

Review

Possible effects of regulating hydroponic water temperature on plant growth, accumulation of nutrients and other metabolites

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Water temperature can affect many physiological processes during plant growth and development. Temperatures below or above optimum levels may influence plant metabolic activities positively or negatively. This may include accumulation of different metabolites such as phenolic compounds, reactive oxygen species (ROS), nutrient uptake, chlorophyll pigment formation, the photosynthesis process and finally the growth and development of the plant. The optimum temperature of the growth medium can contribute to improving and optimising the earlier mentioned plant physiological processes. Information on how the temperature of hydroponic solution influences certain flowering plant production in glasshouses during the winter period is limited. This review suggests the possible benefits of regulating temperatures of the hydroponic solution with the aim of optimising production of flower in the glasshouse during winter periods.

Key words: Chlorophyll, nutrient uptake, phenolic compounds, photosynthesis rate, reactive oxygen species.

INTRODUCTION

Temperature is the major environmental factor that influences the vegetative growth processes in plants from the initial stages of development to flower formation (Roh and Hong, 2007). During growth, optimum temperature is required below and above which may impair plant development (Summerfield et al., 1989). Very low or high temperatures in the growth environment may be detrimental to various metabolic processes in plant tissues such as nutrient uptake, chlorophyll formation and photosynthesis (Taylor and Rowley, 1971; Rhee and Gotham, 1981; Markwell et al., 1986). Studies have shown that, when temperatures are lowered, the nutrient uptake, chlorophyll pigmentation and photosynthesis rate are negatively affected. However, at optimum levels the metabolism rates in plants are improved (Taylor and Rowley, 1971; Macduff et al., 1986; Engels et al., 1992; Kurek et al., 2007) and increase plant growth (Went, 1953

González-Meler et al., 1999; Frantz et al., 2004). Furthermore, stress due to very low temperature may induce plants to produce different species of reactive oxygen species (ROS) such as, superoxide (O_2^-), hydrogen peroxide (H_2O_2), oxygen (O_2) and HO (hydrogen oxide) which may ultimately culminate into oxidative stress, thus, damaging the plant cells. Generally, an increase or decrease in temperature above or below the optimum level is known to alter several physiological processes in plants and damage the plant cells, thus, altering the growth (Wahid, 2007; Yang et al., 2009).

The accumulation of other metabolites such as anthocyanins and flavonoid in plants may be influenced by temperature (Kleinhenz et al., 2003; Ling et al., 2007). Studies have shown that, in several plants, increasing thermal stress slightly above or below the optimum range may induce the production and accumulation of phenolic compounds such as flavonoids and anthocyanins (Rivero et al., 2001; Taulavuori et al., 2004; Guy et al., 2008; Padda and Picha, 2008), a defensive mechanism employed by plants against this type of stress. In several plants, thermal regulation of hydroponic solution

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temperature may optimise the plant physiological processes mentioned earlier, thus, affecting the quality of the plant.

Due to a decrease in temperature, commercial growers experience a lower level of ornamental plant production during winter than in summer (Olivier, 1974; Mills et al., 1990). However, there is a high demand for flowers during winter season when temperatures are below optimum for flower production. During this period, the production levels are lower due to lowered temperature (Olivier, 1974; Mills et al., 1990). By modifying irrigation water temperature to optimum levels, specific ornamental plants can be grown hydroponically in greenhouses during the winter period. Heating of hydroponic solution in greenhouse production has shown success in other parts of the world in a variety of crops (Moorby and Graves, 1980; Rovira, 2005; Kozai, 2006; Sethi and Sharma, 2007). This review exploits the potential of increasing production of flowers during winter season by regulating temperatures in the hydroponic solution to optimize plant growth.

EFFECTS OF REGULATING HYDROPONIC WATER TEMPERATURE ON PROFILING OF SECONDARY METABOLITES PRODUCTION SUCH AS FLAVONOID AND ANTHOCYANINS

Phenolic compounds are the major molecules among plant secondary metabolites and they play a very important role in plant development (Ndakidemi and Dakora, 2003; Makoi and Ndakidemi, 2007). In the vacuole of a plant organ such as leaves and flowers, anthocyanins plays major role in flower colour and fragrance (Harborne, 1980; Schijlen et al., 2004). Anthocyanins and flavonoid accumulation in plants is influenced by environmental factors such as light, temperature and other stress levels (Kleinhenz et al., 2003; Ndakidemi and Dakora 2003; Ling et al., 2007; Makoi et al., 2010). Like all other organisms, plants may exhibit the maximum rate of metabolite production at an optimum temperature for which they have adapted (Aldred et al., 1999).

