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The inhibition of exogenous ethylene generated by solid ethylene-releasing agents on sprouting of potato tubers in relation to carbohydrate metabolism

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RESEARCH ARTICLE

Abstract

The effects of exogenous ethylene generated by solid ethylene-releasing agents on carbohydrate metabolism and sprouting in potato tubers at 15 °C were investigated in this study. Potato tubers were randomly divided into 4 groups, and treated with 0, 1, 2, and 3 bags of solid ethylene-releasing agents. The initial time of potato tuber sprouting and sprouting index were recorded. The rate of respiration, total sugar, total reducing sugar, starch, fructose, glucose, and sucrose content during the sprouting were determined. Our result indicated that exogenous ethylene inhibited the sprouting of potato tubers (sprout index from 0.583 to 1.125), whereas little effect on the initial time of sprouting was observed. Moreover, exogenous ethylene enhanced respiration slightly (less than 8.2%), elevated the total sugar (from 17.73 to 32.58 mg/g) and reduced sugar levels (from 0.23 to 4.43 mg/g). Nevertheless, the starch, glucose, and fructose content varied minimally. The sucrose content was decreased significantly by exogenous ethylene. Therefore, exogenous ethylene treatment could inhibit the potato sprouting process, and a dose-dependent relationship was observed between exogenous ethylene and sprouting index. The inhibitory effect of sprouting was related to carbohydrate metabolism, including changes in the total sugar, total reducing sugar, and sucrose content, to some extent.

Keywords: potato tuber, exogenous ethylene, solid ethylene releasing agents, sprouting, carbohydrate metabolism

1. Introduction

According to Salunkhe *et al.* (1974), one-fourth of all produce that is harvested is not consumed because of spoilage occurring between the time of harvest and the time of purchase by the consumer. As a result, billions of dollars are lost annually to growers, shippers, warehouse owners, and processors. The nutritive value and overall quality of potatoes can be diminished by sprouting. Therefore, sprout management is an important aspect of successful storage to maintain a good quality of tubers for the intended purpose. Numerous of reports showed that ethylene could control sprouting effectively (Prange *et al.*, 1998). Ethylene gas has been registered since 2002 in Canada and 2003 in the UK (Daniels-Lake *et al.*, 2005) because it is relatively innocuous to humans and other animals (median lethal dose (LD_{50}) for mice in air was 950,000 mg/kg) in comparison with several chemical sprouting inhibitors, e.g., chlorpropham (or CIPC), which has an oral LD_{50} in rat that is >2,000-4,200 mg/kg body mass (FAO, 2005). In many plants, including broccoli (*Brassica oleracea* var. *italica*) (Gapper *et al.*, 2005), onion (*Allium cepa*) (Chope *et al.*, 2012; Cools *et al.*, 2011), alfalfa (*Medicago sativa*) somatic embryos (Kępczyńska and Zielińska, 2013), it has been proved that sugars act as important molecules that relay information relation to the dormancy or sprouting.

An increasing in the concentration of CO_2 in the storage atmosphere, led to the consequent increase in the rate of dormancy breakage; hence, Coleman (1998) hypothesised that dormancy breakage was related to the changes in carbohydrate concentrations in potato tubers. The effect of ethylene on dormancy breakage was probably attributed to changes in the sucrose concentrations in potato tubers; moreover, there might be relation between carbohydrate and ethylene concentration, when the atmospheric CO_2

concentration was elevated, the sucrose level was increased owning to the upregulation of the expression of genes in the ethylene biosynthetic pathway (Seneweera *et al.*, 2003). Transgenic approaches, targeted to carbohydrate metabolism in the plant, have shown that modifications in the carbohydrate metabolism affect tuber dormancy and sprouting (Vreugdenhil, 2007).

