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

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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

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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® 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:

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

Σ = 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_{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^{-1} in low volume spray. During growth tuber were irrigated in total amount of about 40 $m^3\,ha^{-1}$ and fertilized by ammonium nitrate. Seven treatments of 25 gr ha^{-1} Mancozeb 75% (Manzidan, Dow AgroSiences) were applied during foliage development. After 90 d, at which point the daughter tubers had reached an average diameter of 45 mm, foliage was