Ethylene inhibited sprouting of potato tubers by influencing the carbohydrate metabolism pathway

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Abstract The aim of this study was to investigate the role of ethylene to control sprouting of potatoes by observing the effect of exogenous ethylene on carbohydrate metabolism and key enzymes. The initial time of potato tuber sprouting and sprouting index were recorded, and rate of respiration, total sugar, total reducing sugar, starch, fructose, glucose, sucrose and the activities of acid invertase (AI), neutral invertase (NI), sucrose synthase (SS), sucrose phosphate synthase (SPS), starch phosphorylase and amylase during sprouting were measured. Exogenous ethylene inhibited sprouting of potato tubers. Moreover, exogenous ethylene increased respiration total sugar, AI activity, SPS activity, SS activity, and reduced sugar and assay activity. Nevertheless, starch, glucose, fructose, NI activity and starch phosphorylase activity showed lower variation. Lower sprouting resulted into potatoes with higher levels of total sugar, total reducing sugar and glucose, and lower level of fructose and sucrose. And sprouting could be inhibited by increasing the activities of SS, SPS and AI by treatment with $199.3 \mu\text{L L}^{-1}$ exogenous ethylene. Overall, exogenous ethylene inhibited sprouting of potato tubers by influencing its carbohydrate metabolism.

Keywords Potato tuber · Exogenous ethylene · Sprouting · Carbohydrate metabolism · Key enzymes

Introduction

Potato is one of the most important food crops in the world and is a main staple food for human consumption (Saraiva 2004), and sprout management was an important aspect of successful storage and distribution, to maintain good quality of the tubers for the intended purpose. Exogenous ethylene had been shown to inhibit potato sprouting, as described in several reports (Daniels-Lake et al. 2006, 2011). The effect of ethylene on sprouting was probably connected with changes in sucrose concentrations in potato tubers, there might be relation between carbohydrate and ethylene. Transgenic approaches, targeted to carbohydrate pathways in the plant, have shown that modifying carbohydrate metabolism affected tuber dormancy and sprouting (Vreugdenhil 2007).

Although there had been some research about sprout-inhibitory of ethylene (Prange et al. 2005) and its effect on sugar accumulation (Zhao et al. 2015; Foukaraki et al. 2016a, b), the reports about overall effect on carbohydrate and its mechanism was rare. In this work, potato tubers were treated by solid ethylene releasing agents as a matter of convenience, sprouting index, rate of respiration, starch and sugar contents, the activity of key sugar metabolizing enzymes were determined. The aim of this work was undertaken to examine how exogenous ethylene inhibited sprouting of potato tubers by regulating the carbohydrate metabolism pathway.

Materials and methods

Chemicals

Chromatographic grade acetonitrile and ultrapure water were used for HPLC analysis. All other chemicals used were of analytical grade.

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Plant material and ethylene treatments

“*Favorita*” potato stored in cold storage (about 4 °C) for 3 months, had passed dormant period, were immediately delivered to the laboratory, where tubers free of visual defects and of uniform size were selected. Potatoes were divided into three groups (about 15 kg) and packed in plastic bags, each containing the same number and three replicates of tubers.

The potatoes were treated by exogenous ethylene as follows. Three groups of potatoes were separated as control M_0 no treatment was done, M_1 and M_2 were treated by 91.7 and 199.3 $\mu\text{L L}^{-1}$ exogenous ethylene, respectively. At last, the potatoes were stored at 15 °C. The sampling for detecting sugar content and key enzymes of the potatoes was done on 0, 4, 8, 12, 16, 20 and 24 days, after treatment, respectively.

Sprouting index

Buds were considered to have sprouted once a sprout of minimum length 2 mm had formed, as defined by Zhao et al. (2015). Initial germination time and sprouting indexes of all treatment were recorded at sampling dates. The method was as follows: if all bud eye of the tuber didn't germinated, it was considered as level-0; level-1 was the tuber that the germination percentage of bud eye was lower than 25 %; level-2 was the tuber that the germination percentage of bud eye was between 25 to 50 %; level-3 was the tuber that germination percentage of bud eye was higher than 50 %. Calculation formula for evaluating the sprouting index was as follow:

$$\text{Sprouting index} = \sum_{i=0}^3 iX_i \times 100/T$$

In which: I = sprouting level; X_i = the tuber number of level- i ; T = the total number of tuber in plastic bag.