As with carbohydrate metabolism and sprouting in potato tubers, Sonnewald (2001) determined that at the onset of sprouting, potato tubers turned into a source organ supporting the growth of the developing sprout. During this process, starch and protein degradation were initiated and soluble sugars and amino acids were formed. Nevertheless, initial support of sprout growth probably did not require mobilisation of a reserve but relied on pre-existing soluble sugars and amino acids. Sprouting regulation often involves several different metabolic pathways, and 2 sprout inhibitors can react. For example, ethylene and 1-methylcyclopropene suppress sprouting in onion via different mechanisms (Chope and Terry, 2008; Cools *et al.*, 2011).

Although some research has been conducted on the inhibitory effects of ethylene on sprouting (Prange *et al.*, 1998, 2005; Wills *et al.*, 2004), there are few reports investigating the overall effect of ethylene on carbohydrate and the underlying mechanisms. Studies investigating the effects of exogenous ethylene, a known sprouting regulator of potato, on sprouting behaviours and all kinds of carbohydrates have been undertaken. In this work, potato tubers were treated with solid ethylene-releasing agents as a matter of convenience, which is different from the ethylene gas or liquid ethephon that was used in previous reports. Then, the sprouting index, rate of respiration, total sugar, total reducing sugar, starch levels, and sucrose, fructose, and glucose content were determined. This study aimed to determine whether carbohydrate metabolism was involved in the inhibition of exogenous ethylene in potato sprouting.

2. Materials and methods

Chemicals

Chromatographic grade acetonitrile and ultrapure water were used for high-performance liquid chromatography (HPLC) analysis. All other chemicals used were of analytical grade.

Plant material and ethylene treatments

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

The potatoes were treated with solid ethylene-releasing agents (2.5 g per bag, the content of effective component is 20%, patent number CN101715810A) as follows: solid ethylene-releasing agents were dipped in water for 2 min and placed in the plastic bag, and the plastic bag was sealed immediately. Four groups of potatoes were separated: M_1 received no treatment and M_2, M_3, and M_4 were treated with 1, 2, and 3 bags of solid ethylene-releasing agents, respectively. At last, the potatoes were stored at 15 °C.

Every 3 days of storage, the fresh potatoes (3 bags per treatment each time) were taken out for respiration analysis: this process was continued for 18 days. The samples were washed, and a sample that was 10 mm in diameter from the top to the base of the tuber was taken with a puncher, quickly frozen in liquid nitrogen, and subjected to freeze-drying for about 24 h using a FD-1A-80 Vacuum Freeze Drying Machine (Beijing Boyikang Laboratory Apparatus Co. Ltd., Beijing, China P.R.). The dried potato slices were ground to fine powder in a JYL-B031 Multi-Mill (Jiuyang Co. Ltd, Jiangsu, China P.R.) and passed through a 24-mesh sieve. The powders were sealed in plastic bags and stored at room temperature until analysis.

Sprouting index

Buds were considered to have sprouted once a sprout of a minimum length of 2 mm had formed, as defined by Coleman (1998). The initial germination time and sprouting indexes of all treatments were recorded at sampling dates. The germination was classified as follows: level 0 = all the eyes of the tuber did not germinate; level 1 = the tuber germination percentage of bud eyes was lower than 25%; level 2 = the tuber germination percentage of bud eyes was between 25 and 50%; and level 3 = the tuber germination percentage of bud eyes was higher than 50%. The formula for evaluating the sprouting index was as follows:

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

Where 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 in Hajirezaei (2003). The rate of respiration was reported as mg/kg/h.

Total sugar, reducing sugar and starch

Extraction 1: 0.25 g potato samples was extracted using water bath at 60 °C for 20 min with 50-60 ml water. Extraction 2: 0.2 g samples was heated for 30 min in a boiling water bath with 10 ml 6 M HCl and 15 ml water. Extraction 3: 0.2 g potato samples was heated and dissolved with 3.2 ml 60% perchloric acid and 3 ml water.

Extraction 1 and 2 were assayed using 3,5-dinitrosalicylic acid reagent for total sugar and reducing sugar, respectively, as described by Hu *et al.* (2008). The sugar concentration was determined according to the absorbance value at a wavelength of 540 nm by using a glucose calibration curve. 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.

