (Solanum tuberosum L.) cultivars, Kexin No.1 (drought tolerance) and Favorita (drought sensitive), were used in the trials. The sowing dates were 18 May and 15 May in 2013 and 2014, respectively. The fertilizer contained N (535 kg/ha), P₂O₅ (375 kg/ha), and K₂O (750 kg/ha), in which N (47 kg/ha), P₂O₅ (75 kg/ha), and K₂O (62 kg/ha) were applied as sowing. The N (146 kg/ha) and P₂O₅ (300 kg/ha) on 19 July, N (244 kg/ha) and K₂O (413 kg/ha) on 9 August, N (98 kg/ha) and K₂O (275 kg/ha) on 19 August were topdressed in 2013, Urea, single superphosphate and K₂SO₄ were used as the fertilizer types of N, P₂O₅ and K₂O, respectively. The same fertilizer type and amount were applied on 10 July 2025 July and 9 August in 2014, respectively.

Three irrigation treatments were 65% (control), 50% (moderate DI), 35% (severe DI) in relative soil water content (RWC) at the seedling stage. The seedling
stage was set up as 1–19 days after emergence (DAE) in 2013, and 1–24 DAE for Kexion No.1, 1–21 DAE for Favorita in 2014. After the seedling stage, the normal irrigation was applied 70%, 75%, 60% RWC in the tuber initiation (until 32 DAE), bulking (33–86 DAE) and maturation (>87 DAE) stages, respectively. A randomized block design was used with three replications in both years. The plot was 12 m × 6 m with 0.75 m row spacing and 0.25 m plant spacing. A buffer area 2 m in width was established between the plots to prevent border effects and water leakage.

A micro-spraying tape with 3 m range was put into the middle of each plot used for water supply, and a water meter was equipped for irrigation amount control in each treatment (Wang et al., 2018). Sufficient water was supplied before emergence for all treatments, to guarantee even seedling emergence. After 80% of the seedlings had emerged, RWC was monitored every 3 days using a drying method: the soil was sampled at 4:00 pm and oven-dried overnight; the irrigation amount was calculated and irrigated the following morning. An RWC deviation of 2% was permitted for each treatment (i.e. the target RWC for the control at the seedling stage was 65%; if the tested value of the 0–60 cm soil layer was lower than 63 ~ 65%, irrigated water was applied to achieve 67% RWC). The irrigation quota, based on Seyed et al. (2010), was calculated as follows:
\[
I = 0.6*A*(R_{aim} - R_{test})*p_b
\]
where I is irrigation quota (t), A is irrigated area (m²), \(R_{aim}\) is aimed-for RWC (%), \(R_{test}\) is tested RWC (%), and \(p_b\) is soil bulk density (g/cm³).

**Pot experiment**

Pot experiments were performed in a greenhouse at the Inner Mongolia Agricultural University Experimental Station in 2015. Plastic pots (15 L) were filled with 20 kg washed river sand. Two virus-free micro-tubers (weight: 10–12 g) were planted as seed material in each pot at a depth of 8 cm. Kexion No.1 was used as the experimental material. The pots were irrigated with an 800 ml/pot of distilled water for each of seven applications before emergence. The plants were irrigated every 3–4 days after emergence to ensure sufficient water supply. Irrigations were alternately performed using a nutrient solution and distilled water, at a ratio of two applications of nutrient solution to one of water. The composition of the nutrient solution was detailed in our previous report (Suyala et al., 2017).

Three treatments (0, 5 and 10 μM) of exogenous ABA were applied with every application of irrigated water and nutrient solution until 3 DAE; four applications of ABA-containing solution were administered overall, and totally 0.96 and 1.92 g/seedling ABA amounts were input for the 5 and 10 μM ABA treatments, respectively. Twenty pots were used for each treatment.

**Sampling and measurements**

The soil was sampled at a depth of 0–60 cm using a soil core 2.5 cm in diameter to measure RWC. When the soil samples had been dried to a constant weight at 105°C, the RWC was calculated. The RWC was the percentage of actual soil water content, accounting for maximum field water capacity (Rab et al., 2011). Soil samples were collected from the midpoint between two seedlings in the plant row with three replicates for each treatment. The same method was used for water monitoring in the pot experiment but the sampling hole had to be filled using a new medium after sampling.