Respiration

Whole tuber respiration was evaluated by CO_2 production using an infrared gas analysis in an open system (Compact Minicuvette System CMS-400, Walz GmbH, Effeltrich, Germany) as described by Hajirezaei et al. (2003). The rate of respiration was reported as $\text{mg (kg h}^{-1}\text{)}$.

Soluble sugar determination

Total sugar, reducing sugar and starch

Extraction (1): 0.25 g of potato samples was extracted using water bath at 60 °C for 20 min with 50–60 ml water. Extraction (2): 0.2 g of samples was heated for

30 min in boiling water bath with 10 ml 6 M HCl and 15 ml water. Extraction (3): 0.2 g of potato samples was heated and dissolved with 3.2 ml 60 % perchloric acid and 3 ml water.

Extraction (1) and (2) were assayed using DNS reagent for total sugar and reducing sugar, respectively, as described in Hu et al. (2008). Read the value of sugar concentration corresponding to the absorbance from the calibration curve of glucose at a wavelength of 540 nm. Starch content was estimated by the method of Men and Liu (1995). This method involves dissolving starch in perchloric acid, diluting with distilled water, reacting with iodine solution and measuring the absorbance at a wavelength of 660 nm. Total sugar, reducing sugar and starch content was reported as micromoles of glucose and soluble starch equivalents (GAE) per milligram of dry weight. All spectrophotometric assays were run on a V-1100D spectrophotometer (Mapada, China).

Fructose, glucose, and sucrose

The procedure for carbohydrate determination has been previously described in detail (Olsen et al. 2003). Tuber tissue (1.5 g) was extracted in 40 mL of 80 % ethanol for 30 min by ultrasonic extraction using a SB-25-12DT ultrasonic cleaner (Scientz, China), filtered (Whatman No. 1). The extraction was evaporated under vacuum at 50 °C by RE-52AA rotary evaporator (Puredu, China), the residue was dissolved in 10 ml of mobile phase. The final extract was filtered through a 0.45 μm pore-size membrane filter, and immediately injected to HPLC as 20 μL . High performance liquid chromatography (Shimadzu, Japan) include hypersil NH_2 column (5 μm , 250 $\times$ 4.6 mm, Dalian Elite Analytical Instruments Co. Ltd., Deaic, China) and RID-10A detector. The column and detector temperature was 35 and 40 °C. The mobile phase was acetonitrile: water (70:30, v/v) with a flow rate of 1 ml min^{-1} . Peak areas for respective sugars (fructose, glucose, and sucrose) were recorded and sugar concentration (mg g^{-1} of tissue dry weight) was calculated using standard substance.

Enzyme assays

All procedures related to enzyme extraction were carried out at 4 °C or lower. Plant samples were extracted in 0.1 M PBS buffer (pH 7.5) containing 5 mM MgCl_2 , 1 mM EDTA, 1 mM EDTA 0.1 % (v/v) β -mercaptoethanol and 0.1 % (v/v) Triton X-100, at 4 °C, centrifuged at 10,000 rpm and 4 °C for 10 min, then the supernatant fluid into 10 ml calibration tube. The activities of SPS, SS, acid and neutral invertase were determined from the same extract.