The total sugar, reducing sugar and starch content was reported as micromoles of glucose and soluble starch equivalents per milligram of dry weight. All spectrophotometric assays were performed on a V-1100D spectrophotometer (Mapada, Shanghai, China P.R.).

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, Ningbo, China P.R.), and was filtered (Whatman no. 1; Hangzhou Special Paper Industry Co., Ltd., Hangzhou, China). The extraction was evaporated under vacuum at 50 °C by RE-52AA rotary evaporator (Puredu, Shanghai, China P.R.), and 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 20 μl sample was immediately subjected to high performance liquid chromatography (HPLC; Shimadzu, Kyoto, Japan). HPLC included a Hypersil NH_2 column (5 μm, 250×4.6 mm; Dalian Elite Analytical Instruments Co. Ltd., Deaic, China P.R.) and RID-10A detector. The column and detector temperature was 35 and 40 °C, respectively. The mobile phase was acetonitrile:water (70:30, v/v) with a flow rate of 1 ml/min. Peak areas for respective sugars (fructose, glucose, and sucrose) were recorded, and the sugar concentration (mg/g of tissue dry weight) was calculated using a standard substance.

Statistical analysis

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

3. Results

Sprouting indexes

Figure l shows that the initial germination time of tubers of M_1 and M_2, M_3, and M_4 were 4 and 5 days after treatment, respectively. Tubers exposed to ethylene (M_2, M_3, and M_4) exhibited lower sprouting indexes in proximal parts than the control (M_1) until the 9th day; then, the sprouting indexes of M_2 and M_4 increased rapidly. At the end of this experiment, the sprouting indexes of M_2 and M_4 were higher than M_1 except for the last time point. The sprouting index of M_3 was the lowest.

Our results indicated that solid ethylene releasing agents could inhibit potato sprouting, which was also described in several reports (Daniels-Lake *et al.*, 2006; Jeong *et al.*, 2002; Prange *et al.*, 2005). Increasing its amount could reinforced the effect, while it may be not true that high concentrations of ethylene improve the inhibition, as described in previous reports (Daniels-Lake *et al.*, 2005; Wills *et al.*, 2004).

Moreover, the initial germination time of potato had no significant changes compared to other reports. For example, Prange *et al.* (1998) used 40 μl/l of ethylene gas to treat potatoes (Russet Burbank) at 9 °C, sprouting was delayed by 5-15 weeks. In report of Wills *et al.* (2004), 0.01 to 10 μl/l of ethylene gas delayed the sprout time (cv. Sebago) 20 to 32 days at 20 °C. These results may be caused by the cultivars and the storage temperature (Daniels-Lake *et al.*, 2006). In addition, the amount of ethylene was an important factor in

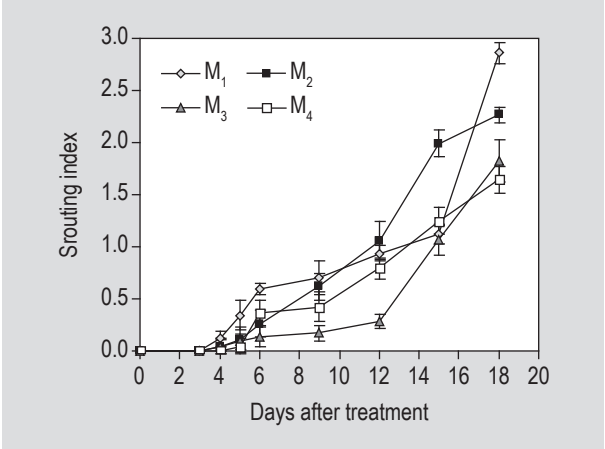

Figure 1. Effect of exogenous ethylene on sprouting indexes of potato tubers. Each value represents mean ± standard deviation of three replicates. M_1 = control; M_2, M_3, and M_4 = potato tubers treated by 1, 2, and 3 bags solid ethylene releasing agents, respectively.

the results. Suttle (1998) alluded to contradictory findings related to exogenous ethylene; Suttle (1998) reported that, depending on the concentration and duration of exposure, exogenous ethylene can hasten or delay tuber sprouting.

