



## Postharvest temperature has a greater impact on apical dominance of potato seed-tuber than field growing-degree days exposure

Raz Danieli<sup>a,b,1</sup>, Lior Blank<sup>c,1</sup>, Bolaji Babajide Salam<sup>a,b</sup>, Siva Kumar Malka<sup>a</sup>, Paula Teper-Bamnlker<sup>a</sup>, Avinoam Daus<sup>a</sup>, Uri Zig<sup>d</sup>, Michal Amichay<sup>e</sup>, Zion Shemer<sup>e</sup>, Amit Gal-On<sup>c</sup>, Dani Eshel<sup>a,\*</sup>

<sup>a</sup> Department of Postharvest Science, Volcani Center, ARO, Rishon LeZion, Israel

<sup>b</sup> The Robert H. Smith Institute of Plant Sciences and Genetics in Agriculture, The Hebrew University of Jerusalem, Robert H. Smith Faculty of Agriculture Food and Environment, Rehovot, Israel

<sup>c</sup> Department of Plant Pathology and Weed Research, ARO, Volcani Center, Rishon LeZion, Israel

<sup>d</sup> Hevel Maon Enterprises, Negev, Israel

<sup>e</sup> Ramat Negev Desert Agro-research station, Halutza, Israel

### ARTICLE INFO

#### Keywords:

Dormancy  
Growing-degree days  
Postharvest physiology  
Potato  
Propagation  
Stem branching

### ABSTRACT

The potato tuber is a swollen stem, which is used as the propagation material for commercial potato crops. At the end of a period of dormancy, the number of sprouts growing from the tuber nodes represent loss of tuber apical dominance (AD) resulting in branching. In Mediterranean countries, seed tubers cannot be kept in cold storage for a long period as it leads to over-branching of the seed tuber after replanting. In order to test the hypothesis that temperature exposure in the field effects dormancy length and/or AD postharvest, we exposed seed tubers to different numbers of growing-degree days (GDD) during their development. Seed tubers were cultivated at 0, 300 and 880 m above sea level (ASL), at three different planting dates. Crops were exposed to 780–1250 GDD and extended growth period induce linear accumulating GDD. For both cultivars, ‘Desiree’ and ‘Nicola’, there was a low correlation between GDD in the field and the number of days of storage at 2 °C before 70% of the tubers were released from dormancy. The main factor affecting the duration of dormancy period was the cultivar. In both cultivars, there was a low correlation between the seed-tuber crop’s exposure to GDD and the number of stems that emerged from the replanted tubers. The number of produced stems was mainly affected by the length of the storage period until replanting. Tubers that were replanted in the fall (following 130–190 d of storage) produced two to four stems each; whereas tubers replanted in the spring (following 210–270 d of storage) produced four to seven stems. There was a low correlation between mother-plant exposure to GDD in the field and total yield of the daughter plants. In both cultivars, exposure of the mother plants to different numbers of GDD did not have any significant effect on the size distribution of the tubers produced by the daughter plants. Extending the storage period did consistently induce yield of smaller sized tubers. We suggest that potato seed-tubers do not “remember” their GDD history and their AD is mainly affected by the duration of cold storage.

### 1. Introduction

The potato (*Solanum tuberosum* L.) tuber is a swollen underground stem formed by the swelling of subapical underground stolons (Harris, 1992). As the tuber elongates, a growing number of lateral bud (LB) meristems (called eyes) are formed in a spiral arrangement on its surface (Goodwin, 1967). After harvest, tuber buds are generally dormant and will not sprout or grow, even if the tubers are placed under optimal

conditions for sprouting (reviewed by Wiltshire and Cobb, 1996). The dormancy observed among harvested potato tubers is defined as endodormancy and is due to an unknown endogenous signal (or signals) that mediates the suppression of meristem growth (reviewed by Sonnewald and Sonnewald, 2014). Following a transition period of 1–15 weeks, depending on the storage conditions and the cultivar, dormancy is broken and ABs start to grow (Wiltshire and Cobb, 1996; Eshel, 2015). Typically one eye/sprout becomes dominant and inhibits

\* Corresponding author.

E-mail address: [dani@agri.gov.il](mailto:dani@agri.gov.il) (D. Eshel).

<sup>1</sup> These authors contributed equally to this article.

the growth of the other eyes, which are paradormant (Suttle, 2007; Teper-Bamnolker et al., 2012).

The nutrition hypothesis assumes that access to plant nutrients is the major factor regulating LBs growth (Phillips, 1975; Van den Ende, 2014; Buskila et al., 2016). Research centering on this hypothesis has shown that varying nitrogen supply can control the degree of AD (McIntyre, 1987; McIntyre, 1997), with nitrogen limitation delaying the activation of LBs (de Jong et al., 2014). This hypothesis has been narrowed down to the sugar nutrients, proposing that AD is maintained largely by the sugar demand of the shoot tip, which limits the amount of sugar available to the LBs (Mason et al., 2014; Rameau et al., 2014).

Apical dominance in potato tubers results in the apical bud (AB) exerting control over LB outgrowth. It is similar to the AD exerted by the shoot tip in many different plants (for review see Phillips, 1975; Cline, 1991; Dun et al., 2006; Leyser, 2009). Buskila et al. (2016) suggested that AD and its release may be divided into four developmental stages: the dormant-tuber stage, for which more than 2 weeks are needed for the AB to sprout at 14 °C; the active-tuber stage, during which LBs are dormant and less than 2 weeks is needed for the AB to sprout at 14 °C; the AD stage, during which LBs are suppressed by the AB; and AD loss, at which point the sprouting tuber has lost its AD and there are several developing LBs.

The dominance of the growing AB over the LBs decreases during storage and is one of the earliest morphophysiological indicators of the tuber's physiological age (Eshel, 2015). Teper-Bamnolker et al. (2012) observed three main types of loss of AD among stored potato tubers: loss of dominance of the Abs over those situated more basipetally on the tuber (Type I), loss of dominance of the main bud in any given eye over the subtending axillary buds within the same eye (Type II) and loss of dominance of the developing sprouts over their own branching, meaning that side stems do not emerge from the base of the sprout as in Type II (Type III). If tubers are kept in cold storage for a long time, they tend to sprout multiple stems and that phenomenon is referred to as tuber branching (Teper-Bamnolker et al., 2012; Salam et al., 2017).

