Greenhouse vapour pressure deficit and lighting conditions during growth can influence postharvest quality through the functioning of stomata

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Abstract

There is a tendency in horticulture to grow plants in greenhouses with high humidity and prolonged light periods, especially in winter. Although plants grow well in greenhouses with high relative humidity (RH) (low vapour pressure deficit; VPD), the plants produced under such greenhouse climates have limited control over water loss after harvest, leading to uncontrolled transpiration and decreased water content in the postharvest stage. This results in shortened vase-life of cut flowers and decreased quality of leafy vegetables. When plants had been produced in greenhouses with moderate humidity and natural day length, their stomata close when they are exposed to stomata closure-promoting environments (low RH, desiccation and darkness), as usually happens during the postharvest stage. However, in greenhouses with low VPD conditions and long photoperiods, stomata will not fully close during the postharvest stage; even decreased leaf water content will not result in full stomatal closure (stomatal malfunctioning) in products coming from those greenhouses. In this paper, greenhouse climate factors during the growth of plants that induce stomatal malfunctioning in the postharvest stage will be characterised. Approaches will be discussed to improve stomatal functionality under such greenhouse conditions in order to increase vase- and shelf-lives of products.

Keywords: greenhouse, postharvest quality, relative humidity, stomata, VPD

INTRODUCTION

To make more efficient use of land and energy, greenhouse production systems for vegetables and ornamental plants are vastly developing all over the world. Higher yield in greenhouses compared to field production is a result of controlled environmental conditions, more intensive production and prolonged cropping periods. Although, the costs of greenhouse production per unit of area are higher; the higher yield per area and higher visual quality in greenhouse products than the field production usually compensate the extra costs (Bot, 2003). To reach the best end-quality of horticultural products, three types of research have been conducted. The first type comprised studies that focused on some issues which are important before culturing the plants, such as selection of proper genetic materials and establishment of suitable growing platforms. The second type investigated issues during growth by researching optimal environmental and agronomical conditions for growing plants. The third and final research type focused on the postharvest performance of products by inventing highly sophisticated storage options and finding the optimal conditions to retain the quality of the harvested products (Chiesa, 2003; Witkowska, 2013). There are also some additional studies which made a link among the three types of research by focusing on the influence of preharvest factors on postharvest quality (Gruda, 2005; Hewett, 2006; van Meeteren and Aliniaeifard, 2016).

Environmental factors inside the greenhouse play important roles, not only for crop growth and production, but also for postharvest quality of greenhouse products. The
optimal environmental conditions and technology for growing plants in greenhouses do not necessarily guarantee optimum postharvest product quality. Growing plants in some environmental conditions may result in optimal growth of the plants in the greenhouse, but are a cause of several postharvest problems for the products generated in such greenhouses. Greenhouse production under such environmental conditions could lead to short shelf-life for vegetables and short vase-life for cut flowers, and in the worst situations, lead to deterioration of the products (van Meeteren and Aliniaeifard, 2016).

The importance of various preharvest factors (e.g., cultivar, agronomic practices, climatic conditions, degree of maturity at harvest time, time of harvest, and prevalence of diseases and pests) (Tijkens et al., 2003; Gruda, 2005; Hewett, 2006; Moretti et al., 2010; Tibaldi et al., 2011; Fanourakis et al., 2013b; Luna et al., 2013; Tudela et al., 2013) and postharvest factors (e.g., storage conditions, packaging and processing, transport and distribution) (Watada et al., 1996; Chiesa, 2003; Moretti et al., 2010) for the postharvest quality of horticultural products have been previously reported. Among the environmental preharvest factors, relative humidity (RH) (Rezaei Nejad and van Meeteren, 2005; Islam et al., 2010; Fanourakis et al., 2011, 2013b; Aliniaeifard, 2014; Aliniaeifard and van Meeteren, 2016) and lighting conditions (Slootweg and van Meeteren, 1991; Fjeld et al., 1994; Mortensen and Fjeld, 1998; Mortensen and Gislerød, 1999, 2011; Pettersen et al., 2007; Arve et al., 2013; Witkowska, 2013; Islam, 2014; Mortensen, 2014; Ouzounis et al., 2016) attracted lots of attention for their impact on postharvest quality of horticultural products.

Stomata are responsible for gas exchange between a plant and the surrounding atmosphere. Environmental factors can affect this gas exchange through influencing the functioning of stomata. Water vapour loss is a determinant factor for the quality of horticultural products (especially cut flowers and leafy vegetables). Here, we provide evidence that stomata form the memory of plants’ environmental conditions during growth to quality attributes at the postharvest stage.