Rate of respiration

The rates of respiration of different treatment during storage are shown in Figure 2. All treatments display almost the same changes in the process, where there was a slightly increase in the first 3 days. Thereafter, the rate of respiration decreased; this decrease was steep at first, then gradual, and then did not change. This trend was almost the same as that report of Downes *et al.* (2010). It was likely that the sprout removal after the induction of sprouting caused a reduction in the rate of tuber metabolism (Alexopoulos *et al.*, 2008).

SPSS analysis revealed that the rank of respiration from different treatments was $M_2 < M_1 < M_4 < M_3$, and no overall significant differences were found among them ($P>0.05$). It seemed that solid ethylene releasing agents could minimise the increase in respiration rate except in M_2, but the effect was not more evident with an increased amount of ethylene. This result was in line with the results using onion at 20 and 28 °C (Cools *et al.*, 2011; Downes *et al.*, 2010) and potato tubers at 6 °C (Foukaraki *et al.*, 2012) which had a high respiration rate. The relationship was proved by Alexopoulos *et al.* (2009), who found that bromoethane could induce an increase in ethylene and respiration of potato seeds.

Furthermore, there might be a negative relationship between the respiration rate and sprouting. In view of the good inhibition of sprouting, it appeared that maintaining high respiration was ideal at 15 °C.

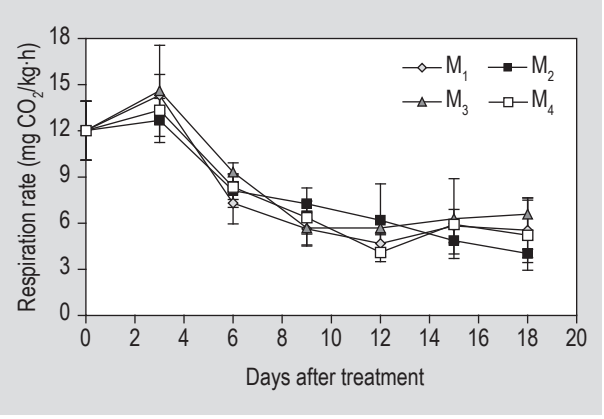

Figure 2. Effect of exogenous ethylene on the rate of respiration of potato tubers. Each value represents mean ± standard deviation of three replicates. M_1 = control; M_2, M_3, and M_4 = potato tubers treated by 1, 2, and 3 bags solid ethylene releasing agents, respectively.

Total sugar

As illustrated in Figure 3A, the total sugar content of all treatments increased remarkably in the first 3 days, following which, the level of increase was relatively lower. M_4 only a subtle decrease between the 3rd to the 12th day. The total sugar content of M_1, M_2, M_3, and M_4 rose 133.40, 139.24, 147.31 and 153.68 mg/g in the whole process, respectively.

During the whole process, the total sugar content of tubers treated with ethylene was remarkably high than that of the control ($P<0.05$). Moreover, the total sugar content of M_4 was lower than that of M_3 ($P<0.05$) and slightly higher than that of M_2 ($P>0.05$).

The increase in total sugar was strengthened by exogenous ethylene, which was consistent with the result of Foukaraki *et al.* (2012) was found in potato tubers that were treated with ethylene (10 µl/l) at 6 °C. The dose relationship between ethylene and total sugar was just contrary to the relationship between ethylene and sprouting index, which suggested that lower sprouting indexes tended to correlate with high levels of total sugar.