Three plants per plot were harvested for analysis during the seedling, tuber initiation, tuber bulking and maturation stages of potato. The measured date varied depended on cultivar and experimental year. For the pot experiment, 10 seedlings (i.e. five pots) were collected at 50 and 57 days after sowing (DAS) for each treatment. After the leaf, shoot, root, stolon and tuber from a plant had been separated, they were dried for 30 min at 105°C, and then at 80°C until they reached a constant weight; the dry weight was then measured. Three independent samples within each plot were averaged and then for further variance analyses, same method was used for the following parameters analyses.

Before drying, leaf area was measured using a leaf area meter (Model LI-3100; LI-COR, Inc., Lincoln, NE, USA) Leaf area index (LAI) was determined as leaf area per unit of ground only in the field experiment.

Tuber initiation were determined under the field experiment in 2014. Ten plants were selected randomly during the seedling stage. The diameter of swelling part over than 0.5 cm was regarded as formed tuber.

**Quantification of hormones** was performed using ELISA (Zhao et al., 2006). During and after treatments at the seedling stage, 1–2 g of fresh leaf, root, and stolon samples were collected and immediately placed in liquid nitrogen, and then stored at –80°C until analysis. The fourth compound leaf from the apex, a 2-cm segment of stolon from the tip and root were sampled. The sampling dates were 7, 12 and 22 DAE for Kexion No.1, and 12, 17 and 22 DAE for Favorita in 2013, and 9, 13, 17 and 21 DAE for Kexion No.1 and 10, 14, 18 and 22 DAE for Favorita in 2014. The methods of extracting, purifying and quantifying ABA, ZR, GA (GA1 and GA3), and IAA using ELISA have been described previously by Zhang et al. (2010). The hormonal concentrations were expressed as fresh weight (FW).
**Yield harvests** were done on 11 September 2013, and on 17 August for Favorita and 13 September for Kexin No.1 in 2014; 2 square meters (except for border plants) per plot were randomly selected and harvested for yield determination. This process was repeated three times for each treatment.

**Statistical analyses**

The results were analyzed using SPSS software (version 19.0; SPSS Inc., Chicago, IL, USA). A P-value of 0.05 was considered significant.

**Results**

**Yield response to water deficiency at the seedling stage**

The maximum yield of Kexin No.1 and Favorita at harvest reached 55.7 and 54.4 t/ha in 2013 (Figure 1a), and 60.8 and 62.9 t/ha in 2014 (Figure 1b), respectively. The yield with 50% RWC was significantly higher than that of the control (65% of the maximum field water capacity at the seedling stage). However, severe DI (35% RWC) at the seedling stage resulted in a decreased tuber yield, to a level significantly lower than the control in Favorita in both experimental years (Figure 1).

Tuber number is an important determinant for final yield, the initiation of tuber was determined under different water deficiency at the seedling stage in 2014. The results showed that more tubers initiated under 35% treatment at 20 DAE, higher than control and 50% water treatment; at the 25 DAE 50% water treatment exhibited the highest while lowest for control on tuber numbers (Table 1).

**Leaf area index, dry matter accumulation and distribution**

The LAI was reduced under soil water deficiency conditions at the potato seedling stage; the greater the water deficiency, the more LAI was decreased (Figure 2). This phenomenon was seen in both cultivars in 2013 and 2014. However, the water deficiency treatments at the seedling stage exhibited higher LAI than the control after around 40 DAE. Subsequently, moderate DI (50% RWC) maintained the highest LAI, while the control (65% RWC) induced the lowest LAI, up to the end of the growth period. Consistent results were observed in both Kexin No.1 and Favorita in both experimental years (Figure 2).