GREENHOUSE VAPOUR PRESSURE DEFICIT (VPD) AND QUALITY OF PRODUCT

One of the most important factors influencing the shelf- or vase-life of horticultural products is the internal water balance of the leaf, which is dependent on the water uptake and transpirational water loss. Negative water balance occurs when the water uptake by plant/product is lower than the water loss. Negative water balance induces wilting of the leaf/plant and as a result poor quality of the horticultural products (e.g., reduced shelf-life in leafy vegetables or decreased vase-life of cut flowers) (van Meeteren and Aliniaeifard, 2016).

Greenhouses are usually characterised by their partial or full isolation from the outside environment. This practice helps to save energy inside the greenhouses. One consequence of such practices is an increase in the RH of the greenhouse atmosphere. However, production of plants in greenhouses characterised with continuous high RH (>85%) may result in problems with diseases like powdery mildew and botrytis, poor plant quality and nutrient deficiency due to reduced transpiration (Hannusch and Boland, 1996a, b; Torre et al., 2001; Tullus et al., 2012). Furthermore, it has been frequently reported that plants produced at high RH [low vapour pressure deficit (VPD)] have negative water balance after harvest, which results in reduced vase-life in cut flowers and reduced shelf-life in leafy vegetables, due to high transpiration rate when exposed to common postharvest conditions such as high VPD, darkness and desiccation (Fanourakis et al., 2011, 2013b, 2016; Arve et al., 2013; Giday et al., 2013b; In et al., 2013; Aliniaeifard, 2014; Aliniaeifard et al., 2014; Aliniaeifard and van Meeteren, 2016). For instance, roses grown under continuous low VPD are characterised with higher water loss than roses grown under higher VPDs, resulting in shorter vase-life of low VPD-grown plants than the plants grown under higher VPDs (Mortensen and Fjeld, 1998; Torre and Fjeld, 2001). The negative effects of low VPD during growth on postharvest life of flowers have also been observed in some other ornamental plants such as Begonia, Chrysanthemum, Euphorbia and Kalanchoe (Ferrante et al., 2015; van Meeteren and Aliniaeifard, 2016; Aliniaeifard and van Meeteren, 2016). Moreover, production of herbs and leafy vegetables under low VPD conditions would also result in uncontrolled water loss by their leaves and as a result decreased shelf- and vase-lives.
Water evaporation through leaves occurs via two main pathways, namely stomata and cuticle. When plants are grown in low VPD conditions, their ability to close stomata in response to closing stimuli decreases. As a consequence they show an extreme water loss phenotype when they are exposed to environments with high evaporative demands as well as to stomatal closing signals such as abscisic acid (ABA) (Rezaei Nejad and van Meeteren, 2005; Aliniaeifard, 2014; Aliniaeifard et al., 2014; Aliniaeifard and van Meeteren, 2014, 2016; Maleki Asayesh et al., 2017a, b). Many studies have attempted to discover the reasons for the extreme water loss characteristics of low VPD-grown plants in stomatal closure-promoting environments (Rezaei Nejad and van Meeteren, 2006; Aliniaeifard and van Meeteren, 2013, 2014; Fanourakis et al., 2013a; Giday et al., 2013a; Aliniaeifard, 2014; Aliniaeifard et al., 2014; Maleki Asayesh et al., 2017b). Morphological and anatomical alterations (such as thinner leaves with different patterns of palisade and spongy cell arrangements and thinner cuticular layer) have been reported for the leaves of plants that developed in low VPD conditions (Torre et al., 2003; Maleki Asayesh et al., 2017b), which resulted in some conclusions in this regard (Torre et al., 2003; Fanourakis et al., 2011). Since both stomata and cuticle participate in water loss from the leaf, it is important to know how much involvement the two have in water loss from plants developed in low VPD conditions. It has been revealed that although cuticular transpiration is higher in plants grown in low VPDs, its role in water vapour loss is still too small to be the main pathway for the high water loss characteristics of low VPD-grown plants (Fanourakis et al., 2013a; Maleki Asayesh et al., 2017b). Furthermore, exposure of leaves to low VPD conditions shorter than the time required to induce anatomical and morphological alterations (e.g., 4 days exposure of fully developed leaves to low VPD) also resulted in the same water loss characteristics for both plants (4 days low VPD-exposed and low VPD-grown) (Aliniaeifard et al., 2014; Aliniaeifard and van Meeteren, 2016). This confirms that extreme water loss characteristics for long-term low VPD-exposed plants must therefore be largely due to increased stomatal transpiration (Fanourakis et al., 2013a; Aliniaeifard et al., 2014; Maleki Asayesh et al., 2017a).