Plant emergence, AD, tuber set and tuber size are all affected by the physiological age of seed tubers, which can substantially impact overall crop value (Knowles and Knowles, 2016). Sprout type is one of the earliest morphophysiological indicators of a seed tuber's physiological age (Eshel and Teper-Bamnolker, 2012; Eshel, 2015). The physiological age of a seed tuber is the physiological stage that influences its productive capacity (Struik, 2007). The physiological status of a seed tuber at any time is determined by genotype, chronological age and environmental conditions from tuber initiation through the emergence of the daughter plant (reviewed by Caldiz, 2009). Struik (2007) suggested that the cumulative temperature during postharvest storage is the most important factor affecting physiological aging, although its effect is moderated by light conditions and genetic factors. The physiological age of seed tubers affects future crop performance (O'Brien et al., 1983; Vakis, 1986; Van Loon, 1987; Moll, 1994).

A few studies have suggested that the physiological status of a seed tuber at any particular moment is determined by genotype, chronological age and environmental conditions from tuber initiation until new plant emergence (reviewed by Caldiz, 2009). In this study, our objective was to evaluate the effect of growing temperature and duration of cold storage on the performance of propagation material after replanting. We conducted an extensive three-year field study and found that storage duration has a stronger effect on the field productivity of potato seed tubers than the exposure to GDD during the growth of the seed-tuber crop.

## 2. Materials and methods

### 2.1. Plant material

Two different potato cultivars were used: 'Nicola' and 'Desiree'. Each of these cultivars has a different dormancy period. 'Nicola' is

considered a short-dormancy cultivar and 'Desiree' is considered to be a long-dormancy cultivar. Pre-basic-grade seed tubers were imported from Scotland in December 2013 and December 2014 and used as initial propagation material. The tubers used for the field trials had an average diameter of 35–45 mm.

### 2.2. Seed-tuber crops

Pre-basic-grade potato seed tubers were planted in three different locations and at three different dates in the years 2014 and 2015, so that the developing crops would be exposed to different numbers of GDD. Field trials were conducted at three locations in the northern Negev region of Israel: Kibbutz Saad [0 m above sea level (ASL)], Ashalim (300 m ASL) and Mitzpe Ramon (880 m ASL; Fig. 1).

Planting was carried out at three different times. The first planting was done in January, which is when local commercial growers generally plant potatoes and when temperatures are low. The second planting was done in February, which local growers consider to be a late planting time. The third planting was done in March, a time that is considered too late (i.e., too warm) by commercial growers (Fig. 1). When daughter tubers reached an average size of 45 mm (measured after sampling of 10 plants originated from the same planting date), the haulm was chopped and tubers were harvested after 14 d of skin set (during mid-May to June).

### 2.3. Calculation of GDD

Eight HOBO 8 K Pendant<sup>®</sup> temperature data-loggers (Onset; Bourne, MA, USA) were placed in each field, at a depth of 10 cm, which is where we would expect the daughter tubers to develop. Measurements were taken every 15 min for 5–6 months in each field. GDD was calculated using the following equation:

$$\Sigma \left( \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}} \right) \quad (1)$$

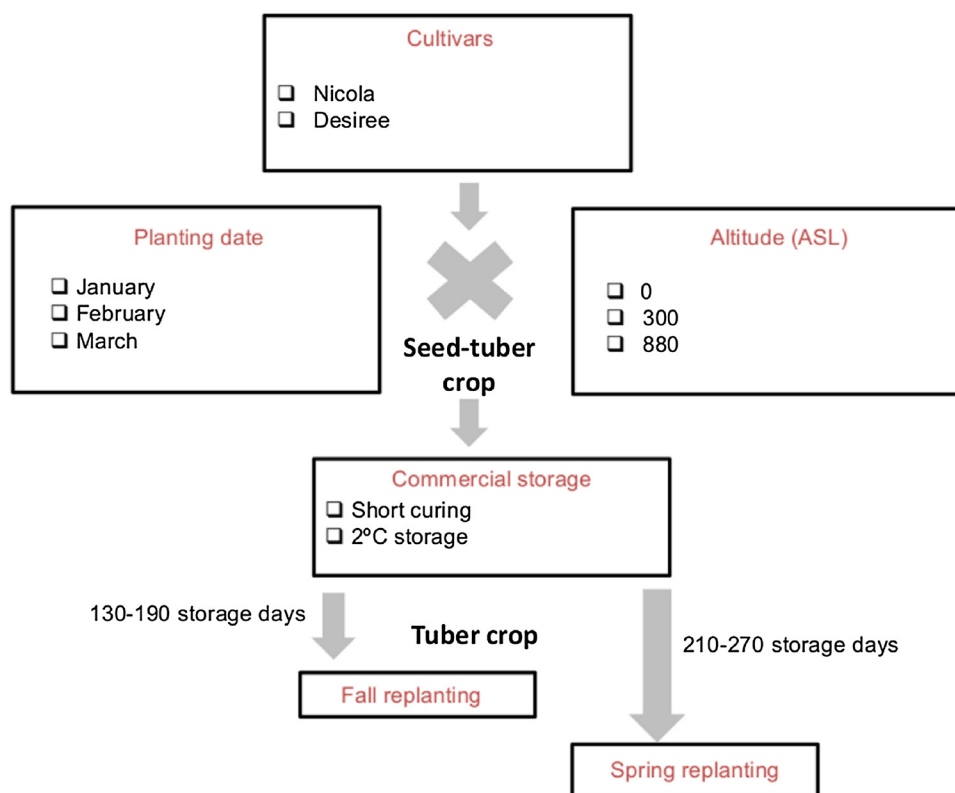
$\Sigma$  = the number of days in the period beginning 1 month after the planting date and ending on the day the haulm was chopped;  $T_{\max}$  = highest temperature;  $T_{\min}$  = lowest temperature;  $T_{\text{base}} = 2$  °C, at temperature at which we assume no growth occurs.

### 2.4. Determining the length of the dormancy period

After harvest, tubers were kept at 12 °C for 10 d of wound-healing and then transferred to a storage room kept at 2 °C and 95% RH (Fig. 1). For each treatment, every 2 weeks, we transferred 30 tubers from an environment kept at 2 °C to one kept at 14 °C and 85% RH, until sprouting, and counted the number of sprouting tubers every 10 d. A tuber was considered to be sprouting when at least one sprout had reached a length of at least 2 mm after 2 weeks at 14 °C. In this manner, we calculated the average number of days until 70% of the tubers had been released from dormancy.