It has been reported that, cultivation of crops under cold temperature decreases metabolites as a result of a low rate of yield (Van Der Ploeg and Heuvelink, 2005; Thakur et al., 2010). Studies have shown that, the accumulation of phenolic compounds such as anthocyanins and flavonoid by plants in winter can differ in comparison to summer, due to temperature variations (Mori et al., 2005; Olsen et al., 2008; Kassim et al., 2009). Different mechanisms are proposed. For example, variations in temperature may exert thermal stress on the plants tissues, consequently, interfering with the activity of the various plant enzymes and hence, the production of metabolites. In this context, significant changes in phenolic compound metabolism may be affected by extended periods of low temperature which may result in chilling

injury. Taulavuori et al. (2004) and Padda and Picha (2008) reported that, a plant exposed to low temperatures resulted in an increased content of phenolic compound in their tissues. Moreover, anthocyanins are highly water soluble and are therefore produced under different stress levels, such as temperature stress.

Research evidence suggests that, plants may exhibit the maximum rate of metabolite production at a given optimum temperature. In most plants, increasing thermal stress slightly above the optimum range may induce the production and accumulation of metabolites such as flavonoids and anthocyanins (Rivero et al., 2001; Guy et al., 2008). Elevated temperatures above the optimum level similarly increases enzyme activity (Pearcy, 1977) and results in the production of different types of metabolites. The effect of thermal stress is often manifested by the appearance of physiological injuries into the plant tissues thus, resulting into the excessive production of secondary metabolites (Revero et al., 2001), a strategy used to protect the plant from further stress damage. To verify this, Wahid (2007) reported that, accumulation of anthocyanins in *Photinia* spp. and aster (*Aster amellus*) flower were increased with exposure to high temperature. Other studies involving *Rehmannia glutinosa* have reported decreased content of phenolic compounds at very high temperatures (Chung et al., 2006).

Little information is available on the influence of hydroponic solution temperatures on the pigment formation for plants grown under glasshouse conditions during winter. From this background, it is therefore important to establish the effects of temperature gradients on metabolite production in plants grown in the hydroponic media with varied temperatures during the winter period.

EFFECTS OF REGULATING HYDROPONIC WATER TEMPERATURE ON REACTIVE OXYGEN SPECIES IN DIFFERENT PLANT TISSUES

Reactive oxygen species (ROS) are warning signals for plants subjected to stress, including cold stress (Nobuhiro and Ron, 2006). Reactive oxygen species such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), oxygen (O_2) and HO (hydrogen oxide) are toxic molecules producing oxidative damage to proteins, DNA and lipids, which may finally affect plant growth and development (Ping et al., 2008). Excessive accumulation of ROS in plants occurs when stress is severe and causes oxidative injury (Ling et al., 2007). It is likely that, ROS produced at low temperatures can cause damage to cellular components by disrupting metabolic function (Anderson et al., 2005). Some research evidence indicates that, cold stress enhances the transcription of protein and activity of different reactive oxygen species-scavenging enzymes in plants (Nobuhiro and Ron, 2006).

However, the exposure to low temperatures may increase the amount of reactive oxygen species (Ping et al.,

2008), an antioxidant strategic defence mechanism enabling plants to adapt to heat stressed environments. The ROS-scavenging mechanisms have an important role in protecting plants against temperature stresses (Miller et al., 2006).

Accordingly, ROS production is increased by oxidative stress under unfavourable environmental conditions such as those involving temperature changes to extreme limits (Gechev et al., 2006). The accumulation of ROS in plants can lead to many physiological injuries of tissues, loss of membrane integrity and chlorophyll bleaching (Xu et al., 2006; Liu and Pang, 2010). Furthermore, ROS is accredited for decreasing membrane stability and facilitating lipid peroxidation (Sairam et al., 2002).

Generally, most plants display their antioxidative enzyme activities at a temperature of 25°C (Peltzer et al., 2002). However, the exposure of plants to low temperature may increase the amount of ROS as an antioxidant strategic defence mechanism enabling plants to adapt in low temperature stressed environments (Ping et al., 2008). Studies conducted in low temperature environments revealed reductions in enzymatic activation energies due to production of ROS (Peltzer et al., 2002).