Assay of activity acid invertase (AI) and neutral invertase (NI)

The measurement of activity of AI and NI was carried out according to the Nielsen et al. (1991). Procedure with some minor modifications. The soluble AI activity was assayed by adding 50 μ l reaction buffers (0.1 M pH 5.5 acetic acid buffer and 1 % sucrose) to 50 μ l crude enzyme, and incubated at 34 °C for 1 h. The controlled trial is that 50 μ l crude enzyme incubated at 100 °C for 10 min. The reaction was stopped by boiling the mixture for 5 min and adding 1.5 ml of 3, 5-dinitrosalicylic acid, after incubated in a water bath at 100 °C for 5 min. The mixture was set to the volume to 25 ml with distilled water. The soluble AI activity was assayed from the obtained light absorption value at a wavelength of 540 nm. The assay for NI activity was similar to that of AI except that the reaction was performed in phosphate buffer (pH 7.5). The resulting reducing sugars were estimated by Nelson-Somogyi method. Invertase activity was expressed in units of $\text{mg g}^{-1} \text{h}^{-1}$ FM.

Assay of sucrose synthase (SS) and sucrose phosphate synthase (SPS) activity

For the assay of sucrose phosphate synthase (SPS) and sucrose synthase (SS), the respective tissues were extracted following the method of Miron and Schaffer (1991). Assay mixture for SPS contained 0.1 M borate buffer (pH 8.0), 15 mM MgCl_2 , 5 mM fructose-6-phosphate, 15 mM glucose-6-phosphate, 10 mM UDP-glucose and enzyme extract. After incubation at 30 °C for 1 h, the reaction was stopped by adding 0.2 ml of 30 % KOH and then cooled to room temperature. The sucrose formed was determined by anthrone reagent. Background was determined by adding the stopping base before adding the enzyme. The reaction mixture for SS assay was similar to SPS assay but it contained 0.06 M fructose instead of fructose-6-phosphate and was devoid of glucose-6-phosphate. The sucrose hydrolysed during SS catalyzed reaction and sucrose formed during SPS catalyzed reaction were estimated according to Vassey et al. (1991). The enzyme activities were expressed as nmol sucrose hydrolysed or formed $\text{mg g}^{-1} \text{h}^{-1}$ FM, respectively.

Assay of starch phosphorylase activity

For determination of starch phosphorylase activity (Dubey and Singh 1999), plant materials from each treatment were homogenized in 5 ml buffer containing 100 mM sodium succinate (pH 5.8), 10 % glycerinum, 1 mM EDTA, 15 mM β -mercaptoethanol, 1 mM EDTA, 5 mM MgCl_2 and centrifuged at 15,000 rpm for 20 min at 4 °C. The

assay mixture contained 0.8 ml SDB [100 mM sodium succinate (pH 5.8), 0.1 % bovine serum albumin (w/v), 10 mM β -mercaptoethanol, 0.2 mM EDTA, 10 % glycerinum], substrate mixture [100 mM sodium succinate (pH 5.8), 5 % soluble starch (w/v), 0.1 mM glucose-1-phosphate 0.2 mM AMP] and enzyme extract to make the total volume up to 1.0 ml. The reaction was stopped after 10 min by adding 2.6 ml [2.6 g ammonium molybdate in 100 ml 14 % [v/v] sulfuric add]. The mixture was centrifuged and phosphorus content in the supernatant was estimated following the method of Fiske and Subbarow. The enzyme activity was calculated as nmol of P_i liberated $\text{mg g}^{-1} \text{h}^{-1}$ FM.

Assay of amylase

Amylase was assayed in colorimetry according to the method of Zhou (1995). The extract was performed in ice-bath. The homogenate was centrifuged at 3000 rpm for 15 min. The resulting supernatant was kept at 40 °C water-bath for 5 min following addition of 1 % starch solution, then kept boiling for 5 min after addition of DNS. The enzyme activity was measured by the absorbency of a wavelength of 525 nm, and was showed in the amount of maltose transformed in 5 min. The standard curve was obtained in the same way.

Statistical analysis

The statistical analysis was carried out using SPSS 17.0 (SPSS Inc., Chicago, IL). Results were expressed as mean values $\pm$ standard deviation. Means were compared by multivariate analysis followed by the Duncan's test. A difference was considered statistically significant when $P < 0.05$.