Starch

After 18 days, the starch content in potatoes of M_1, M_2, M_3, and M_4, decreased to 51.50, 17.26, 50.59, and 6.41 mg/g (Figure 3B), respectively. Starch degradation has been discussed as an important event related to the induction of sprouting (Fernie and Illmitzer, 2001). However, the starch content of M_2 and M_4 only slightly changed and was significantly higher than that of the control (M_1), especially in the later part of the experiment. In contrast, no obvious difference was observed between M_2 and M_4, and the starch content of M_3 was always lower than that of the control ($P<0.05$). It seemed that the effect on starch content was related to the amount of solid ethylene releasing agents.

Daniels-Lake *et al.* (2005) reported that starch breakdown was promoted by exogenous ethylene, while this was present only in M_3 in our experiments. Enhanced respiration (Figure 2) might explain this phenomenon; if the difference between M_1 and M_4 was ignored, it might be suggested that respiration promotes starch breakdown. Hajirezaei *et al.* (2003) also reported that the breakdown rate of starch was negatively correlated with respiration in potatoes. Nevertheless, it did not appear to have a close relationship with sprouting behaviour. Kalt *et al.* (1999) also observed the same result. This view was in agreement with that of a previous report of Biemelt *et al.* (2000), which showed that starch degradation was not a prerequisite for the initiation of sprouting. Considering the best sprouting inhibition effect, it could be assumed that a low starch level was beneficial to decrease of sprouting indexes.

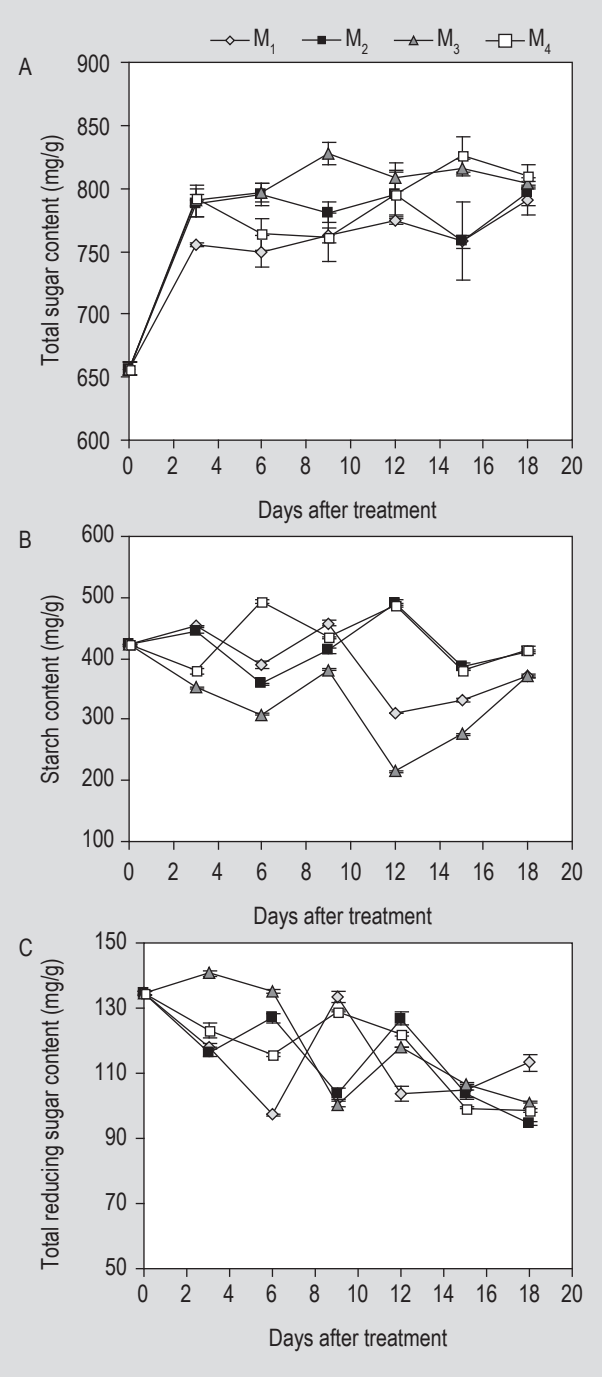

Figure 3. Effect of exogenous ethylene on (A) the total sugar, (B) starch, and (C) total reducing sugar content of potato tubers. Each value represents mean ± standard deviation of three replicates. M_1 = control; M_2, M_3, and M_4 = potato tubers treated by 1, 2 and 3 bags solid ethylene releasing agents, respectively.