Many scholars have indicated that high temperatures may enhance the production of ROS including singlet oxygen (O_2), superoxide radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^{\cdot}) (Liu and Huang, 2000; Suzuki and Mittler, 2006). These may cause lipid peroxidation and pigments membrane instability (Xu et al., 2006; Lopez-Vazquez et al., 2007), then, negatively affecting plant metabolism and limiting growth and yield (Sairam and Tyagi, 2004). In heated environments, the protection against oxidative stress is an important component in determining the survival of a plant under heat stress (Gong et al., 1997; Dat et al., 1998). Assessing the accumulation of ROS in glasshouse grown plants under different hydroponic temperature regimes will enable us to understanding how ROS can affect growth and development of such plants grown under a controlled environment during winter period. Further research is necessary to establish the mechanisms involved in the production of antioxidants in cells exposed to heat stress.

EFFECTS OF REGULATING HYDROPONIC WATER TEMPERATURE ON NUTRIENT UPTAKE AND ACCUMULATION IN PLANT TISSUES

Plant nutrients have a great potential for increasing yield and are capable of promoting plant growth (Ndakidemi and Semoka, 2006). Nutrient uptake and accumulation in plant tissues may be influenced by temperature, amongst various other environmental factors (Reay et al., 1999; Aðalsteinsson and Jensén, 2006). Calatayud et al. (2008) revealed that, in most plant species, nutrient uptake by roots decreased at low temperatures. Temperatures of growth media may influence chemical reaction rates of

nutrients in the solution, nutrient transport in the medium, physiological aspects related to ion uptake rate and functioning of soil microbial communities (Pregitzer and King, 2005). Therefore, it is of paramount importance to regulate hydroponic solution temperatures in situations whereby, plants are grown in a controlled environment during winter months. Optimizing temperature in the growth medium can be achieved by warming the nutrient solution (Morgan et al., 1980).

Studies have shown that, elevated temperatures increased nutrient uptake in cucumber (*Cucumis sativus* L.) and enhanced plant growth leading to significant increase in yield (Daskalaki and Burrage, 1998). Experiments involving Jojoba (*Simmondsia chinensis*) showed that, the uptake rate of N, P, K, Na, Fe, Mn and Zn were significantly reduced at low temperatures compared with those exposed to temperatures as high as 33°C (Reyes et al., 1977). Furthermore, nutrient concentrations in roots were similarly higher in plants grown at 33°C than at 21 or 27°C (Reyes et al., 1977). Studies by Hood and Mills (1994) and Scoltzfus et al. (1998) showed that, increasing temperature from 15 to 29°C increased uptake of P, K, Ca, Mg, Fe, Mn, Zn and B and finally, the plant growth. Nutrient uptake, especially N in pine (*Pinus sylvestris* L.) increased with increasing root temperature from 8 to 16°C (Vapaavuori et al., 1992). In cucumber (*C. sativus* L.), uptake of N, P, K, Ca and Mg was increased when the temperature was raised in a closed hydroponic system from 12 to 20°C (Daskalaki and Burrage, 1998).

On the other hand, low temperatures are known to induce B deficiency and leaf damage in crop plants (Huang et al., 2005). For example in cucumber, low temperature (10°C) doubled nitrate accumulation in the root zone when compared with the root zone temperatures of 18 and 26°C (Kim et al., 2002). This was probably due to restricted mobility and volatilisation of nitrates at low temperatures (Thomas and Kissel, 1970), depending on the type of nutrients. Nutrient uptake for plants grown in glasshouses may be positively and adversely affected by manipulating the hydroponic solution temperature to the optimum level. Studies should therefore be conducted to establish the optimum temperatures to meet nutrient uptake demands of specific plants during winter season.

EFFECTS OF VARYING HYDROPONIC WATER TEMPERATURE ON CHLOROPHYLL PIGMENTATION

Colour pigmentation in plants, especially chlorophyll is important to their growth and development. The amount of chlorophyll formed in plants is strongly influenced by environmental factors including temperature changes (Hauvax and Lannoye, 1984; Tian et al., 1996; Shvarts et al., 1997; Yun et al., 1998; Kleinhenz et al., 2003). The influence of temperature on chlorophyll formation involves several mechanisms. At optimum temperatures, the

