Plant Prod. Sci. 12(4) : 449—452 (2009)

【Short Report】

Effects of Drought and Shading on Non-structural Carbohydrate Stored in the Stem of Potato (*Solanum tuberosum* L.)

Xu Zheng[1,2], Yutaka Jitsuyama[1], Takayoshi Terauchi[1,3] and Kazuto Iwama[1]

([1]Research Faculty of Agriculture, Hokkaido University. Sapporo, 060-8589, Japan;
[2] China Guangxi Academy of Agricultural Sciences, Nanning, 530007, China;
[3]Sugarcane Experimental Station in Tanegashima, National Agricultural Research Center for Kyushu Okinawa Region (KONARC), 1742-1 Anno, Nishino-omote, Kagoshima 891-3102, Japan)

Abstract : Most studies on non-structural carbohydrate (NSC) are concentrated on the leaf and tuber, and little is known about NSC in the stem and its function. To test the hypothesis that NSC stored in stem contributes to stable tuber bulking under stress conditions, we grew plants in pots in a greenhouse under drought and shading conditions for 17 d during tuber bulking. Compared with the control, drought and shading significantly reduced leaf and stem dry weights (DW) and total NSC concentration in the main stem base. However, tuber DW increased by 77% in drought and by 46% in shading conditions relative to the control. The contributions of NSC loss in the stem to tuber DW increase in drought and shading conditions were 37% and 54%, respectively. This study suggests that NSC stored in the stem base is supplied to tuber under stress conditions to support tuber bulking.

Key words : Drought, Non-structural carbohydrate (NSC), Potato, Shading, Stem base.

Sucrose and starch are the final photosynthates in leaves, and sucrose translocates to sink organs through the stem in higher plants (Blankenship, 2002). Non-structural carbohydrate (NSC) can be stored in crop stems (Wardlaw and Willenbrink, 2000). Much of this NSC can be remobilized and transported to developing organs to increase their growth and yield (Setter et al., 1998).

Photosynthesis is limited by environmental factors, such as water, light, CO_2, and temperature (Flexas et al., 2006), and the limited photosynthesis results in less photosynthate translocation to sinks (Roitsch, 1999). When photosynthetic activity is depressed by stress, plant growth (Xu and Huang, 2000) and grain filling (Yang and Zhang, 2006) become more dependent on remobilized stem reserves. In wheat stem, larger storage polymers (fructans) are decomposed to smaller polymers under drought conditions (Virgona and Barlow, 1991), and total NSC concentration decreases when the daily radiation is lower than 16.6 MJ m^{-2} day^{-1} during the mid-milk ripe stage (Takahashi et al., 1993). The contribution of NSC stored in the stem to the grain yield of cereal crops can be more than 50% under stress conditions, but it is 5-33% in non-stress conditions (Hirano et al., 1998; Wardlaw and Willenbrink, 2000). These results suggest that stem reserves might act as a short-term buffer to maintain the supply of photosynthate to developing organs when the supply of photosynthate from source leaves can not satisfy the requirement of sinks (Takahashi et al., 1994; Wardlaw and Willenbrink, 2000).

In potato, because the leaf is the source organ and the tuber is the main storage organ, studies on NSC have almost concentrated on the leaf and tuber (Hartmutkolbe and Stephan-Beckmann, 1997a, 1997b; Kehr et al., 1998; Geigenberger and Stitt, 2000; Ghosh et al., 2000). However the potato stem also acts as a storage organ for NSC (Sato, 1981). Starch grains are observed in all parenchymatous tissues in the stem during the first half of the growth period and disappear during the last half (Yoshida, 1969). The NSC content of the stem changes with time, and weather conditions markedly influence the starch content (Hartmutkolbe and Stephanbeckmann, 1997a). The stem dry weight reach 340 g m^{-2} at the maximum shoot growth stage (around the end of flowering) (Zheng, unpublished), which suggests that a large amount of NSC is stored in the stem. However, the function of NSC stored in the stem is still unclear.