### 2.5. Tuber crops

After storage, tubers sourced from all treatments (three growing areas and two to three planting dates) were replanted in one field, located at 300 m ASL, with 25-cm spacing (in row) in plots of 4 × 2 m that were arranged in randomized blocks with four replicates of each treatment. The field was cultivated according to the local commercial practice, briefly, seed tubers were treated preplanting with Pencycuron (Monceren 250; Bayer CropSciences) by applying 500 ml ton<sup>-1</sup> in low volume spray. During growth tuber were irrigated in total amount of about 40 m<sup>3</sup> ha<sup>-1</sup> and fertilized by ammonium nitrate. Seven treatments of 25 gr ha<sup>-1</sup> Mancozeb 75% (Manzidan, Dow AgroSciences) were applied during foliage development. After 90 d, at which point the daughter tubers had reached an average diameter of 45 mm, foliage was



**Fig. 1.** Field experiments in 2014 and 2015. Seed tuber-crops: Two potato cultivars were planted in three time points (January, February and March) at three different altitudes [0,300 and 880 m above sea level (ASL)]. All tubers were cured for 10 d and then transferred to 2 °C storage. Tuber crop: After storage, tubers were replanted for the next fall or spring season.

flailing by chain topper. Replanting was done twice for each lot, during the fall (after 130–190 d of storage) and spring (after 210–270 d of storage) seasons of 2014–2016 (Fig. 1).

## 2.6. Counting emerging stems

To study the effect of mother-plant GDD exposure on the field performance of the daughter plants, stored seed tubers from all treatments were replanted in the same field. About 30 d after planting, 40 plants were sampled (randomly 10 plants in each replicate) and their aerial stem emergence was evaluated.

## 2.7. Tuber crop yield

Tuber yield was evaluated in two different ways: the size distribution of the harvested crop and total yield. From each replicate, we sampled a plot of 4 m<sup>2</sup>. The collected tubers were then sorted into five size categories based on their diameter: 0–30 mm, 30–45 mm, 45–55 mm, 55–65 mm and greater than 65 mm. The tubers in each size category were weighed. Total yield was calculated as the sum of the weights of all of the tubers in all of the size categories. The results are displayed as ton ha<sup>-1</sup>.

## 2.8. Statistical analysis

To get a better understanding of the independent contribution of each variable, we applied hierarchical partitioning (Blank and Blaustein, 2014; Blank et al., 2016) using the Hier.part package (Nally and Walsh, 2004). We calculated  $R_N^2$  values (Nagelkerke, 1991) using the fmsb package (Nakazawa, 2014). All statistical analyses were carried out with R 3.1.0 (R Core Development Team).

## 3. Results

### 3.1. Effects of elevation and planting date on GDD exposure

In order to determine the effects of elevation and planting time on the GDD exposure of the daughter tubers, we measured the temperature in-row, at a depth of 10 cm, from the tuberization stage through haulm-chopping. Between February and July (2014 and 2015), the lowest daily underground (10 cm depth) average temperature was observed in the field located at 880 m ASL, where temperatures ranged between 7 and 22 °C. In both years, the temperature in that field was generally 2 and 4 °C lower than the temperature in the plots at 300 m ASL and at sea level, respectively (Fig. 2). The greatest difference was observed between May and July, when the ground temperature in the field at 880 m ASL was 18–20 °C, equivalent to the April ground temperature in the two other fields. Altitude also affected the daily day–night differences in temperature. Those differences were greater in the fields at 300 and 880 m ASL, in which we observed differences of 4–11 °C between day and night temperatures. In all treatments during 2014 and 2015, the period of time between the first tuberization of the daughter plants and the day that the haulm was chopped (at which point average tuber diameter was 45 mm) was 52–78 d in the year 2014 and 43–75 d in 2015 (Fig. 3). Crops planted at the earlier periods (January and February) took longer to develop (data not shown). The developing tubers were exposed to 780–1250 GDD in 2014 and 780–1000 GDD in 2015. As expected, the extended growth period induce linear accumulating GDD (Fig. 3).

### 3.2. The effect of field GDD on the length of the postharvest endodormancy period

In both cultivars, the linear regression between mother-plant GDD exposure and the amount of time the tubers needed to be stored at 2 °C before 70% of the tubers were released from dormancy was found to be low and not statistically significant (Fig. 4). Cultivar was the main

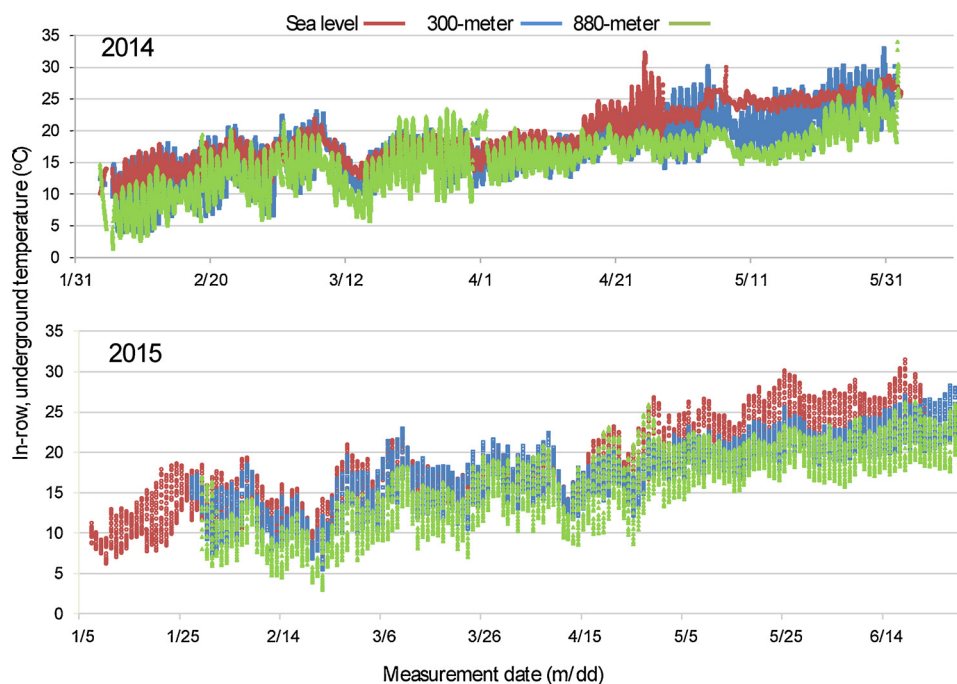


Fig. 2. Underground temperature as measured in 2014 and 2015 at Kibbutz Saad (0 m ASL), Ashalim (300 m ASL) and Mitzpe Ramon (880 m ASL). Sensors were placed in the rows at a depth of 10 cm (the depth at which daughter tubers are formed).