synthesis of metabolites such as carbohydrates may be enhanced, thus, leading to increased chlorophyll in the leaves (Reay et al., 1998; Al-Hamdani and Ghazal, 2009). Scientific evidence points out that, plants subjected to various levels of stress (high temperatures) can damage their cells and eventually affect chlorophyll quality (López-Ayerra et al., 1998). Vu and Yelenosky (1987) reported that, the amount of chloroplast proteins tends to drop with increasing growth temperatures. The experiments involving testing of maize at various temperatures revealed that, their exposure to higher temperatures triggered membrane damage and lowered the chlorophyll concentration in the plant tissues (Yang et al., 1996). In barley (*Hordeum vulgare* L.), other researchers (Ilík et al., 2000) reported plasmalemma and chloroplast membrane damage, loss in cell permeability, thylakoids burst and the formation of condensed structures due to high temperature. Funamoto et al. (2003) also showed that, in broccoli (*Brassica oleracea*), chlorophyll degradation by heat treatment was mainly due to the suppression of chlorophyll peroxidase activities in microsomes and cytosol.

Low temperature treatments may also affect chlorophyll quality in plants as the cells are subjected to cold stress (López-Ayerra et al., 1998). Studies have shown that, orange trees (*Citrus sinensis* L. Osbeck) grown under low temperatures contained less chlorophyll than those grown at high temperatures (Vu and Yelenosky, 1987). In spinach (*Spinacia oleracea* L.), lipid peroxidation and chlorophyll levels were reduced by cold temperatures (López-Ayerra et al., 1998) by a mechanism which involved shrinking and damaging of the elastic cells due to cold stress. Generally, when plants are subjected to low temperature stress, the development of chlorotic bands on leaves may appear (Vu and Yelenosky, 1987). Under such circumstances, a decrease in chlorophyll content may be a consequence of oxidative stress which leads to chlorophyll deficiency (Bacelar et al., 2006). With regard to thermo regulation in hydroponic systems, no information is available on the influence of temperatures on the production of chlorophyll pigments in plants grown during the winter period.

POSSIBLE EFFECTS OF REGULATING HYDROPONIC WATER TEMPERATURE REGIMES ON THE PHOTOSYNTHESIS RATE

Temperature is an important environmental factor to plants, which directly influences their photosynthetic functions (Vu and Yelenosky, 1987; Collatz et al., 1991; Williams and Black, 1993; Ling et al., 2007). An increase in temperature to optimum levels may favourably shift electron transport and make the plant to synthesise adequate metabolites such as carbohydrates thus, leading to optimum growth (Piere and Urs, 2005). It is well known that, warm temperature conditions affect plant growth structures including all physiological processes in plants

such as membrane structure, stomatal conductance and protein synthesis. The low temperature effects on photosynthesis may include changes in stomatal and non-stomatal characteristics (Percy, 1977; Berry and Bjorkman 1980; Vu and Yelenosky, 1987; Vierling, 1991; Calatayud et al., 2008). Studies on olive plants showed that, low temperatures decreased photosynthesis and this was correlated to its influence on stomatal closure (Bacelar et al., 2006). Temperatures above the optimum levels may also damage various cell functions, as the photosynthesis process is very sensitive to heat stress (Piere and Urs, 2005). Similarly, photosynthesis can also be affected negatively by low root temperature (Calatayud et al., 2008).

According to Lambrea et al. (2005), stimulation of photosynthesis was observed at the growth temperature of 23°C whereas, at 39°C the effects of elevated CO₂ on photosynthesis was induced downward. Generally, increased temperature above the optimum limit may reduce photosynthetic rate (Wahid et al., 2007). For instance, in a study involving rice (*Oryza sativa* L.) plant, Mohammed and Tarpely (2009) indicated that, high temperatures had a negative effect on photosynthesis as well as various enzymes involved in the process. Uniformity of shoots and time to flower on plants is also increased by increasing photosynthetic photon flux (Quedado and Friend, 1978; Karlsson et al., 1989). However, information concerning the effects of hydroponic water temperature during winter on the photosynthesis rate on plants is rather limited in plants grown under glasshouse conditions. Therefore, it is important to document the influence of plants photosynthetic activities when exposed to hydroponic media of different temperature treatments. Such information could assist in developing adaptable hydroponic solution temperature for cultivating glasshouse plants with highly functional substances.