Similar treatment difference was observed in dry matter accumulation (Figure 3). However, dry weight varied among the treatments. At the seedling stage, the dry weight was proportional to the soil water content, and the control was the highest, followed by 50% RWC, and 35% RWC was lowest, although there was no significant difference. On entering the tuber initiation stage (20

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**Table 1. Tuber numbers under different treatments at the seedling stage in 2014.**

| Cultivar | Treatment | Days after emergence |
|----------|-----------|---------------------|
|          |           | 15                  | 20 | 25                  |
| Kexin No.1 | 35%      | 1.35a               | 3.15a | 4.29b             |
|           | 50%      | 1.02a               | 2.56b | 5.02a             |
|           | 65%      | 1.13a               | 2.40b | 3.68c             |
| Favorita  | 35%      | 2.75a               | 4.02a | 4.50b             |
|           | 50%      | 2.00a               | 3.51b | 5.75a             |
|           | 65%      | 2.45a               | 3.19b | 3.47c             |

* Values within a column with the same letter denote no statistically significant difference at *P* < 0.05.
Figure 2. The leaf area index (LAI) of the whole developmental stage for (a) Kexin No.1 and (b) Favorita in 2013, (c) Kexin No.1 and (d) Favorita in 2014 under different soil moisture conditions at the seedling stage (19 days after emergence [DAE] in 2013, 24 and 21 DAE for Kexin No.1 and Favorita in 2014, respectively). Data are means and standard errors of three independent measurements. The same letter denotes no statistically significant difference at \( P < 0.05 \).

DAE in 2013 and 25 DAE in 2014), the moderate water deficit treatment began to catch up with the control, but the severe water deficit treatment remained lower. At the early tuber bulking stage (34–43 DAE), the dry weight of the 50% RWC treatment surpassed that of the control, and that of the 35% RWC treatment remained lower than the control under most conditions, although it occasionally reached the same level as the control (e.g. Kexin No.1 in 2013). At the late tuber bulking stage (63–86 DAE), the 50% RWC treatment had the highest dry weight, followed by the 35% RWC treatment, and the control was lowest significantly in both cultivars and years (Figure 3).

The percentage of dry matter in tubers at harvest in the 50% RWC and the control was significantly higher than that in the 35% RWC for both cultivars and years, although there was no significant difference between the 50% RWC and the control, except for Favorita in 2014 (Table 2).

**Hormone dynamics in relation to changes in soil water**

The ABA concentrations in root, leaf, and stolon increased in response to soil water deficiency at the seedling stage (Table 3) (data were missing for Favorita in 2013). Average 12.7% and 28.2% increase in root, 27.8% and 65.6% increase in leaf, 15.9% and 65.3% increase in stolon of ABA concentration respectively, compared to control under 50% and 35% DI treatments based on two cultivars and experimental years. The consistent treatment difference of ABA concentration in leaf was observed across both cultivars and years (Figure 4). However, after re-watering, ABA recovered to the same level under all treatments (Figure 4a, 4b).

The changes in GA (GA1 and GA3) concentration contrasted with those of ABA under water deficiency conditions at the seedling stage (Table 3). Water deficiency inhibited the accumulation of GAs in root, leaf, and stolon, and the effect was more evident under severe water deficiency (35% RWC) than moderate water deficiency (50% RWC) conditions. Similar patterns were noted in cultivars Kexin No.1 and Favorita in 2013 and 2014. After irrigation was reinstated, the differences among the treatments in terms of GA concentration disappeared (data not shown). The hormones ZR and IAA were also detected in different organs under the water deficiency treatments. However, the effect of water deficiency on their concentrations in root, leaf and stolon was indiscernible (data not shown).

The concentration of ABA in leaf increased gradually with plant development from the seedling stage to the
Figure 3. Dry weight of whole plants during developmental stage for (a) Kexin No.1 and (b) Favorita in 2013, (c) Kexin No.1 and (d) Favorita in 2014 under different soil moisture conditions at the seedling stage (19 days after emergence [DAE] in 2013, 24 and 21 DAE for Kexin No.1 and Favorita in 2014, respectively). Data are means and standard errors of three independent measurements. The same letter denotes no statistically significant difference at $P < 0.05$.