We hypothesized that NSC stored in the potato stem contributes to stable bulking under variable environmental conditions. To test this hypothesis, we examined the contribution of NSC stored in the stem to tuber bulking using plants grown in pots under drought and shading conditions in a greenhouse.

Materials and Methods

1. Plant materials

The study was conducted at the Field Science Center

Received 31 October 2008. Accepted 7 April 2009. Corresponding author: K. Iwama (iwama@res.agr.hokudai.ac.jp, fax+81-11-706-3878).
Abbreviations : DAE, days after emergence; DW, dry weight; LSD, least significant difference; NSC, non-structural carbohydrate.

for the Northern Biosphere of Hokkaido University, Sapporo, Japan (40°04'N, 141°20'E), using a late-maturing cultivar Konafubuki. In a greenhouse, seed tuber, fresh weight 50-60 g, were planted on 14 May 2004 in plastic trays (55×40 cm width, 17 cm depth) filled with vermiculite. After emergence, young plants were thinned by hand to two stems for each seed tuber and then transplanted to pots (25 cm diameter, 30 cm depth) filled with a volcanic ash sandy loam soil. Compound fertilizers (20 g pot^{-1}, N : P_2O_5 : K_2O : MgO =7 : 11 : 9 : 3) were incorporated into the soils. Water was poured to the bottom of each pot every evening to adjust the water level to 10 cm from the pot bottom until the treatment started.

Treatments of drought and shading began at 28 d after emergence (DAE) (about one week after tuber bulking and flower initiation) and finished at 45 DAE. The control plants were irrigated continuously and grew under full light. The plants in the drought treatment were not irrigated but grew under full light. The plants in the shading treatment were irrigated continuously but were shaded by suspending a black polypropylene fabric (Dionet50, Dio Chemicals, Ltd., Tokyo, Japan) 2 m above the soil surface, thereby reducing the light intensity to about 50% of the full light.

2. Sampling

The plants in 8 pots per treatment were sampled one hour after sunrise at 28 DAE (start of the treatment) in the control and at 45 DAE (end of the treatment) in both the control and two treatments. The top part of the main stem (5–10 cm from the stem top) and the main stem base (1–10 cm from the soil surface) were sampled. The samples were immediately put into an ice box and transported to the laboratory. To measure the stem, leaf and tuber DW of each plant, we collected the remaining stems, leaves and tubers from each pot and oven-dried them at 80°C for more than 72 hr. To measure the soil water content, we sampled one soil core (5 cm diameter and 100 cm^3 volume) under the seed tuber in each pot at 45 DAE after the plants were sampled. The soil samples were weighed before (soil wet weight) and after oven-drying at 130°C for more than 72 hr (soil DW). The soil water content was calculated as (soil wet weight – soil DW)/soil wet weight.

In the laboratory, samples of the main stem bases were cleaned with paper and the tissue of 4–6 cm from the cut end was sampled to analyze the NSC. Samples of the top part of the main stem were cut into 5 mm lengths. Then, 3 g fresh tissue from both the main stem base and the top part of main stems were stored at –20°C until carbohydrate analysis. To measure the dry-matter percentage of the samples, we weighed the remaining samples before and after oven-drying at 80°C for more than 72 hr.

3. NSC calculation

The hexose concentration was calculated as the sum of glucose and fructose concentrations. The total NSC concentration was calculated as the sum of hexose, sucrose and starch concentrations. In our previous study, starch was the main NSC of shoot and at least 70% of the total NSC was in the stem base, the middle stem and the top part of stem (data unpublished). Yoshida (1969), who investigated the dynamics of starch grains in potato stem tissues, found that starch grains appear from the base to the middle stem, and then to the top part of stem in the first half of the growth period. Stored starch grains gradually disappeared from the base to middle stem, but not from the top part at the later stage of growth. Therefore, in this study, the NSC content of the stem was calculated as the stem DW×the average of NSC concentrations in the top part and base of the main stem. The loss of NSC in the stem during treatment period was calculated as the NSC content before treatment – that after treatment. The contribution of NSC loss in the stem to the increase in tuber DW during the treatment was calculated as the loss of NSC in the stem/increased tuber DW×100.