EFFECTS OF TEMPERATURE CHANGES IN HYDROPONIC WATER ON PLANT GROWTH AND DEVELOPMENT

Water temperature is an important growth factor that may influence plant development in hydroponic systems. Therefore, it is beneficial to study the optimum temperature requirements for different crops grown in climates with adverse winter conditions. Water temperature plays a vital role in plant development (Chung et al., 2006). At optimum temperatures, water can nourish growth while at lower or high levels, plant growth can be negatively affected (He et al., 2002). In plants, water is required to maintain cell turgidity so as to ensure continuous column of moisture in the cells (Stewart and Dwyer, 1983; Noguchi and Terashima, 1997; Outlaw, 2003). It is also indispensable to the intracellular chemical processes that keep the plant growing (Outlaw, 2003; Yamori et al., 2006). Cold water may cause frost damage to plants by

forming sharp-edged ice crystals, which puncture cell walls. Studies have shown that, at lower temperatures (10°C), flower abortion in different plant species occurred because pollen and ovule fertility were highly sensitive to cold temperatures (Jakobsen and Martens, 1994; Domínguez et al., 2005; Singh et al., 2008). In the flower industry, these effects on flower physiology can lead to a drastic reduction in economic yield (Diepenbrock, 2000; Thakur et al., 2010).

Temperature may also affect many other growth physiological processes at different developmental stages of the plant. Studies have shown that, most tender plants will grow well in temperatures ranging from 6 to 24°C and half-hardy plants from 10 to 18°C, whereas hardy plants may survive in temperature range of 7 and 16°C (Bubel, 2007; Gesch and Forcella, 2007). Therefore, when water temperatures drop below 6°C in such type of plants, thermal modifications can be essential to sustain growth.

The effects of temperature on vegetative plant growth and flower development will vary depending on the growth stage of the plant (Selander and Welander, 1984). In a glasshouse experiment the effect of temperature on *Primula vulgaris* showed that, an increasing temperature up to 18°C delayed flower opening and decreased the number of flowering shoots, whereas at a lower temperature (12°C) inhibition of flower development was overcome (Selander and Welander, 1984). In other studies involving *Aeschynanthus speciosus*, increasing the temperature from 12 to 21°C resulted in higher percentage of flowering plants with increased number of leaves formed (Welander, 1984). In separate studies, the number of days to flowering of *Centradenia inaequilateralis* and flower formation was significantly affected by increasing temperature (Tromp, 1984; Friis and Christensen, 1989; Zhu et al., 1997; Roh and Hong, 2007). Other studies conducted in the glasshouse to test the effect of temperature in *P. vulgaris*, showed that increasing the temperature to 18°C delayed flower opening and decreased the number of flowering shoots whereas at 12°C flower development was enhanced and the plant performed well (Selander and Welander, 1984; Roussopoulos et al., 1998). Similarly, studies on a different plant (*Chrysanthemum*) showed that, increasing temperature from 14 to 26°C delayed flowering for more than 30 days (Karlsson et al., 1989). In passion fruit (*Passiflora edulis*), temperatures ranging from 25 to 30°C limited flowering, while, temperatures ranging from 10 to 15°C reduced the yield of vegetative growth (Menzel et al., 1987). Therefore, it is important to establish other possible effects of regulating temperatures in the hydroponic solution on plant growth and development in the glasshouse during winter periods.

CONCLUSIONS

Temperature changes in hydroponic media may affect

the development of plants. Most plants are unable to grow at sub-optimum levels. When temperatures are not at optimum level, several physiological functions such as photosynthesis, chlorophyll formation and pigmentation, nutrient uptake, accumulation and synthesis of secondary metabolites in plants are affected. Thermo regulation of hydroponic solution in the glasshouse is a technique which can be used to optimise the production of flowers or flowering plants during winter periods.