Total reducing sugar

As shown in Figure 3C, the total reducing sugar content decreased gradually; the value was reduced 15.8, 29.7, 24.9, and 26.7% in M_1, M_2, M_3, and M_4, respectively, after 18 days. The reducing sugar content of M_2, M_3, and M_4 were higher than that of M_1, and were significantly different from that of control except M_2. The total reducing sugar content of M_4 was significantly lower than that of M_3 (P<0.05), although the amount of exogenous ethylene was elevated.

This could indicate that exogenous ethylene could decrease the total reducing sugar. Therefore, the higher level of reducing sugar might indicate lower sprouting indexes in potatoes.

Sucrose, fructose and glucose

The changes in the levels of 3 kinds of monosaccharide (fructose, glucose and sucrose) in tubers are shown in Figure 4. During storage, their content declined, and this decline was especially strong in sucrose (more than 22%). Nevertheless, the effect of exogenous ethylene on monosaccharide content varied. The declining trend of 3 kinds of monosaccharide was inconsistent with the trend in Russet Burbank potatoes at 3 °C (Coleman, 1998) and 9 °C (Kalt *et al.*,1999), and similar to the report about glucose content (declined 30% after 40 days; Frazier *et al.*, 2006), while the sucrose content had little change. The reason might be the different cultivar of potatoes used in the studies, which could result in carbohydrate presenting various responses to external stimulation (Buono *et al.*, 2009).

Compared to the control (M_1), the fructose content of M_2 increased slightly (P>0.05), while that of M_3 and M_4 significantly declined (P<0.05), and that of M_4 was slightly lower than that of M_3 (P>0.05) (Figure 4A). As shown in Figure 4B, the glucose content of M_2 and M_3 was higher than that of the control (P<0.05), and there was no significant difference between them. However, the glucose content of M_4 was obviously lower than that of other groups (P<0.01). The sucrose content in tubers was significantly decreased by exposure to exogenous ethylene, and the effect of different treatment was in the order of $M_3 < M_4 < M_2 < M_1$. In addition, a significant difference could be found between any 2 treatments (P<0.05). Seneweera *et al.* (2003) found the converse; that is, sucrose decreased with enhanced expression of genes in the ethylene biosynthetic pathway. This could result from the difference between endogenous and exogenous ethylene. Suttle (1998) demonstrated that endogenous ethylene is essential for full expression of potato microtuber endodormancy, and its involvement may be restricted to the initial period of endodormancy development.

The effect of ethylene on levels of fructose and glucose also varied with the amount of solid ethylene-releasing agents (Figure 4A and 4B). A high level of exogenous ethylene could decrease the fructose content, while a lower level of ethylene maintained the fructose content. Exogenous ethylene might enhance the glucose level (Downes *et al.*,