Results and discussion

Sprouting indexes and rate of respiration

The initial germination time of tubers of M_0 , M_1 and M_2 were 4, 4 and 5 days after treatment, (Fig. 1). Tubers exposed to ethylene (M_1 and M_2) exhibited lower sprouting indexes in proximal parts compared to the control (M_0) until 12 days, then, sprouting indexes of M_1 increased rapidly, and at the end of this experiment, they were higher than M_0 except for the last point (Fig. 1). After 24 days, the sprouting indexes of M_2 was the least, which was lower than that of M_1 ($P > 0.05$) and M_0 ($P < 0.05$).

Time-dependent changes in respiration rate were shown in Fig. 2 after the start of the ethylene treatment, tuber respiration rate began to increase rapidly. Respiration rates

were highest at 4 days after ethylene treatment, and then slowly declined. Compared to the untreated samples, $199.3 \mu\text{L L}^{-1}$ ethylene increased respiration by 15 %, while, respiration rates was significantly reduced by $91.7 \mu\text{L L}^{-1}$ ethylene.

Exogenous ethylene increased tuber respiration rates, affected tuber dormancy and sprouting (Gottschalk 2011). The trend of respiration rate in the present work was almost same as the previous report of Downes et al. (2010) that onion bulb respiration rate increased immediately after being treated with ethylene (Alexopoulos et al., 2008). And the result was also in line with potato tubers at 6 °C (Foukaraki et al., 2010).

Fig. 1 Sprouting indexes of potato tubers. Each value represents mean $\pm$ standard deviation of three replicates

Fig. 2 Respiration rate of potato tubers. Each value represents mean $\pm$ standard deviation of three replicates

Carbohydrate metabolism

Sugar contents and starch

As observed in Fig. 3a, the contents of total sugar in potato tubers of different treatments had a trend of increasing in the whole process. During first 4 days of storage the total sugar increased while, M_2 presented little decreasing between 4 and 12 days. After 24 days, the total sugar content of M_0 , M_1 , M_2 increased 62.73, 68.54, and 82.92 mg/g, respectively. Compared to the control, total sugar content of M_1 increased little ($P > 0.05$), but M_1 was higher than M_0 in the whole process. Exogenous ethylene of $199.3 \mu\text{L L}^{-1}$ promoted total sugar content, which was significant different from that of 12–20 days. It could be confirmed that total sugar could be strengthened by exogenous ethylene. Foukaraki et al. (2012) found that ethylene-treated tubers contained higher levels of total sugars, the present result confirmed that the increasing of total sugar be strengthened by exogenous ethylene.

Exogenous ethylene had remarkable effects on total reducing sugar content (Fig. 3b). After 24 days, the total reducing sugar content of M_0 , M_1 , and M_2 were decreased to 116.03, 100.9, 106.77 mg/g (Fig. 3b), respectively. Compared to the control, reducing sugar content of M_1 and M_2 were lower, and there was a significant difference between them ($P < 0.05$), and the total reducing sugar content of M_1 was much lower than M_2 ($P < 0.05$). An interaction between ethylene and CO_2 in the storage atmosphere has been reported, with higher concentrations of ethylene increasing tuber reducing sugar content (Daniels-Lake et al. 2009), the reason might be the different cultivar of potatoes used in study, in which the carbohydrate could present various responses to external stimulation.

As shown in Fig. 3c, the starch content decreases gradually. During first 4 days, the starch content of all treatments increased and then there was a large reduction from 4 to 8 days. The content of starch in M_0 , M_1 and M_2 reduced by 27.83, 19.23 and 37.19 %, respectively, after 24 days. At the end of storage, M_1 was higher markedly compare to M_2 ($P < 0.05$), while M_0 was much lower than M_1 and higher than M_2 ($P < 0.05$). Starch degradation had been discussed as an important event related to the induction of sprouting (Hajirezaei et al. 2003), who got that breakdown rate of starch was negatively correlated with respiration in potatoes. The results was in corroborated with previous report of Biemelt et al. (2000) showing that starch degradation was not a prerequisite for the initiation of sprouting. Considering the best sprouting inhibition effect, it could be assumed that lower starch level was beneficial for reducing the sprouting indexes. Exogenous

Fig. 3 Total sugar (a), total reducing sugar (b), starch (c) content of potato tubers. Each value represents mean $\pm$ standard deviation of three replicates

ethylene could reduce the disappearing of total reducing sugar.