REFERENCES

- Anderson MD, Prasad TK, Stewart CR (1995). Change in isozyme profile of catalase, peroxidase and glutathione reductase during acclimation to chilling in mesocotyls of maize seedlings. *Plant Physiol.* 109:1247-1257.
- Aldred D, Magan N, Lane BS (1999). Influence of water and nutrients on growth and production of squalenstatin S1 by a *Phoma sp.* *J. Appl. Microbiol.* 87: 842-848.
- Aðalsteinsson S, Jensén P (2006). Influence of temperature on root development and phosphate influx in winter wheat grown at different P levels. *Physiol. Plant* 80: 69-74.
- Bacelar EA, Santos DL, Moutinho-Pereira JM, Gonçalves BC, Ferreira HF, Correia CM (2006). Immediate responses and adaptive strategies of three olive cultivars under contrasting water availability regimes: Changes on structure and chemical compositions of foliage and oxidative damage. *Plant Sci.* 170: 596-605.
- Berry J, Bjorkman O (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* 31: 491-543.
- Bubel N (2007). The new seed-starters Handbook. Available online: http://www.green-seeds.com/pdf/seed_starters.pdf p. 300.
- Calatayud A, Gorbe E, Roca D, Martines PF (2008). Effects of two nutrient solution temperatures on nitrate uptake, nitrate reductase activity, NH₄⁺ concentration and chlorophyll a fluorescence in rose plants. *Environ. Exp. Bot.* 64: 65-74.
- Chung I11M, Kim JJ, Lim JD, Yu CY, Kim SH, Hahn SJ (2006). Comparison of resveratrol, SOD activity, phenolic compounds and free amino acids in *Rehmannia glutinosa* under temperature and water stress. *Environ. Exp. Bot.* 56: 44-53.
- Collatz GJ, Ball TJ, Griwet C, Berry AJ (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. For. Meteorol.* 54: 107-136.
- Daskalaki A, Burrage SW (1998). Solution temperature and the uptake of water and nutrients by cucumber (*Cucumis sativus L.*). *Acta Hort.* 458:317-322.
- Dat JF, Foyer CH, Scott, IM (1998). Changes in salicylic acid and antioxidants during induction of thermo tolerance in mustard seedlings. *Plant Physiol.* 118: 1455-1461.
- Diepenbrock W (2000). Yield analysis of winter oilseed rape (*Brassica napus L.*): A review. *Field Crops Res.* 67: 35-49.
- Engels C, Munkle L, Marschner H (1992). Effect of root zone temperature and shoot demand on uptake and xylem transport of macronutrients in Maize (*Zea mays L.*). *J. Exp. Bot.* 43: 537-547.
- Frantz JM, Cometti NN, Bugbee B (2004). Night temperature has a minimal effect on respiration and growth rapidly growing plants. *Ann. Bot.* 94: 155-166.
- Friis K, Christensen OV (1989). Flowering of *Centradenia inaequilateralis* 'Cascade' as influenced by temperature and photoperiod. *Sci. Hortic.* 41: 125-130.
- Funamoto Y, Yamauchi N, Shigyo M (2003). Involvement of peroxidase in chlorophyll degradation in stored broccoli (*Brassica oleracea L.*) and inhibition of the activity by heat treatment. *Postharvest Biol. Technol.* 28: 39-46.
- Gechev TS, Van Breusegem F, Stone JM, Denev I, Laloi C (2006). Reactive oxygen species as signals that modulate plant stress responses and programmed cell death. *BioEssay.* 28: 1091-1101.
- Gesch RW, Forcella F (2007). Differential sensitivity to temperature of *Cuphea* vegetative and reproductive growth. *Ind. Crops and*