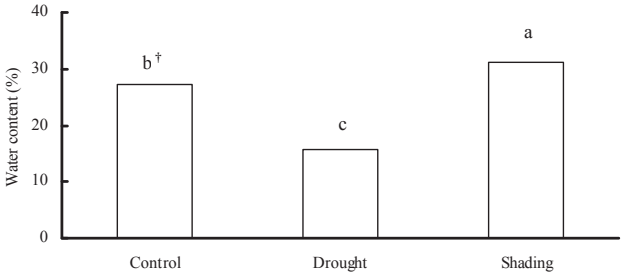

Fig. 1. Soil water content in each treatment at 45 d after emergence. † Different letters indicate differences among treatments based on the LSD test ($P \leqq 0.05$).

4. Statistical analysis

ANOVA was made by using SPSS Base 14.0 J for Windows (SPSS Inc., U.S.A.). The least significant difference (LSD) test at 0.05 probability level was used to evaluate the effects of the treatments on DW of each organ, NSC concentration and NSC contents of the stem, and soil water. The t-test was used to find the differences between the NSC content of the stem before and after the treatment in the control plants.

Results

1. Soil water content

Significant differences in soil water contents among the three treatments were observed at 45 DAE (Fig. 1). Compared with the control, the soil water content in the shading treatment was significantly higher and smaller in the drought treatment.

2. Effect of drought and shading on dry weight

In the control, leaf and stem DWs did not change significantly during the treatment period, but the total

Table 1. Effect of drought and shading on dry weight of pot-grown potatoes (g plant^{-1}).

Treatment	Leaf	Stem	Tuber	Total
Before treatment	17.9	40.0	21.4	79.3
t-test †	ns	ns	**	*
After treatment				
Control	18.0 a ‡	34.6 a	52.8 a	105.4 a
Drought	12.4 c	25.1 b	45.6 b	83.2 b
Shading	15.1 b	27.7 b	35.8 c	78.6 b

† ns, not significant ($P > 0.05$); *,**, significant at $P \leqq 0.05$, and 0.01, respectively, between the values before (28 d after emergence) and after the treatment (45 d after emergence) in the control. ‡ Means followed by the same letters within a column are not significantly different among the control and treatments based on the LSD test ($P > 0.05$).

Table 2. Effect of drought and shading on non-structural carbohydrate (NSC) concentration (mg g^{-1}DW) and content (g plant^{-1}) in the potato stem.

Treatment	NSC concentration (mg g^{-1}DW)								NSC content (g plant^{-1})† in the stem			
	Top part of stem				Stem base							
	Hexose‡	Sucrose	Starch	Total	Hexose	Sucrose	Starch	Total	Hexose	Sucrose	Starch	Total
Before treatment#)	132	3	325	459	93	3	244	340	4.5	0.1	11.4	16.0
t-test§	**	ns	ns	*	ns	**	ns	ns	ns	*	ns	ns
After treatment#)												
Control	67 a¶	12 a	229 a	308 a	112 a	30 a	207 a	349 a	3.1 a	0.7 a	7.6 a	11.4 a
Drought	75 a	16 a	211 a	302 a	93 ab	5 c	162 b	260 b	2.1 b	0.3 c	4.7 b	7.1 b
Shading	79 a	20 a	215 a	314 a	78 b	18 b	183 ab	279 b	2.2 b	0.5 b	5.5 b	8.2 b

† NSC content of the stem = (the sum of NSC concentration in the top part and base of the main stem) /2×stem DW. ‡ Hexose, fructose + glucose. #), Before treatment is at 28 d after emergence (DAE); After treatment is at 45 DAE. § ns, not significant ($P > 0.05$), *,**: significant at $P \leqq 0.05$, and 0.01, respectively, between the control treatment before and after treatment. ¶ Means followed by the same letters within a column are not significantly different based on the LSD test ($P > 0.05$).