Sucrose, fructose and glucose content

The changes of glucose, fructose and sucrose in tubers were shown in Fig. 4. The effect of exogenous ethylene on three kinds of monosaccharide were varied. As shown in Fig. 4a, the glucose content of M₂ was higher than the control ($P < 0.05$), while glucose content of M₁ was lower, and there was no significant difference between them. The change in glucose was similar earlier report (Frazier et al. 2006). Compared to M₀, fructose content of M₂ was declined significantly ($P < 0.05$), and M₁ was lower than M₀ ($P < 0.05$) (Fig. 4b), however, fructose content of all the three treatments changed little. In addition, significant difference could be found between any two of treatments ($P < 0.05$). It proved that higher level of exogenous

ethylene could decrease fructose content. Sucrose was reported as a prerequisite signalling molecule for hormonal dormancy control (Foukaraki et al. 2016a, b). Sucrose content in tubers was significantly decreased by exposure to exogenous ethylene, the effect of different treatment was in the order of M₁ < M₂ < M₀. In addition, significant difference was also observed between any two treatments ($P < 0.05$).

Ethylene might enhance the level of glucose (Foukaraki et al. 2012), and the effect reversed with increasing content of ethylene. Cools et al. (2011) observed that the levels of three sugars in onion were decreased to a variable extent on ethylene treatment which was consistent agreed with our results.

Based on the above analysis the lower sprouting development tended to present higher levels of respiration, total sugar, total reducing sugar, glucose, and lower fructose and sucrose in potatoes. In this work, the results show

Fig. 4 Glucose (a), fructose (b) and sucrose (c) content of potato tubers. Each value represents mean $\pm$ standard deviation of three replicates

that $199.3 \mu\text{L L}^{-1}$ exogenous ethylene could inhibited sprouting of potato and enhanced respiration total sugar, disappearing of total reducing sugar, decrease sucrose content.

Enzymes in carbohydrate metabolism

Invertase

A continuous increase with time in acid invertase (AI) activity was observed in both treatments (Fig. 5a). It can be seen that, AI activity of M_2 maintained a high level at the first 12 days, while, AI activity of M_1 was lower than the control, and there was a significant difference between them. Both M_0 and M_2 showed a decrease in the sprouting potato tubers between 12 and 16 days, while AI activity of

all treatments increased upto 8 days. After 24 days, the order of AI activity in potato tubers was $M_1 > M_2 > M_0$. Neutral invertase (NI) activity in potato tubers showed a rank of $M_2 > M_0 > M_1$, there was no significant difference from the control (Fig. 5b). Higher concentrations of exogenous ethylene significantly promoted the NI activity but significantly inhibited the activity of NI when the concentrations of exogenous ethylene were lower. Figure 5c showed the activity of invertase in potato tubers during 24 days, the activity of invertase was found to be increased in all treatments, (Fig. 5c). Both the activity of M_1 and M_2 were higher than the control M_0 ($P < 0.05$), but there was no significant difference between them.

Yao et al. (2005) pointed out that 400 mg L^{-1} ethephon raised the activities of acid and neutral invertases at late growth stage, which was therefore promoting the sucrose

Fig. 5 Carbohydrate metabolism-related enzyme activities. *Each value represents mean $\pm$ standard deviation of three replicates.* **a** acid invertase (AI), **b** neutral invertase (NI), **c** invertase, **d** sucrose synthase (SS), **e** sucrose phosphate synthase (SPS), **f** starch phosphorylase, **g** amylase

accumulation in the stalks. Wang and Zhang (2000) took apples as materials, spray with 300 mg L⁻¹ ethephon at the early stage of the mature fruit, the results showed that compared with the control and aminooxyacetic acid treatment, the neutral invertase activity were significantly improved, and the ethylene biosynthesis in starkrimson fruit was stimulated.