Table 2. Dry matter distribution in tubers at harvesting (%).

| Treatment | Kexin No.1 2013 | Favorita | Kexin No.1 2014 | Favorita |
|-----------|-----------------|----------|-----------------|----------|
| 35%       | 73.6 ± 2.69 b   | 74.7 ± 4.24 b | 65.6 ± 3.81 b   | 55.3 ± 3.53 b |
| 50%       | 82.0 ± 3.15 a   | 82.1 ± 3.83 a | 74.3 ± 1.65 a   | 73.8 ± 2.34 a |
| 65%       | 78.4 ± 7.22 a   | 81.7 ± 1.15 a | 70.5 ± 4.99 ab  | 58.3 ± 2.89 b |

* Values within a column with the same letter denote no statistically significant difference at $P < 0.05$.

Table 3. ABA and GA concentrations in different organs at the seedling stage under water deficit treatments (ng/gFW).

| Year  | Cultivar | Treatment | Root | Leaf | Stolon | Root | Leaf | Stolon |
|-------|----------|-----------|------|------|--------|------|------|--------|
| 2013  | Kexin No.1 | 35%       | 110.8 ± 4.4a | 140.1 ± 14.0a | 114.9 ± 23.3a | 9.7 ± 0.3b | 10.2 ± 0.2 c | 32.0 ± 0.5b |
|       |          | 50%       | 98.1 ± 2.7b  | 110.9 ± 11.9b | 71.7 ± 2.9b  | 10.0 ± 0.5b | 11.3 ± 0.2b | 32.0 ± 0.5b |
|       |          | 65%       | 89.8 ± 2.4c  | 97.6 ± 6.8c  | 59.0 ± 7.6c  | 11.2 ± 0.4a | 13.9 ± 0.7a | 10.6 ± 0.8a |
| Favorita | 35%       | 78.6 ± 2.4a | 131.2 ± 3.0a | -     | 6.6 ± 0.3c  | 7.4 ± 0.4c  | -     | -     |
|       |          | 50%       | 73.1 ± 1.5a  | 118.4 ± 2.2a | -     | 7.6 ± 0.3b  | 8.5 ± 0.2b  | -     | -     |
|       |          | 65%       | 66.2 ± 1.2b  | 82.3 ± 3.4c  | -     | 8.6 ± 0.4a  | 9.6 ± 0.5a  | -     | -     |
| 2014  | Kexin No.1 | 35%       | 111.8 ± 7.0a | 173.8 ± 13.6a | 87.3 ± 3.4a | 5.0 ± 0.1c  | 8.1 ± 2.1c  | 5.9 ± 0.2b |
|       |          | 50%       | 94.8 ± 1.6b  | 96.9 ± 15.1b | 66.9 ± 1.9b | 5.7 ± 0.4b  | 11.0 ± 0.3b | 6.2 ± 1.1b |
|       |          | 65%       | 76.3 ± 2.9c  | 73.3 ± 2.5c  | 59.1 ± 2.4c | 3.6 ± 0.5a  | 14.9 ± 0.3a | 6.5 ± 0.7a |
| Favorita | 35%       | 76.1 ± 3.3a | 94.6 ± 2.7a  | 103.2 ± 15.3a | 8.3 ± 0.4c  | 7.8 ± 2.1c  | 6.1 ± 0.2c  | -     |
|       |          | 50%       | 65.5 ± 1.9b  | 86.7 ± 1.6b  | 75.9 ± 8.6b | 9.0 ± 0.5b  | 11.0 ± 0.7b | 6.9 ± 0.3b |
|       |          | 65%       | 61.3 ± 0.8b  | 71.3 ± 5.0c  | 57.2 ± 4.2c | 10.6 ± 0.1a | 12.1 ± 0.4a | 8.0 ± 0.6a |

The sampling dates listed in the table were 12 and 13 DAE for cultivar Kexin No.1 and Favorita in 2013, 12 and 14 DAE for cultivar Kexin No.1 and Favorita in 2014, respectively.

GA stands for GA1 + GA3.