The question of why exposure to low VPD for a long time (continuous or more than a few days’ exposure) causes stomatal malfunctioning has been investigated extensively in several studies. A decrease in foliar ABA level due to its catabolism through ABA hydroxylases under low-VPD conditions has been frequently reported (Rezaei Nejad and van Meeteren, 2006; Arve et al., 2013; Aliniaeifard and van Meeteren, 2013, 2014; Giday et al., 2013a, 2014; Aliniaeifard et al., 2014). A low foliar ABA level for more than a threshold time caused abnormal stomatal size and occurrence of sluggish stomata; therefore, stomata are not able to have an adequate response to closing stimuli. Consequently, an extreme water loss phenotype following exposure to desiccation or high VPD would be observed in plants that were grown or exposed long term to low-VPD conditions.

GREENHOUSE LIGHTING CONDITIONS AND QUALITY OF PRODUCTS

Light is one of the environmental factors which determine the rates of water loss and CO₂ uptake through the plant leaves. Light provides the energy source for photosynthesis, and the signals for plant morphogenesis (Chen et al., 2004). Light duration, intensity and spectrum can affect plant gas exchange responses. Lighting conditions can affect quality of the products not only when applied in the postharvest stage (Witkowska, 2013), but also exposure to different lighting conditions in the preharvest stage can affect the postharvest quality of greenhouse-derived products (Mortensen, 2014; van Meeteren and Aliniaeifard, 2016).

In winter, photosynthetically active radiation (PAR) in the greenhouse is often insufficient for constant production of plants. Moreover, duration of the lighting period is very short in many places in the world. Extending the lighting period was the topic of extensive research during the last few decades in order to determine the best duration of lighting period (Slootweg and van Meeteren, 1991; Mortensen and Gislerød, 1999; Arve et al., 2013; Mortensen, 2014). Nowadays, extension of the natural lighting period using
artificial light (supplementary lighting) is common in greenhouses, especially in winter. Supplementary lighting is used to extend the photoperiod and to increase the light intensity especially during winter. For production of some greenhouse crops, such as rose (Rosa × hybrida), pepper (Capsicum annuum) and lettuce (Lactuca sativa), use of supplementary lighting can be extended to 24 h day⁻¹ (continuous lighting). The primary hypothesis for extending the lighting period was increased growth and yield due to longer photosynthesis (Velez-Ramirez et al., 2011). There are some advantages in using a longer light period in greenhouse production. For instance, in roses, total biomass was enhanced by 18% when the lighting period was increased from 18 to 24 h. The number of flowering shoots increased by 12% and fresh weight per shoot by 5% through extending the lighting period to 24 h (Mortensen and Gislerød, 1999). Furthermore, growing plants under continuous light resulted in less infection by powdery mildew (Suthaparan et al., 2010). In miniature roses, decreasing the lighting period to 16 h resulted in more infection with powdery mildew (Mortensen, 2014). Apart from the beneficial effects of extending lighting periods, there are some studies which do not support the idea of growing plants under unnatural prolonged lighting conditions (Mortensen and Gislerød, 1999; Velez-Ramirez et al., 2011). For instance, growing tomato plants under continuous light led to the development of mottled leaf chlorosis and necrotic spots which are lethal for sensitive tomato cultivars (Velez-Ramirez et al., 2011). In the case of rose plants, growing under continuous light would not cause harmful injuries during growth. However, continuous light-grown rose plants showed a decreased vase-life (Mortensen and Fjeld, 1998; Mortensen and Gislerød, 1999). It has been shown that stomata of plants grown under extended lighting periods were not fully responsive to closing stimuli like desiccation, even when exposed to darkness in the postharvest stage, whereas plants grown under natural daylight had a normal stomatal closing response (Slootweg and van Meeteren, 1991). The problem with continuous light-grown plants is especially critical when the roses are harvested and placed under indoor conditions (high VPD). This kind of stomatal malfunctioning causes uncontrolled water loss in the postharvest stage, and as a result, bent neck and leaf drying occurs (Mortensen and Fjeld, 1998).