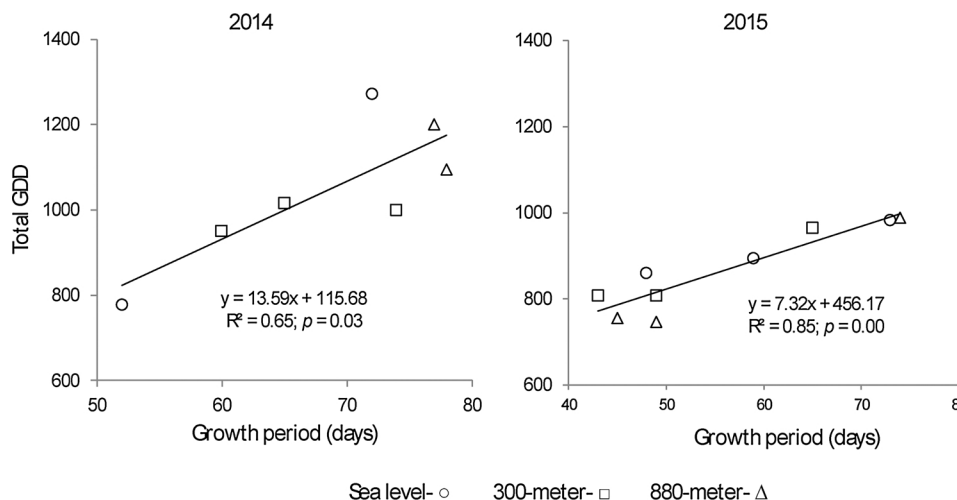


Fig. 3. Effect of the length of the growing period on accumulated GDD in potato plants grown at three different altitudes (0, 300 and 880 m ASL). The growing period is measured as the period beginning one month after planting and ending on the haulm-chopping date.

factor that affected the endodormancy period; ‘Desiree’ exhibited an average endodormancy period of 60–130 d after haulm-chopping and ‘Nicola’ exhibited an average endodormancy period of 40–80 d after haulm-chopping. Slope was significantly only for Desiree in 2015. This result indicated that there was association between endodormancy length and GDD.

### 3.3. The effect of mother-plant GDD exposure on the number of stems and yield of the daughter plants

In order to determine whether mother-plant GDD exposure affected the number of stems produced by the daughter plants grown from the stored tubers, tubers from all treatments were replanted at 300 m ASL. About 30 d after germination, aerial stems were counted. For both cultivars, the linear regression between the GDD exposure of the seed-tuber crop and the number of stems produced by plants grown from the

replanted tuber crop was mostly low (Fig. 5). The main effects, especially in 2014, were seen for duration of the storage period and replanting time (Fig. 5). Tubers that were replanted in the fall (September) produced two to four stems (on average); whereas tubers replanted for the spring season (January) produced four to seven stems on average (Fig. 5).

The effect of GDD on stem number was more pronounced for the longer storage period (spring to spring). The slopes of only two treatment were statistically significant- Nicola in 2014 (spring to fall) (p value = 0.0047) and for Nicola (spring to spring) (p value = 0.019). The fact that mostly the regression between stems number and GDD was not significant indicate that there is not association between this predictor (GDD) and the response (number of stems).

In both cultivars, ‘Desiree’ and ‘Nicola’, the correlation between mother-plant GDD exposure and the total yield of the daughter plants was low (Fig. 6). For example, seed tubers from mother plants exposed

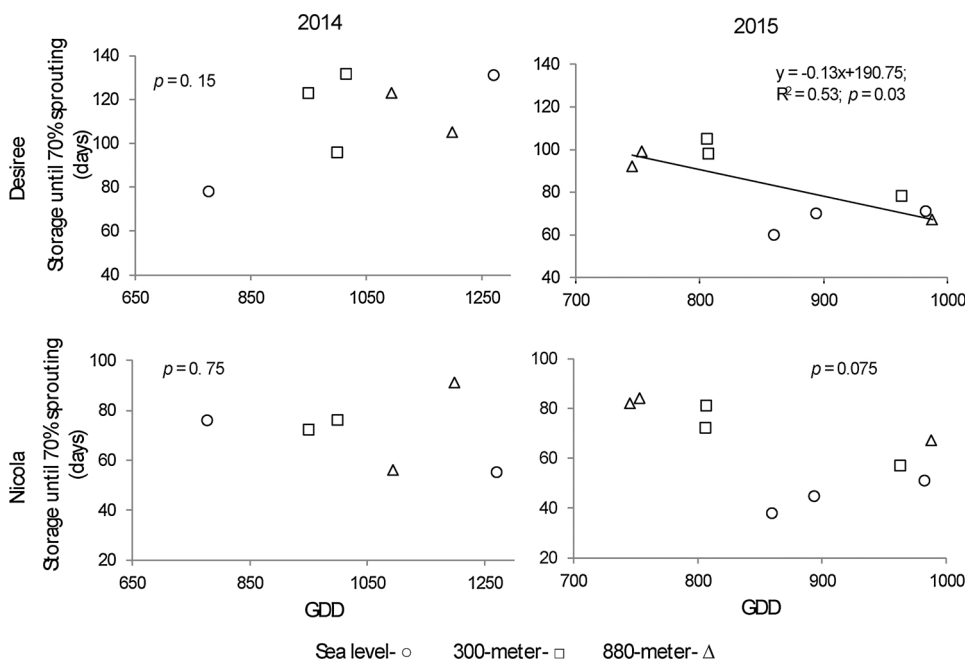


Fig. 4. Effect of preharvest GDD exposure on the duration of postharvest dormancy among the two examined cultivars. Tubers were stored at 2 °C and samples were transferred every 2 weeks to an environment kept at 14 °C. We measured the number of days between the harvest date and the date at which 70% of the tubers had sprouted (i.e., with at least one sprout that was at least 2 mm long after 2 weeks at 14 °C). Linear regressions were calculated to describe the correlation between preharvest GDD exposure and the duration of postharvest dormancy.