Values within a column with the same letter denote no statistically significant difference at $P < 0.05$.

"-", not determined.

The effects of exogenous ABA application

To clarify the possible regulatory influence of ABA on yield formation under water deficiency conditions at the seedling stage, exogenous ABA was applied after plant

tuber initiation stage in both cultivars and years (Figure 4). The ABA concentration in root exhibited similar changes as in leaf with plant development (data not shown). However, GAs, ZR and IAA exhibited no consistent changes or correlations with potato plant development (data not shown).
emergence under sand culture conditions (Table 4). The results indicated that exogenous ABA promoted dry matter accumulation, obtained the higher tuber yield. Moreover, the distribution of dry matter in tubers increased with increased exogenous ABA supply.

Discussion

The application of DI techniques to potato production is beneficial for conserving fresh water and achieving sustainable agricultural development. However, inadequate water supply during the crop’s most sensitive period may result in a dramatic yield decline despite saving some water, which is unexpected in potato production. In this study, we observed that the seedling stage was effective for application of DI. Moderate water deficiency (50% RWC) at that stage significantly increased final tuber yield compared to the control (65% RWC).

Inevitably, too little water (under 35% RWC) had a negative effect, dramatically reducing yield. These results were verified by the results from our two consecutive experimental years, in two potato cultivars (Figure 1).

LAI and dry matter accumulation were reduced by soil water deficiency conditions applied at the seedling stage (Figure 2 and Figure 3). In fact, the number of green leaves and leaf length are reportedly the two parameters most sensitive to moderate drought conditions, according to a previous study (Deblonde & Ledent, 2001). Moreover, weakened stomatal conductance and photosynthesis are well known to occur when plants are faced with water shortages (Liu et al., 2006; Monneveux et al., 2013). Thus, it is not difficult to understand the decline in LAI and dry matter accumulation under water stress conditions at the seedling stage. The growth rate was accelerated following water recovery during the

![Figure 4. Changes of abscisic acid (ABA) concentrations in leaf for (a) Kexin No.1 and (b) Favorita in 2013, (c) Kexin No.1 and (d) Favorita in 2014 during the early developmental period. The sampling dates were 7, 12 and 22 DAE for cultivar Kexin No.1, and 12, 17 and 22 DAE for cultivar Favorita in 2013; and 9, 13, 17 and 21 DAE for Kexin No.1, and 10, 14, 18 and 22 DAE for Favorita in 2014. Arrows in the figures stand for reinstated irrigation date. Data are means of three independent measurements.](image-url)
tuber initiation stage (Figure 2 and Figure 3). Our data showed that the values under moderate water deficiency treatment began to catch up with those in the control at the tuber initiation stage, and surpassed them at the tuber bulking stage during the re-watering process (Figure 2, Figure 3). Even under severe water deficiency conditions (35% RWC in this study), similar tendencies were exhibited, where both LAI and dry matter accumulation values exceeded those in the control by the end of the growth period (Figure 2 and Figure 3); the final yield was less than that in the control only because the dry matter distribution in the tubers was relatively lower (Table 2). It may be that, whether or not severe water deficiency prolongs the growth period and seedlings need more time to recover, if a longer time is allowed for growth, a higher yield might ensue.

In any case, water deficiency at the seedling stage stimulates potato growth during later developmental stages (Figure 2 and Figure 3). To determine the physiological mechanisms underlying this phenomenon, several phytohormones were measured and analyzed, particularly for ABA, which is well known for its response to water stress (Munemasa et al., 2015). Moreover, ABA was reported to have a significant positive effect on tuber development (Liu et al., 2006; Xu et al., 1998). Our results showed that the ABA contents in leaf increased with development proceeded from the seedling stage to tuber initiation stage (Figure 4). Under water stress increased ABA induced more dry matter distribution into tuber and promoted tuber development, which supported by our pot experiment (Table 4). However, severe water deficiency might prolong the growth period which delays the distribution of dry matter from aboveground to tuber, similar phenomenon reported in maize (Liu et al., 2012). Thus, the dry matter distribution into tuber decreased in 35% RWC compared to 50% RWC, regardless of the increase in ABA. We proposed stronger sink induced by moderate water deficiency at the seedling stage provides a basis for later yield promotion as water recovery, which is mediated by earlier ABA signaling. Indeed, more tuber initiated induced by moderate water deficiency at the seedling stage (Table 1).