Sucrose synthase (SS) and sucrose phosphate synthase (SPS)

After 24 days, the SS activity of M₂ was significantly lower than M₁ ($P < 0.05$), although the amount of exogenous ethylene was elevated. Compared to M₀, SS activity of M₁ was increased significantly ($P < 0.05$), and M₂ was slightly lower than M₀ ($P > 0.05$) (Fig. 5d). In addition, significant difference could be found between any two of treatments ($P < 0.05$). In many plants, SS is known to be involved in sucrose cleavage rather than sucrose synthesis (Róth et al. 2007), it proved that higher level of exogenous ethylene could decrease activity of sucrose synthase.

The activity of sucrose phosphate synthase (SPS) was found to be increased by exposure of 199.3 µl L⁻¹ ethylene during 24 days. As illustrated in Fig. 5e. SPS activity of M₂ reached the maximum at 20 days, which was significantly higher than the control, but for M₁, no significant difference from the control was observed. After 24 days, the SPS activity was observed in the order M₂ > M₀ > M₁, which proved that higher level of exogenous ethylene could increase activity of SPS.

Wang et al. (2013) noticed that SPS was negatively correlated with sucrose content in cane, which was contrast with findings of Lingle (1999). Pan et al. (2007) reported that four enzymes made great contribution to sucrose accumulation in sugarcane internodes, and SAI, SS and NI were negatively while SPS was positively correlated with sucrose content in cane, respectively. Verma et al. (2011) emphasized that SPS activity was positively correlated with sucrose content and negatively correlated with hexose sugars content, but SS activity was negatively correlated with sucrose content and positively correlated with hexose sugars content. Changes of sugar contents due to exogenous ethylene treatment were supported by the changes of different sugar metabolizing enzymes. Increase in SPS, SS activity after 24 days (Fig. 5) was related decrease in sucrose content in the potato tubers resulting in a much lower sucrose content in the potato tubers of the exogenous ethylene treated than that of the control.

Starch phosphorylase (SP)

The activity of starch phosphorylase were had little change (Fig. 5f), there was no specific inclining or declining rule

of starch phosphorylase in the three treatments. At the first 4 days activity of starch phosphorylase of all treatments increased and reached the maximum at the 4 days, then, the activities of M₀, M₁ and M₂ were decreased during 4 to 12 days, and reached the minimum at the 12 days. After 24 days, the starch phosphorylase activity was in the order of M₂ > M₀ > M₁, and there was no significant difference between them. Chen and Cai (2005) also noticed that ethylene could stimulate the activities of acid invertase, amylase, sucrose synthase and sucrose phosphate synthase, inhibited the activity of amylase, while no significant effects to starch phosphorylase.

Amylase

In the process of exogenous ethylene exposure, the activity of amylase increased rapidly and reached a peak, and then decreased. At the first 4 days, the amylase activity of M₀ was lower than M₁ and M₂, both of M₀ and M₂ were highest at 8 days, while amylase activity of M₁ was highest at 12 days. After 24 days, the order of amylase activity in potato tubers was M₀ > M₁ > M₂.

Overall, ethylene was showed to stimulate the activities of acid invertase, amylase, sucrose synthase and sucrose phosphate synthase, inhibited the activity of amylase, while no significant effects to the neutral invertase and starch phosphorylase ($P > 0.05$).

Conclusion

Exogenous ethylene inhibited sprouting of potato, and increased respiration, total sugar, glucose, reduced fructose and sucrose. Besides, the lower sprouting development tended to present higher levels of respiration, total sugar, total reducing sugar and glucose, lower fructose and sucrose in potatoes. sprouting could be inhibited by increasing the activities of SS, SPS and AI by treatment with 199.3 µl L⁻¹ exogenous ethylene. Exogenous ethylene inhibited sprouting of potato tubers by influencing its carbohydrate metabolism.