- Products, 25: 305-309.
- González-Meler MA, Ribas-Carbo M, Giles L, Siedow JN (1999). The effect of growth and measurement temperature on the activity of the alternative respiratory pathway. *Plant Physiol.* 120: 765-772.
- Guy C, Kaplan F, Kopka J, Selbig J, Hinch DK (2008). Metabolomics of temperature stress. *Physiol. Plant.* 132: 220-235.
- He L, Nada K, Kasukabe Y, Tachibana S (2002). Enhanced susceptibility of photosynthesis to low-temperature photo inhibition due to interruption of chill-induced increase of S-adenosylmethionine decarboxylase activity in leaves of Spinach (*Spinach oleraceae* L.). *Plant Cell Physiol.* 43: 196-206.
- Hood TM, Mills HA (1994). Root-zone temperature affects nutrient uptake and growth of snapdragon. *J. Plant Nutr.* 17: 279-291.
- Huang L, Ye Z, Bell RW, Dell B (2005). Boron nutrition and chilling tolerance of warm climate crop species. *Ann. Bot.* 96: 755-767.
- Havaux M, Lannoye R (1984). Effects of chilling temperatures on prompt and delayed chlorophyll fluorescence in maize and barley leaves. *Photosynthetica*, 18: 117-127.
- Ilík PR, Kouřil R, Fiala J, Nauš J, Vácha F (2000). Spectral characterization of chlorophyll fluorescence in barley leaves during linear heating. Analysis of high-temperature fluorescence rise around 60°C. *J. Photochem. Photobiol. Biol.* 59: 103-114.
- Jakobsen HB, Martens H (1994). Influence of temperature and ageing of ovules and pollen on reproductive success in *Trifolium repens* L. *Ann. Bot.* 74: 493-501.
- Karlsson MG, Heins RD, Erwin JE, Berghage RD, Carlson WH, Biernbaum JA (1989). Irradiance and temperature effects on time of development and flower size in *Chrysanthemum*. *Sci. Hortic.* 39: 257-267.
- Kassim A, Poette J, Paterson A, Zait D, McCallum S, Woodhead M, Smith K, Hackett C, Graham J (2009). Environmental and seasonal influences on red raspberry anthocyanin antioxidant contents and identification of quantitative trait loci (QTL). *Mol. Nutr. Food Res.* 53:625-634.
- Kim TH, Chun YT, Kim KY, Chung SJ (2002). Root zone temperature effects on nitrate assimilation and xylem transport in hydroponically grown cucumber plants. *Acta Hort.* 588: 59-62.
- Kleinhenz MD, French DG, Gazula A, Scheerens JC (2003). Variety, shading and growth stage effects on pigment concentration in Lettuce grown under contrasting temperature regimes. *HortTechnol.* 13: 677-683.
- Kozai T (2006). Closed systems for high quality transplants using minimum resources. *Plant Tiss. Cult. Eng.* 6: 275-312.
- Lambrea M, Stoyanova-Koleva D, Baldjiev G, Tsonev T (2005). Early acclimation apparatus of bean plants during short-term exposure to elevated CO₂ concentration under high temperature and light intensity. *Agric. Ecosyst. Environ.* 106: 219-22.
- Ling S, Zhan S, Shu- Lan S, Chang- Lian P, Xiao-Jing W, Zhi-Fang L (2007). Antioxidation of anthocyanins in photosynthesis under high temperature stress. *J. Integr. Plant Biol.* 49: 1341-1351.
- Liu F, Pang SJ (2010). Stress tolerance and antioxidant enzymatic activities in the metabolism of the reactive oxygen species in two intertidal red algae *Grateloupia turuturu* and *Palmaria palmata*. *J. Exp. Mar. Biol. Ecol.* 382: 82-87.
- Liu X, Huang B (2000). Heat stress injury in relation to membrane lipid peroxidation in creeping bent grass. *Crop Sci.* 40: 503-510.
- López-Ayerra B, Murcia MA, Garcia-Carmona F (1998). Lipid peroxidation and chlorophyll levels in spinach during refrigerated storage and after industrial processing. *Food Chem.* 61: 113-118.
- Macduff JH, Wild A, Hopper MJ, Dhanoa MS (1986). Effects of temperature on parameters of root growth relevant to nutrient uptake: Measurements on oilseed rape and barley grown in flowing nutrient solution. *Plant Soil.* 94: 321-332.
- Makoi JHJR, Belane A, Chimphango, Dakora FD (2010). Seeds flavonoids and anthocyanins as markers of enhanced plant defence in nodulated cowpea (*Vigna unguiculata* L. Walp.). *Field Crops Res.* 118: 21-27.
- Makoi JHJR, Ndakidemi PA. (2007). Biological, ecological and agronomic significance of plant phenolic compound in rhizosphere of the symbiotic legumes. *Afr. J. Biotechnol.* 6: 1358-1368.
- Markwell JP, Danko SJ, Bauwe H, Osterman J, Gorz HJ (1986). A temperature-sensitive chlorophyllb-deficient mutant of Sweetclover (*Melilotus alba*). *Plant Physiol.* 81: 329-334.
- Menzel CM, Simpson DR, Winks CW (1987). Effect of temperature on growth, flowering and nutrient uptake of three passion fruit cultivars and low irradiance. *Sci. Hortic.* 31: 259-268.