Moreover, GAs promote stolon elongation and inhibit tuber formation (Cheng et al., 2017; Ševčíková et al., 2017). We detected no regular changes in GAs as plant development proceeded under normal or water-stress conditions (data not shown). It is possible that the GA has different structural variants: GA1 and GA3 were measured in this study, but there are many other undetermined GAs. Additionally, many results were for seedlings under tissue-culture or pot conditions, which differ significantly from field conditions (Kloosterman et al., 2007; Xu et al., 1998). There was also no discernible pattern in IAA and ZR amounts according to development at the seedling stage (data not shown). Moreover, the role of IAA in the tuberization process may be affected by auxin redistribution in stolon, but not by the change in its concentration, but by auxin redistribution in stolon (Roumeliotis et al., 2013).

Under water stress conditions at the seedling stage, ABA increased while GA levels declined, and the changes were proportional to the degree of water deficiency (Table 3). Following a period of stress, when the RWC recovered to the control level under all treatments, ABA and GAs showed the same level across treatments. However, no consistent changes were discernible in ZR or IAA amounts according to the type of soil water stress (data not shown). This demonstrated that ABA and GAs are major elements in the response to water stress at the seedling stage. A previous study also indicated that ABA could inhibit GA activity (Vreugdenhil., 2007). It is possible that the changes in GA concentrations under water stress seen in this study were induced by ABA. Thus, we propose that ABA is the key element in plant responses to water stress, and in regulating sink enhancement from seedling stage to tuber initiation stage.

Exogenous ABA, applied at the seedling stage, produced similar effects under moderate water stress, with both matter accumulation and yield formation accelerated during later stages. Moreover, more dry matter was distributed into the tubers (Table 4). Thus, ABA promotes sink capacity (tuber formation and enlargement) when potato seedlings are threatened by water stress at the seedling stage. It has reported that stronger sink activity promoted photosynthetic ability and CO₂ fixation in sweet potato (Sawada et al., 2003). This feedback mechanism may also occur in potato. Enhanced photosynthetic capacity is also beneficial for dry matter accumulation and tuber development during later developmental stages.

The point also supported by the difference between drought tolerance and sensitive cultivars, Kexin No.1 and Favorita respectively in this study. The tolerance cultivar exhibits higher ABA level than sensitive one in leaf and root under normal water supply. When faced water deficiency more ABA was induced and accumulated in drought tolerance cultivar compared to that in sensitive one (Table 3). Finally, the yield of tolerance cultivar is less cut down under severe water deficiency than sensitive cultivar (Figure 1).

We propose that root elongation and sink enhancement when plants experience water deficiency mediated by ABA is the major cause. Several reports have demonstrated that ABA mediates root elongation and root hair initiation under moderate water stress in various plants.
(Sharp et al., 1994; W. Xu et al., 2013). The positive effects of moderate ABA on root elongation in potato were also noted by our research group (unpublished data). When potato plants experience water stress at the seedling stage, the root systems developed better when the stress is not too severe. After water recuperation during later developmental stages, a well-developed root system is beneficial for the absorption of water and mineral nutrients, laying a foundation for increased LAI and dry matter accumulation and, ultimately, yield. Furthermore, increased tuber initiation and bulking induced by ABA strengthened the sink of plant when it faced water deficiency. The stronger sink promotes photosynthesis and matter accumulation by a feedback mechanism. However, more details of the mechanism are required.

Acknowledgments

This work was supported by the National Science Foundation of China (3216150149, 31460321), the Key Project of Inner Mongolia Autonomous Region (2020DZ0005, 2021SZD0004) and Research start-up funds of IMAU (NDYB2017-19).

Disclosure statement

No potential conflict of interest was reported by the author(s).

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