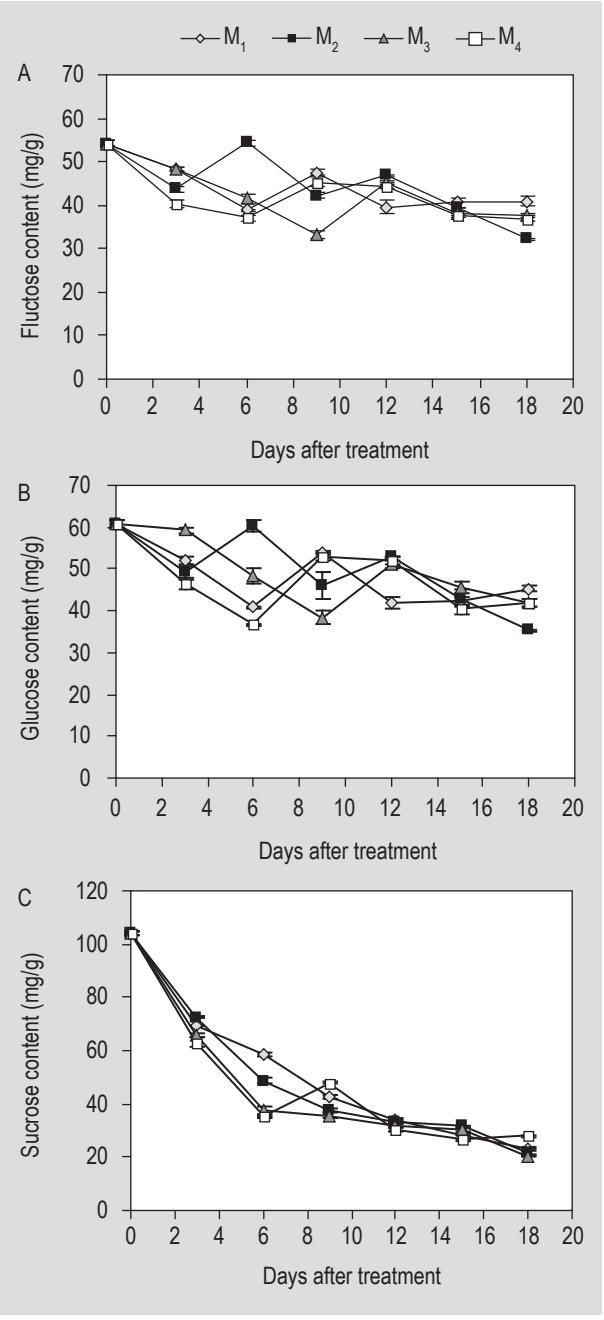

Figure 4. Effect of exogenous ethylene on (A) fructose, (B) glucose and (C) sucrose content of potato tubers. Each value represents mean ± standard deviation of three replicates. M_1 = control; M_2, M_3, and M_4 = potato tubers treated by 1, 2, and 3 bags solid ethylene-releasing agents, respectively.

2010; Foukaraki *et al.*, 2010, 2012), and the effect was reversed with increasing amounts of ethylene. It was also hypothesised that the levels of fructose and sucrose reduced, and that of glucose increased in response to reduced sprouting indexes in potatoes. In addition, the sucrose level decreased significantly in response to exogenous ethylene, and the effect was strengthened with increased volumes of exogenous ethylene. Cools *et al.* (2011) observed that the levels of 3 sugars in onion were decreased to different degrees in onion by ethylene when sprouting was inhibited, which agreed with our result concerning sucrose and partially agreed with our fructose and glucose results. A similar result was also observed in *Amaranthus caudatus L.* seeds treated with ethephon (Białecka and Kępczyński, 2007). The different results might be from the response of different plants to exogenous ethylene.

4. Conclusions

Exogenous ethylene inhibited sprouting in potatoes, increased respiration, total sugar, and total reducing sugar, and reduced fructose and sucrose. In addition, the lower sprouting development tended to correlate with higher levels of respiration, total sugar, total reducing sugar and glucose, and lower levels of fructose and sucrose in potatoes. However, the inhibitory effect of sprouting may result from the change in total sugar, reducing sugar and sucrose.

Furthermore, we found that there was no significant change in the initial germination time of potatoes. Therefore, the mode of ethylene release by the solid releasing-agents needs to be optimised in further research. It may also be useful to fine-tune the concentration of ethylene-releasing solid to apply to the tubers to elicit efficacious results. The time of exposure to the solid may be less critical because Rylski *et al.* (1974) and others have already demonstrated that long-term exposure to ethylene inhibits subsequent sprout growth.

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