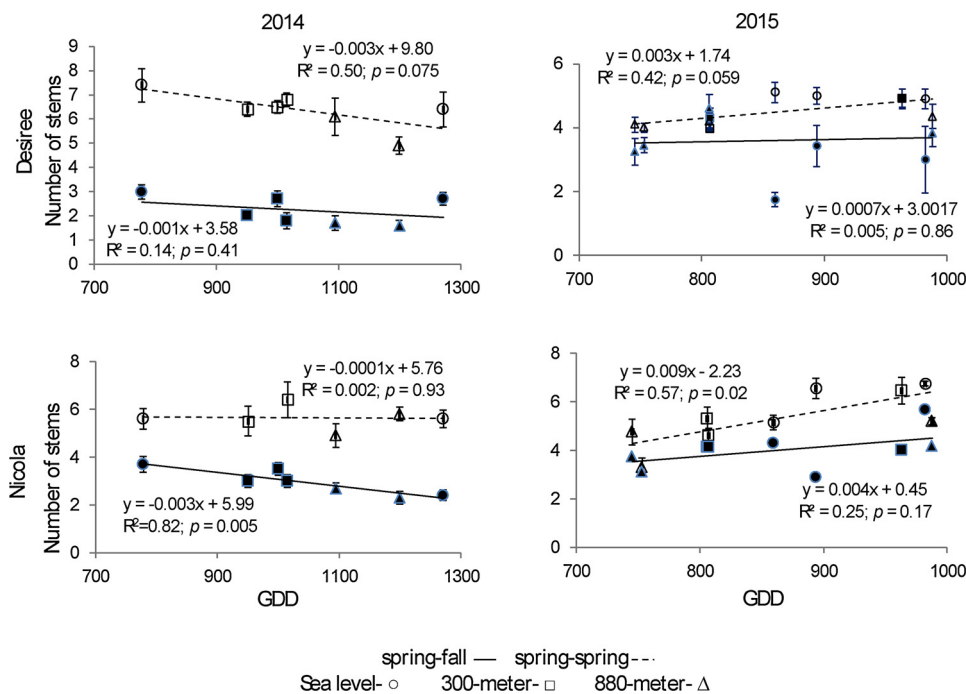


Fig. 5. Effects of GDD exposure of the seed crop and storage duration on the number of stems in the field for ‘Desiree’ and ‘Nicola’. Seed-tuber crops were grown during the spring season of 2014 or 2015 at three different altitudes (0, 300 and 880 m ASL). Harvested tubers were stored at 2 °C until the next fall or spring season. Each data point represents the average number of stems among 40 plants (10 plants in four replicates) at 30 d after germination. Error bars represent the standard error.

to 750 GDD during their development produced yields similar to those of seed tubers from mother plants that had been exposed to 1300 GDD (Fig. 6). A longer storage period induced a minor and non-significant increase in total yield in 2014 (Fig. 6).

Our analysis showed that storage duration did have an effect on the size distribution of the tuber crops (Fig. 7). GDD was divided into three categories: 700–850 d, 850–1000 d and 1000–1200 d. Storage duration was also divided into three categories: 130–170 d 170–220 d and 220–270 d. For both cultivars, GDD exposure of the mother plants did not have any dramatic effect on the size distribution of the tubers produced by the daughter plants (Fig. 7). However, reducing the duration of the storage period resulted in the production of larger tubers (Fig. 7).

The effect of storage duration on stem number was found to be

statistically significant for both cultivars. There were no significant differences between years (Table 1). Both GDD and duration of the storage period explained the variation in the number of stems better than they explained the variation in yield. This difference was more obvious for ‘Desiree’ (Table 2). Among both cultivars, storage duration accounted for much more of the variation in yield and stem number than GDD did (Table 3).

#### 4. Discussion

##### 4.1. Tuber postharvest dormancy is not affected by field GDD exposure

Dormancy is thought to be a physiological adaptation to intermittent periods of environmental limitations. This survival mechanism

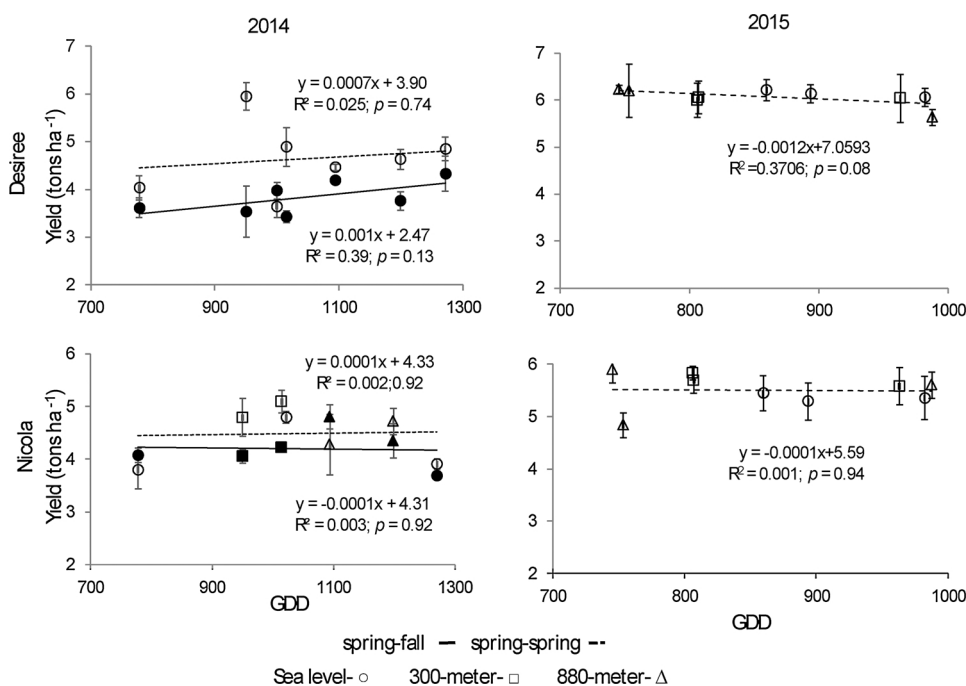


Fig. 6. Effect of GDD exposure of the seed crop on total yield after storage for 'Desiree' and 'Nicola' seed tubers. Seed-tuber crops were grown during the spring season of 2014 or 2015 at three different altitudes (0, 300 and 880 m ASL) and stored at 2 °C until the next fall or spring season. We sampled a plot of 4 m<sup>2</sup> for each replicate. Values represent an average of four replicates. Error bars represent the standard error.