DW increased significantly due to increased tuber DW (Table 1).

During the treatment period, drought and shading significantly reduced the leaf, stem and tuber DWs compared with the control; but senescence was not observed in leaf or stem. Tuber DW increased 31.4, 24.2 and 14.4 g plant^{-1} in the control, drought and shading treatments, respectively. Relative to the control, the tuber DW increase was 77% and 46% in the drought and shading treatments, respectively. Thus, total DWs in both drought and shading treatments were significantly lighter than in the control.

3. Effect of drought and shading on NSC concentration

In the control, the hexose, starch and total NSC concentrations in the main stem base did not change significantly during the treatment period (Table 2). In contrast, the hexose and total NSC concentrations decreased significantly in the top part of the main stem.

During the treatment period, the NSC concentrations in the top part of the main stem showed no significant difference between the control and treatments (Table 2). In the main stem base, however, drought significantly reduced the sucrose and starch concentrations, and shading significantly reduced the sucrose and hexose concentrations. Thus, both drought and shading significantly reduced the total NSC concentration.

4. Effects of drought and shading on NSC content

In the control plants, hexose, starch and total NSC contents of the stem did not change significantly during the treatment period (Table 2). Drought and shading significantly reduced the content of all NSCs and total NSC in the stem compared with the control.

During the treatment period, all NSCs in the stem decreased in both control and the two treatments, except the sucrose content (Table 3). The total amount of stem NSC loss was about 4.6, 8.9 and 7.8 g plant^{-1} in the control, drought and shading treatments, respectively. Starch was the main lost NSC and explained about 77% of the total NSC loss on the average three treatments. The proportion of NSC loss in the stem to the increased tuber DW was 14.6% in the control treatment, 36.8% in the drought treatment and 53.9% in the shading treatment, that is, 2.5 times and

Table 3. Loss of non-structural carbohydrate (NSC) in the potato stem and contribution of NSC loss in the potato stem to the tuber dry weight increase during the treatment period†.

Treatment	Changes in NSC content (g plant^{-1})				Contribution of lost stem NSC to increased tuber dry weight (%)
	Hexose	Sucrose	Starch	Total NSC	
Control	−1.4	0.6	−3.8	−4.6 (100)	14.6 (100)
Drought	−2.4	0.1	−6.7	−8.9 (193)	36.8 (252)
Shading	−2.3	0.4	−5.9	−7.8 (170)	53.9 (369)

† Treatment period: 28 to 45 d after emergence.

3.7 times higher in the drought and shading treatments, respectively, than in the control.

Discussion

In this study, tuber DW increased by 24.2 g plant^{-1} during drought treatment and 14.4 g plant^{-1} during shading treatment (Table 1), and the total NSC concentration in the main stem base in both treatments significantly decreased compared with the control plants (Table 2). These results suggest that NSC stored in the potato stem base is remobilized and transported to tubers. Yang et al. (2001) reported that soil drying increases both α-amylase and SPS activities, leading to fast hydrolysis of starch and increased remobilization of carbon in rice stems to grains. Total NSC concentration in stems of rice (Yoshida, 1972) and of wheat (Takahashi et al., 1993) decreases and this carbohydrate storage serves as a buffer to support grain filling at low intensity light during grain filling.