Extending the lighting period can negatively affect the quality of herbs through the functioning of the stomata (Islam et al., 2010; Tibaldi et al., 2011). For example, in basil (Ocimum basilicum) and lemon balm (Melissa officinalis) higher rates of water loss were recorded in plants produced in 24-h light compared to the rate of water loss in plants exposed to a 16- or 20-h photoperiod. Lighting period and light intensity can affect the amount of healthy compounds in the essential oil of medicinal plants. For example, linalyl acetate is one of the constituents in the essential oil of oregano plants. This compound is characterised by high anti-inflammatory activity (Peana et al., 2002). It has been reported that in full-light conditions, as a result of more open stomata and high transpiration rate, the amount of linalyl acetate in oregano plants decreased due to high foliar water loss, while growing oregano plants in pots under 50% shade resulted in a higher percentage of linalyl acetate in the essential oil (Tibaldi et al., 2011).

HOW TO PREVENT STOMATAL MALFUNCTION

As mentioned in the previous sections, to save energy and increase yield, there is a tendency to produce plants in greenhouses with low VPD and extended lighting duration. Plants produced in such greenhouses have shortened vase- or shelf-lives. The main reason for this shortened vase- and shelf-life is uncontrolled water loss due to decreased stomatal functionality in the products coming from those greenhouses. The question is how can we prevent stomatal malfunctioning and as a result extend the postharvest life of the plants?

Regarding other plant traits, there is genotypic variation among genotypes for their stomatal responsiveness to closing stimuli when they are grown under environmental conditions that induce stomatal malfunctioning (Fanourakis et al., 2011, 2012; Giday et al., 2013a, b). Therefore the easy solution for preventing stomatal malfunction is to select tolerant cultivars and/or use them in breeding programmes (Fanourakis et al., 2012).

As indicated, greenhouse crops exposed to additional lighting time (via supplementary
lighting) than the natural time have less functional stomata and as a result a shorter postharvest life than the plants produced under natural day/night cycles (Fjeld et al., 1994; Mortensen and Fjeld, 1998; Mortensen and Gislerød, 1999, 2011). It has been found that by increasing the intensity of supplementary irradiance during the growth of plants exposed to 20-h light, it was possible to improve the postharvest quality of the products (Fjeld et al., 1994).

Plants grown under continuous light had low β-glucosidase activity which is responsible for converting ABA-GE (reserve of ABA) to ABA. β-Glucosidase activity increased when plants were exposed to a photoperiod with certain duration of darkness period, and as a consequence stomatal functionality increased, resulting in higher vase-life (Arve et al., 2013).

In most of the experiments that showed a link between plant growth under artificial extension of the lighting period and malfunctioning of the stomata, the plants were also grown under low VPD conditions. It has been reported that by increasing the VPD during plant growth, it would be feasible to have a normal closing response of the stomata even when the plants are grown under continuous light conditions (Mortensen and Fjeld, 1998; Mortensen and Gislerød, 1999; Pettersen et al., 2006, 2007; Arve et al., 2013). This finding resulted in the conduction of several studies towards finding the reasons for stomatal malfunctioning under low VPD conditions (as reviewed by Aliniaeifard and van Meeteren, 2013). Since it has been revealed that the low foliar ABA concentration is the main reason for the occurrence of stomatal malfunctioning, approaches which therefore induce accumulation of ABA can prevent malfunctioning of stomata (Aliniaeifard and van Meeteren, 2013, 2014, 2016; Aliniaeifard et al., 2014; Maleki Asayesh et al., 2017a). Application of ABA to roots or spraying it to the leaf during growth of the plants under low VPD conditions prevented the problem of stomatal malfunctioning (Ffanourakis et al., 2011; Aliniaeifard et al., 2014; Aliniaeifard and van Meeteren, 2014; Giday et al., 2014). In other studies, increasing the VPD during a critical stage of stomatal development resulted in a normal closing response of stomata (Ghashghaie et al., 1992; Fanourakis et al., 2011; Maleki Asayesh et al., 2017a). It is also likely that short interruptions of the low VPD every few (about 3) days by high VPD will prevent induction of stomatal malfunction (van Meeteren et al., 2009).

CONCLUSIONS

Nowadays, supplementary lighting and a low VPD are common during greenhouse production of crops. Although, growing plants in such conditions has some advantages during plant growth, it negatively influences the water balance of the products in the postharvest stage. Extended lighting periods and low VPD during growth of the plants will induce a lasting decreased stomatal response to closing stimuli. As a consequence of stomatal malfunctioning, the harvested greenhouse products would have low capacity to control water loss, leading to shortened vase-life of cut flowers and shortened shelf-life of leafy vegetables and herbs. Since VPD is the main determinant factor during growth which influences postharvest performance of the products, in the management of the greenhouse environment we should avoid plant exposure to continuous and long-term low VPD, especially in the critical stage of plant development.

Literature cited