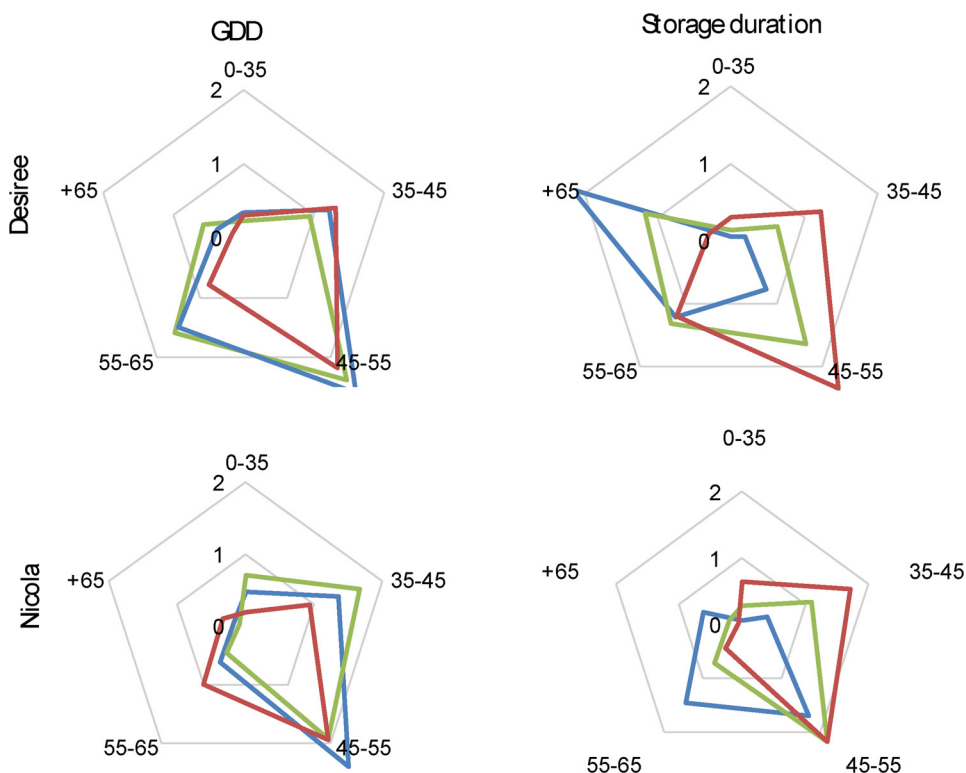


Fig. 7. Radar chart comparing the size distribution of the tuber crops as affected by the GDD exposure and duration of storage of the seed crop (first crop). GDD data were divided into three categories: 700–850 d (blue), 850–1000 d (green) and 1000–1200 d (red). Storage duration data were also divided into three categories: 130–170 d (blue) 170–220 d (green) and 220–270 d (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prevents the sprouting of daughter tubers after they are formed (Suttle, 2007). Previous studies have suggested that the duration of the endodormancy period is primarily dependent on genotype, but it has also been suggested that other factors, such as the conditions under which the crop was grown and storage conditions after tuber harvest may also affect the duration of the endodormancy period (Turnbull and Hanke, 1985; Wiltshire and Cobb, 1996). Our study showed that the GDD conditions during the development of the seed-tuber crop had no significant effect on the length of the endodormancy period following the cold storage of harvested tubers (Fig. 4). This finding suggests that as long as the tuber is attached to the mother plant, it does not

“remember” the exposure to GDD or that the postharvest effect of that exposure is negligible.

A few studies have shown that postharvest heat stress may induce early sprouting. Exposing potato tubers to a temperature of 33 °C for 2–3 weeks induced early sprouting when tubers were incubated at 14 °C immediately after the incubation at 33 °C (Salam et al., 2017). These results are in agreement with an earlier report on loss of AD in potato tubers upon short-term exposure to a range of high temperatures of 30–50 °C (Juknevičienė et al., 2011). Similarly, exposure of stems to extreme temperatures has been previously shown to induce early bud burst in trees such as ‘Anna’ apple (*Malus domestica* Borkh.; Wang and

**Table 1**  
Analysis of variance (ANOVA) results showing the effects of GDD, duration of the storage period (in days) and year on stem number in ‘Nicola’ and ‘Desiree’.

‘Desiree’	df	Sum Sq	Mean Sq	F	Pr (> F)
GDD	1	39.1	39.1	6.499	0.0151
Storage duration	1	514.1	514.1	85.537	3.7E-11
Year	1	2.9	2.9	0.481	0.4924
Residuals	37	222.4	6		

‘Nicola’	df	Sum Sq	Mean Sq	F	Pr (> F)
GDD	1	13.04	13.04	3.325	0.076
Storage duration	1	98.92	98.92	25.225	0.000
Year	1	0.34	0.34	0.088	0.769
Residuals	38	149.01	3.92		

**Table 2**  
The explained variance ( $R^2$ ) in a model including GDD and storage duration as independent variables and yield and number of stems as dependent variables.

		Yield	Number of stems
‘Desiree’	GDD + storage duration	0.16	0.71
‘Nicola’	GDD + storage duration	0.35	0.43

**Table 3**  
The independent contributions of GDD and storage duration (in days) to the explanation of yield and the number of stems, as determined by hierarchical partitioning for ‘Desiree’ and ‘Nicola’.

Hierarchical partitioning		Yield (UNITS)	Number of stems
‘Desiree’	GDD	23	3.5
	Storage duration	77	96.5
‘Nicola’	GDD	33	9
	Storage duration	67	94

Faust, 1994), red-osier dogwood (*Cornus sericea* L.; Shirazi and Fuchigami, 1995), poplar (*Populus nigra* Charkowiensis x *P. nigra* incassata; Wisniewski et al., 1997) and nectarine (*Prunus persica* var. *nectariana* cv. Shuguang; Yue et al., 2013). We can assume that the relatively mild conditions (avg. temperature of 7–25 °C) experienced during this study and the wide daily fluctuation in underground temperatures did not apply any acute stress to the developing daughter tubers (Fig. 2).

#### 4.2. The number of stems is determined mainly by the duration of the cold-storage period

The physiological age of seed tubers affects future crop performance (i.e., stem emergence rate, emergence rate, number of emerged stems per mother tuber, time to tuber initiation, crop vigor and growth, dry matter distribution and tuber yield) (O’Brien et al., 1983; Vakis, 1986; Van Loon, 1987; Moll, 1994; Knowles and Knowles, 2006). Struik (2007) defined the physiological age of a seed tuber as the physiological stage that influences its productive capacity. This suggests that the cumulative temperature during storage is the predominant factor affecting physiological aging, although its effect is moderated by light conditions and genetic factors.

In our study, we did not find any significant effect of GDD exposure during tuber growth on stem number or yield after replanting (Figs. 5 and 6). In our system, duration of storage had the strongest effect on those parameters. Storage at 2 °C prevented sprouting until planting in both seasons, fall and spring. A previous study showed that storage temperatures higher than 4 °C increase respiration and accelerate the physiological aging of seed tubers. Tubers exposed to a brief high-temperature, age-priming treatment and then kept at 4 °C for the remainder of a 190- to 200-day storage period maintained a higher basal

metabolic (respiration) rate throughout the storage period, as compared with tubers stored at 4 °C for the entire season (Blauer et al., 2013).

A few studies have demonstrated that high temperatures during tuber formation promote aging postharvest and after replanting (Went, 1959; Caldiz et al., 1985; Caldiz et al., 1999). The physiological age index developed by Caldiz et al. (2001) suggests that the main period that should be considered in determining tuber age is the period from the haulm-chopping date of the seed crop ( $T_0$ ) through the postharvest sampling date or planting date. In our study, only storage duration had a significant effect on stem number, a clear marker of tuber physiological age (Eshel and Teper-Bamnlker, 2012).

Our recent study of postharvest sugar accumulation in potato tubers showed that the sweetening of the tuber parenchyma during cold storage is correlated with the production of multiple stems (Salam et al., 2017). During tuber development, the storage parenchyma converts soluble assimilates (i.e., sucrose, amino acids) into polymeric reserves i.e., starch and storage proteins; (Prat et al., 1990; Visser et al., 1994). At maturity, over 70% of the tuber carbohydrate reserves are sequestered as starch, which must be converted into transport-compatible solutes for sprouting initiation and growth (Sonnewald, 2001; Viola et al., 2007). Within the tuber, a rapid shift from storage metabolism (starch synthesis) to reserve mobilization during postharvest storage suggests a transition from sink to source.