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References

- Alexopoulos AA, Aivalakis G, Akoumianakis KA, Passam HC (2008) Effect of gibberellic acid on the duration of dormancy of potato tubers produced by plants derived from true potato seed. *Postharvest Biol Technol* 49(3):424–430

- Białecka B, Kępczyński J (2007) Changes in concentrations of soluble carbohydrates during germination of *Amaranthus caudatus* L. seeds in relation to ethylene, gibberellin A3 and methyl jasmonate. *Plant Growth Regul* 51(1):21–31
- Biemelt S, Hajirezaei M, Hentschel E, Sonnewald U (2000) Comparative analysis of abscisic acid content and starch degradation during storage of tubers harvested from different potato varieties. *Potato Res* 43(4):371–382
- Chen HP, Cai SY (2005) Correlation between active oxygen, ethylene and amylase of banana fruit in different grades of maturity. *Subtropical Plant Sci* 34(3):8–10
- Cools K, Chope GA, Hammond JP, Thompson AJ, Terry LA (2011) Ethylene and 1-methylcyclopropene differentially regulate gene expression during onion sprout suppression. *Plant Physiol* 156(3):1639–1652
- Daniels-Lake BJ, Prange RK (2009) The interaction effect of carbon dioxide and ethylene in the storage atmosphere on potato fry color is dose-related. *HortScience* 44:1641–1644
- Daniels-Lake BJ, Prange RK, Kalt W, Walsh JR (2006) Methods to minimize the effect of ethylene sprout inhibitor on potato fry colour. *Potato Res* 49(4):303–326
- Daniels-Lake BJ, Pruski K, Prange RK (2011) Using ethylene gas and chlorpropham potato sprout inhibitors together. *Potato Res* 54(3):223–236
- Downes K, Chope GA, Terry LA (2010) Postharvest application of ethylene and 1-methylcyclopropene either before or after curing affects onion (*Allium cepa* L) bulb quality during long term cold storage. *Postharvest Biol Tec* 55(1):36–44
- Dubey RS, Singh AK (1999) Salinity induces accumulation of soluble sugars and alter the activity of sugar metabolizing enzymes in rice plants. *Biol Plant* 42:233–239
- Fernie AR, Willmitzer L (2001) Molecular and biochemical triggers of potato tuber development. *Plant Physiol* 127(4):1459–1465
- Foukaraki, S.G., Chope, G.A., Terry, L.A., 2010. Ethylene exposure after dormancy break is as effective as continuous ethylene to control sprout growth in some UK-grown potato cultivars. In: XXVIII International Horticultural Congress on Science and Horticulture for People (IHC2010): International Symposium. 934. 1175–1181
- Foukaraki, S.G., Chope, G.A., Terry, L.A., 2012. 1-MCP application before continuous ethylene storage suppresses sugar accumulation in the UK-grown potato cultivar ‘Marfona’. *Acta Horticulturae*
- Foukaraki SG, Cools K, Chope GA, Terry LA (2016a) Impact of ethylene and 1-MCP on sprouting and sugar accumulation in stored potatoes. *Postharvest Biol Technol* 114:95–103
- Foukaraki SG, Cools K, Terry LA (2016b) Differential effect of ethylene supplementation and inhibition on abscisic acid metabolism of potato (*Solanum tuberosum* L.) tubers during storage. *Postharvest Biol Technol* 112:87–94
- Frazier MJ, Kleinkopf GE, Brey RR, Olsen NL (2006) Potato sprout inhibition and tuber quality after treatment with high-energy ionizing radiation. *Am Potato J Res* 83(1):31–39
- Gottschalk K (2011) Recent developments in potato storage in Europe. *Am Potato J Res* 38:85–99