In wheat and rice crops, NSC stored in the stem acts as a buffer to maintain a steady rate of grain filling, especially when photosynthesis is seriously impaired due to drought or shading (Judel and Mengel 1982; Blacklow et al. 1984). Under normal conditions, the amount of stem NSC is more than 40% of the stem DW, and the contribution of these stored reserves is 5–20% of the grain yield (Shakiba et al., 1996). Under drought or heat stress after anthesis, however, photosynthetic activity is depressed and grain filling is more dependent on mobilized stem reserves and it contributed to 22–60% of the grain yield (Davidson and Chevalier, 1992; Blum et al., 1994). In this study, loss of NSC in the stem in drought and shading treatments contributed to about 37% and 54% of increased tuber DW, respectively, which was 2.5 and 3.7 times, respectively, higher than in the control (Table 3). These results indicate that translocation of NSC from the stem to the tuber is promoted under stress conditions to reduce the effect of depressed photosynthesis. These results also indicate that the NSC stored in potato stem plays an important role in increasing tuber DW under stress conditions as in rice and wheat.

In conclusion, our study showed that NSC stored in potato stem acts as a buffer to maintain tuber bulking. The stored NSC is used during the growing season and its translocation from the stem to the tuber is promoted under stress conditions to reduce the effect of depressed photosynthesis on tuber DW increase. The NSC stored in the potato stem plays an important role in increasing dry yield under stress conditions as in rice and wheat.

Acknowledgements

We thank S. Ichikawa and the students of the Crop Science Laboratory, Hokkaido University, for their technical assistance and support in management.

References

Blacklow, W.M. et al. 1984. Plant Sci. Lett. 36 : 213-218.
Blankenship, R.E. 2002. In L. Taiz and E. Zeiger eds., Plant Physiology (3rd ed.). Sinauer Assoc. Inc. Publ., Sunderland, Mass. 111-144.
Blum, A. et al. 1994. Aust. J. Plant Physiol. 21 : 771-781.
Davidson, D.J. and Chevalier, P.M. 1992. Crop Sci. 32 : 186-190.
Flexas, J. et al. 2006. Physiol. Plant. 127 : 343-352.
Geigenberger, P. and Stitt, M. 2000. Plant J. 23 : 795-806.
Ghosh, S.C. et al. 2000. Jpn. J. Trop. Agr. 44 : 158-166*.
Hartmutkolbe and Stephan-beckmann, S. 1997a. Potato Res. 40 : 111-129.
Hartmutkolbe and Stephan-beckmann, S. 1997b. Potato Res. 40 : 135-153.
Hirano, M. et al. 1998. Jpn. J. Crop Sci. 67 : 208-215*.
Judel, G.K. and Mengel, K. 1982. Crop Sci. 22 : 958-962.
Kehr, J. et al. 1998. Plant J. 16 : 497-503.
Roitsch, T. 1999. Curr. Opin. Plant Biol. 2 : 198-206.
Sato, K. 1981. Jpn. J. Crop Sci. 50 : 267-275**.
Setter, T.L. et al. 1998. In S. Nagarajan, G. Singh and B.S. Tyagi eds. Wheat Research Needs beyond 2000 AD. Narosa Publishing House, New Delhi, 237-255.
Shakiba, M.R. et al. 1996. J. Genet. Breed. 50 : 91-100.
Takahashi, T. et al. 1993. Jpn. J. Crop Sci. 62 : 560-564.
Takahashi, T. et al. 1994. Jpn. J. Crop Sci. 63 : 75-80.
Virgona, J.M. and Barlow, E.W.R. 1991. Aust. J. Plant Physiol. 18 : 239-247.
Wardlaw, I.F. and Willenbrink, J. 2000. New Phytol. 148 : 413-422.
Xu, Q. and Huang, B. 2000. Crop Sci. 40 : 1363-1368.
Yang, J. and Zhang, J. 2006. New Phytol. 169 : 223-236.
Yang, J. et al. 2001. J. Exp. Bot. 52 : 2169-2179.
Yoshida, M. 1969. Res. Fac. Agric. Hokkaido Univ. 7 : 209-215**.
Yoshida, S. 1972. Annu. Rev. Plant Physiol. 23 : 437-464.

* In Japanese with English abstract.
** In Japanese with English summary.