Sucrose synthesis appears as a dominant anabolic pathway in the storage parenchyma of dormant and sprouting tubers (Viola et al., 2007). Cold-induced sweetening resulting from the accumulation of reducing sugars in cold-stored potato tubers has been mainly studied for its impact on potato processing (Sowokinos, 2001; Dale and Bradshaw, 2003). During cold-induced sweetening, sucrose synthesis increases and some sucrose is transported to the vacuole, where it is hydrolyzed to glucose and fructose (Isherwood, 1973; Isla et al., 1998; Sowokinos, 2001). This step is predominantly controlled by vacuolar acid invertase, an enzyme strongly associated with the accumulation of reducing sugars during cold storage (Matsuura-Endo et al., 2004). Silencing of the vacuolar acid invertase gene (*VInv*) effectively controls cold-induced sweetening (Bhaskar et al., 2010; Zhu et al., 2016). The increased level of sucrose in *VInv*-silenced lines has been shown to be highly correlated with the loss of AD and an increased number of stems after replanting (Salam et al., 2017).

In this study, the dominant effect of the duration of cold storage on the number of stems produced after replanting emphasizes the importance of the sweetening process and suggests that it is the main cause for tuber branching (Salam et al., 2017). The development of methods to allow the prediction of future stem number based on the analysis of sugar levels in the seed tuber will enable the improved assessment of the physiological quality of seed tubers.

#### Acknowledgements

This research was funded by a grant from the Chief Scientist of the Ministry of Agriculture and Rural Development of Israel (no. 132174113). The manuscript is a contribution of the Agricultural Research Organization, Volcani Center, Rishon LeZion, Israel, No. 796/17.

The authors thank Dr. Leah Tsror and Prof. Abraham Gamliel, from ARO, The Volcani Center for their valuable suggestions and constructive criticism.

#### References

- Bhaskar, P.B., Wu, L., Busse, J.S., Whitty, B.R., Hamernik, A.J., Jansky, S.H., Buell, C.R., Bethke, P.C., Jiang, J., 2010. Suppression of the vacuolar invertase gene prevents cold-induced sweetening in potato. *Plant Physiol.* 154, 939–948.
- Blank, L., Blaustein, L., 2014. A multi-scale analysis of breeding site characteristics of the endangered fire salamander (*Salamandra atra*) at its extreme southern range limit. *Hydrobiologia* 726, 229–244.
- Blank, L., Cohen, Y., Borenstein, M., Shulhani, R., Lofthouse, M., Sofer, M., Shtienberg, D.,