- Hajirezaei MR, Bömke F, Peisker M, Takahta Y, Lerchl J, Kirakosyan A (2003) Decreased sucrose content triggers starch breakdown and respiration in stored potato tubers (*Solanum tuberosum*). *J Exp Bot* 54(382):477–488
- Hu R, Lin L, Liu T, Ouyang P, He B, Liu S (2008) Reducing sugar content in hemicellulose hydrolysate by DNS method: a revisit. *J Biobased Mater Bio* 2(2):156–161
- Kalt W, Prange R, Daniels-Lake BJ, Walsh J, Dean P, Coffin R (1999) Alternative compounds for the maintenance of processing quality of stored potatoes (*Solanum tuberosum*). *J Food Process Preserv* 23(1):71–81
- Lingle SE (1999) Sugar metabolism during growth and development in sugarcane internodes. *Crop Sci* 39:480–486
- Men FY, Liu MY (1995) Physiology of potato. China Agriculture Press, Beijing, pp 317–335
- Miron D, Schaffer AA (1991) Sucrose phosphate synthase, sucrose synthase and invertase activities in developing fruit of *Lycopersicon esculentum* mill and the sucrose accumulating *Lycopersicon hirsutum* Humb and Bonpl. *Plant Physiol* 95:623–627
- Nielsen TH, Skiarbek HC, Karlsen P (1991) Carbohydrate metabolism during fruit development in sweet pepper (*Capsicum annuum*) plants. *Plant Physiol* 82:311–319
- Olsen N, Thornton RE, Baritelle A, Hyge G (2003) The influence of storage conditions on physical and physiological characteristics of Shepody potatoes. *Potato Res* 46(1–2):95–103
- Pan YQ, Luo HL, Li YR (2007) Correlating analysis between sucrose content and the activities of four enzymes related to sucrose metabolism in sugarcane (*Saccharum officinarum* L) internodes. *Plant Physiol Commun* 43(5):861–864
- Prange RK, Daniels-Lake BJ, Jeong JC, Binns M (2005) Effects of ethylene and 1-methylcyclopropene on potato tuber sprout control and fry colour. *Am J Potato Res* 82:123–128
- Róth E, Berna A, Beullens K, Yarramraju S, Lammertyn J, Schenk A, Nicolai B (2007) Postharvest quality of integrated and organically produced apple fruit. *Postharvest Biol Technol* 45(1):11–19
- Saraiva JA (2004) Carvalho A and Machado F, Effect of a 50 MPa pressure treatment on green pea seeds germination. XLII European High Pressure Research Group Meeting, Lausanne
- Vassey TL, Quick WP, Sharkley TD, Stitt M (1991) Water stress, CO₂ and light effects on sucrose phosphate synthase activity in *Phaseolus vulgaris*. *Plant Physiol* 81:37–44
- Verma AK, Upadhyay PC, Verma S, Solomon SB (2011) Functional analysis of sucrose phosphate synthase (SPS) and sucrose synthase (SS) in sugarcane (*Saccharum*) cultivars. *Plant Biol* 13(2):325–332
- Vreugdenhil D (2007) The canon of potato science. *Potato Res* 50(3):371–373
- Wang YZ, Zhang DP (2000) Regulating effects of ethylene on carbohydrate metabolism in ‘Starkrimson’ apple fruit during the ripening period. *Acta Metall Sin* 27(6):391–395
- Wang AQ, Huang WJ, Niu JQ, Liu M, Yang LT, Li YR (2013) Effects of ethephon on key enzymes of sucrose metabolism in relation to sucrose accumulation in sugarcane. *Sugar Tech* 15(2):177–186
- Yao RL, Li YR, Huang YH, Yang LT, Zhang GR (2005) Effects of ethephon on invertases activities in relation to sucrose accumulation in sugarcane. *Guangxi Agric Sci* 36(2):106–109
- Zhao S, Chen QM, Fu MR, Yang XY, Qu QL, Dai HF (2015) The inhibition of exogenous ethylene generated by solid ethylene releasing agents on sprouting of potato tubers in relation to carbohydrate metabolism. *Qual Assur Saf Crop* 7(4):423–429
- Zhou Q (1995) Guide of plant physiological and biochemical experiment. China Agriculture Press, Beijing