2016. Variables associated with severity of bacterial canker and wilt caused by *Clavibacter michiganensis* subsp. *michiganensis* in tomato greenhouses. *Phytopathology* 106, 254–261.
- Blauer, J., Knowles, L., Knowles, N., 2013. Evidence that tuber respiration is the pace-maker of physiological aging in seed potatoes (*Solanum tuberosum* L.). *J. Plant Growth Regul.* 32, 708–720.
- Buskila, Y., Sela, N., Teper-Bamnolker, P., Tal, I., Shani, E., Weinstain, R., Gaba, V., Tam, Y., Lers, A., Eshel, D., 2016. Stronger sink demand for metabolites supports dominance of the apical bud in etiolated growth. *J. Exp. Bot.* 18, 5495–5508.
- Caldiz, D., Panelo, D., Claver, F., Montaldi, E., 1985. The effect of two planting dates on the physiological age and yielding potential of seed potatoes grown in a warm temperate climate in Argentina. *Potato Res.* 28, 425–434.
- Caldiz, D., Caso, O., Vater, G., Fernández, L., 1999. The potential for production of high quality seed potatoes in Tierra del Fuego Island, Argentina. *Potato Res.* 42, 9–23.
- Caldiz, D.O., Fernandez, L.V., Struik, P.C., 2001. Physiological age index: a new, simple and reliable index to assess the physiological age of seed potato tubers based on haulm killing date and length of the incubation period. *Field Crops Res.* 69, 69–79.
- Caldiz, D.O., 2009. Physiological age research during the second half of the twentieth century. *Potato Res.* 52, 295–304.
- Cline, M.G., 1991. Apical dominance. *Bot. Rev.* 57, 318–358.
- Dale, M.F.B., Bradshaw, J.E., 2003. Progress in improving processing attributes in potato. *Trends Plant Sci.* 8, 310–312.
- Dun, E.A., Ferguson, B.J., Beveridge, C.A., 2006. Apical dominance and shoot branching. Divergent opinions or divergent mechanisms? *Plant Physiol.* 142, 812–819.
- de Jong, M., George, G., Ongaro, V., Williamson, L., Willetts, B., Ljung, K., McCulloch, H., Leyser, O., 2014. Auxin and strigolactone signaling are required for modulation of arabidopsis shoot branching by nitrogen supply. *Plant Physiol.* 166, 384–395.
- Eshel, D., Teper-Bamnolker, P., 2012. Can loss of apical dominance in potato tuber serve as a marker of physiological age? *Plant Signaling Behav.* 7, 1158–1162.
- Eshel, D., 2015. Bridging dormancy release and apical dominance in potato tuber. In: Anderson, J.V. (Ed.), *Advances in Plant Dormancy*. Springer International Publishing, Switzerland, pp. 187–196.
- Goodwin, P., 1967. The control and branch growth on potato tubers: I. Anatomy of buds in relation to dormancy and correlative inhibition. *J. Exp. Bot.* 18, 78–86.
- Harris, P.M., 1992. *The Potato Crop: the Scientific Basis for Improvement*. Chapman and Hall, London.
- Isherwood, F.A., 1973. Starch-sugar interconversion in *Solanum tuberosum*. *Phytochemistry* 12, 2579–2591.
- Isla, M.I., Vattuone, M.A., Sampietro, A.R., 1998. Hydrolysis of sucrose within isolated vacuoles from *Solanum tuberosum* L. tubers. *Planta* 205, 601–605.
- Juknevičienė, P., Venskutoniene, E., Pranaitienė, R., Duchovskis, P., 2011. The influence of different temperatures and exposition time on potato tuber sprouting and development of plants. *Žemdirbystė (Agricuture)* 98, 131–138.
- Knowles, N.R., Knowles, L.O., 2006. Manipulating stem number, tuber set, and yield relationships for northern and southern-grown potato seed lots. *Crop Sci.* 46, 284–296.
- Knowles, L.O., Knowles, N.R., 2016. Optimizing tuber set and size distribution for potato seed (*Solanum tuberosum* L.) expressing varying degrees of apical dominance. *J. Plant Growth Regul.* 35, 574–585.
- Leyser, O., 2009. The control of shoot branching: an example of plant information processing. *Plant Cell Environ.* 32, 694–703.
- Mason, M.G., Ross, J.J., Babst, B.A., Wienclaw, B.N., Beveridge, C.A., 2014. Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc. Natl. Acad. Sci.* 111, 6092–6097.
- Matsuura-Endo, C., Kobayashi, A., Noda, T., Takigawa, S., Yamauchi, H., Mori, M., 2004. Changes in sugar content and activity of vacuolar acid invertase during low-temperature storage of potato tubers from six Japanese cultivars. *J. Plant Res.* 117, 131–137.
- McIntyre, G.I., 1987. The role of water in the regulation of plant development. *Can. J. Bot.* 65, 1287–1298.
- McIntyre, G., 1997. The role of nitrate in the osmotic and nutritional control of plant development. *Funct. Plant Biol.* 24, 103–118.
- Moll, A., 1994. The effects of physiological ageing of seed tubers on growth characteristics of eight potato cultivars tested under controlled conditions. *Potato Res.* 37, 11–20.
- Nagelkerke, N.J., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78, 691–692.
- Nakazawa, M., 2014. *Fmsb: Functions for Medical Statistics Book with Some Demographic Data*. R Package Version 0.4.5.
- Nally, R., Walsh, C.J., 2004. Hierarchical partitioning public-domain software. *Biodivers. Conserv.* 13, 659–660.
- O'Brien, P., Allen, E., Bean, J., Griffith, R., Jones, S.A., Jones, J., 1983. Accumulated day-degrees as a measure of physiological age and the relationships with growth and yield in early potato varieties. *J. Agric. Sci.* 101, 613–631.
- Phillips, I.D.J., 1975. Apical dominance. *Annu. Rev. Plant Physiol.* 26, 341–367.
- Prat, S., Frommer, W.B., Hofgen, R., Keil, M., Kossmann, J., Koster-Topfer, M., Liu, X.J., Muller, B., Pena-Cortes, H., Rocha-Sosa, M., 1990. Gene expression during tuber development in potato plants. *FEBS Lett.* 268, 334–338.
- Rameau, C., Bertheloot, J., Leduc, N., Andrieu, B., Sakr, S., Foucher, F., 2014. Multiple pathways regulate shoot branching. *Front. Plant Sci.* 5, 741.
- Salam, B.B., Malka, S.K., Zhu, X., Gong, H., Ziv, C., Teper-Bamnolker, P., Ori, N., Jiang, J., Eshel, D., 2017. Etiolated stem branching is a result of systemic signaling associated with sucrose level. *Plant Physiol.* 175, 734–745.
- Shirazi, A., Fuchigami, L., 1995. Effects of near-lethal stress on bud dormancy and stem cold hardiness in red-osier dogwood. *Tree Physiol.* 15, 275–279.
- Sonnenwald, S., Sonnenwald, U., 2014. Regulation of potato tuber sprouting. *Planta* 239, 27–38.
- Sonnenwald, U., 2001. Control of potato tuber sprouting. *Trends Plant Sci.* 6, 333–335.
- Sowokinos, J.R., 2001. Biochemical and molecular control of cold-induced sweetening in potatoes. *Am. J. Potato Res.* 78, 221–236.
- Struik, P., 2007. The canon of potato science: 40. Physiological age of seed tubers. *Potato Res.* 50, 375–377.
- Suttle, J.C., 2007. Dormancy and sprouting. In: Vreugdenhil, D. (Ed.), *Potato Physiology and Biotechnology. Advances and Perspectives*. Elsevier, Amsterdam, pp. 287–309.
- Teper-Bamnolker, P., Buskila, Y., Lopesco, Y., Ben-Dor, S., Saad, I., Holdengreber, V., Belausov, E.d., Zemach, H., Ori, N., Lers, A., Eshel, D., 2012. Release of apical dominance in potato tuber is accompanied by programmed cell death in the apical bud meristem. *Plant Physiol.* 158, 2053–2067.
- Turnbull, C.G.N., Hanke, D.E., 1985. The control of bud dormancy in potato tubers. *Planta* 165, 359–365.
- Vakis, N., 1986. Influence of physiological ageing of seed potatoes on yield and earliness. *Potato Res.* 29, 417–425.
- Van Loon, C., 1987. Effect of physiological age on growth vigour of seed potatoes of two cultivars. 4. Influence of storage period and storage temperature on growth and yield in the field. *Potato Res.* 30, 441–450.
- Van den Ende, W., 2014. Sugars take a central position in plant growth, development and stress responses: a focus on apical dominance. *Front. Plant Sci.* 5.
- Viola, R., Pelloux, J., van der Ploeg, A., Gillespie, T., Marquis, N., Roberts, A.G., Hancock, R.D., 2007. Symplastic connection is required for bud outgrowth following dormancy in potato (*Solanum tuberosum* L.) tubers. *Plant. Cell Environ.* 30, 973–983.
- Visser, R.G.F., Vreugdenhil, D., Hendriks, T., Jacobsen, E., 1994. Gene expression and carbohydrate content during stolon to tuber transition in potatoes (*Solanum tuberosum*). *Physiol. Plant.* 90, 285–292.
- Wang, S.Y., Faust, M., 1994. Changes in the antioxidant system associated with budbreak in 'Anna' apple (*Malus domestica* Borkh.) buds. *J. Am. Soc. Hortic. Sci.* 119, 735–741.
- Went, F., 1959. Effects of environment of parent and grandparent generations on tuber production by potatoes. *Am. J. Bot.* 46, 277–282.
- Wiltshire, J.J.J., Cobb, A.H., 1996. A review of the physiology of potato tuber dormancy. *Ann. Appl. Biol.* 129, 553–569.
- Wisniewski, M., Sauter, J., Fuchigami, L., Stepien, V., 1997. Effects of near-lethal heat stress on bud break, heat-shock proteins and ubiquitin in dormant poplar (*Populus nigra* *Charkowiensis* × *P. nigra* *incrassata*). *Tree Physiol.* 17, 453–460.
- Yue, T., Ling, L., Chuan-yuan, L., Dong-mei, L., Xiu-de, C., Dong-sheng, G., 2013. Respiratory response of dormant nectarine vegetative buds to high temperature stress. *J. Integr. Agric.* 12, 80–86.
- Zhu, X., Gong, H., He, Q., Zeng, Z., Busse, J.S., Jin, W., Bethke, P.C., Jiang, J., 2016. Silencing of vacuolar invertase and asparagine synthetase genes and its impact on acrylamide formation of fried potato products. *Plant Biotechnol. J.* 14, 709–718.