- Mohammed AR, Tarpley L (2009). High night time temperatures affect rice productivity through altered pollen germination and spikelet fertility. *Agric. For. Meteorol.* 149: 999-1008.
- Moorby J, Graves CJ (1980). Root and air temperature effects on growth and yield of tomatoes and lettuce. *Acta Hort.* 98: 29-44.
- Miller G, Shulaev V, Mittler R (2008). Reactive oxygen signalling and abiotic stress. *Physiol. Plant.* 133: 481-489.
- Mills PJW, Smith IE, Marais G (1990). A greenhouse design for a cool subtropical climate with mild winters based on microclimatic measurements of protected environments. *Acta Hort.* 281: 83-94.
- Morgan JV, Moustafa AT, Tan A (1980). Factors affecting the growing on stages of Lettuce and *Chrysanthemum* in nutrient solution culture. *Acta Hort.* 98: 253-262.
- Mori K, Sugaya S, Gemma H (2005). Decreased anthocyanin biosynthesis in grape berries grown under elevated night temperature condition. *Sci. Hortic.* 105: 319-330.
- Ndakidemi PA, Semoka JMR (2006). Soil fertility survey in western Usambara Mountains, northern Tanzania. *Pedosphere.* 16: 237-244.
- Ndakidemi PA, Dakora FD (2003). Legume seed flavonoids and nitrogenous metabolites as signals and protectants in early seedling development. *Funct. Plant Biol.* 30: 729-745.
- Nobuhiro S, Ron M (2006). Reactive oxygen species and temperature stresses: A delicate balance between signal and destruction. *Physiol. Plant.* 126: 45-51.
- Noguchi K, Terashima I (1997). Different regulation of leaf respiration between *Spinacia oleracea*, a sun species, and *Alocasia odora*, a shade species. *Physiol. Plant.* 101: 1-7.
- Olivier OJ (1974). All-year-round vegetable production without protection and future prospects in South Africa. *Acta Hort.* 42: 353-362.
- Olsen KM, Slimestad R, Lea US, Brede C, Løvdaal T, Ruoff P, Verheul M, Lillo C (2008). Temperature and nitrogen effects on regulators and products of the flavonoid pathway: experimental and kinetic model studies. *Plant Cell Environ.* 32:286-299.
- Outlaw JrWH (2003). Integration of cellular and physiological functions of guard cells. *Crit. Rev. Plant Sci.* 22: 503-529.
- Padda MS, Picha DH (2008). Effects of low temperature storage on phenolic composition and antioxidant activity of sweetpotatoes. *Postharvest Biol. Technol.* 47: 176-180.
- Pearcy RW (1977). Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.). *Plant Physiol.* 59: 795-799.
- Peltzer D, Dreyer E, Polle A (2002). Differential temperature dependencies of antioxidative enzymes in two contrasting species: *Fagus sylvatica* and *Coleus blumei*. *Plant Physiol. Biochem.* 40: 141-150.
- Pierre H, Urs F (2005). Growth at moderately elevated temperature alters the physiological response of the photosynthetic apparatus to heat stress in pea (*Pisum sativum*) leaves. *Plant Cell Environ.* 28: 302-317.
- Ping L, Wei-Guo S, Ke- Ping M (2008). Differential responses of the activities of antioxidant enzymes to thermal stresses between two invasive *Eupatorium* Species in China. *J. Integr. Plant Biol.* 50: 393-401.
- Pregitzer KS, King JS (2005). Effects of soil temperature on nutrient uptake: nutrient acquisition by plants. Springer Berlin, Heidelberg, pp. 277-310.
- Quedado RM, Friend DJ (1978). Participation of photosynthesis in floral induction of the long day plant *Anagallis arvensis* L. *Plant Physiol.* 62: 802-806.
- Reay PF, Fletcher RH, Thomas VJG (1998). Chlorophylls, carotenoids and anthocyanin concentration in the skin of 'Gala' apples during maturation and the influence of foliar applications on nitrogen and magnesium. *J. Sci. Food Agric.* 76: 63-71.
- Reyes DM, Stolzy LH, Labanauskas CK (1977). Temperature and oxygen effects in soil on nutrient uptake in Jojoba seedlings. *Am. Soc. Agron.* 69: 647-650.
- Rhee GY, Gotham IJ (1981). The effect of environmental factors on

- phytoplankton growth: Temperature and the interactions of temperature with nutrient limitation. *Limnol. Oceanogr.* 26: 635-648.
- Rivero RM, Ruiz JM, García PC, López-Lefebvre LR, Sánchez E, Romero L (2001). Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. *Plant Sci.* 160: 315-321.
- Roh MS, Hong D (2007). Inflorescence development and flowering of *Ornithogalum thyrsoides* hybrid as affected by temperature manipulation during bulb storage. *Sci. Hortic* 113: 60-69.
- Roussopoulos D, Liatakas A, Whittington WJ (1998). Controlled-temperature effects on cotton growth and development. *J. Agric Sci.* 130: 451-462.
- Rovira AD (2005). Root excretions in relation to the rhizosphere effect IV. Influence of plant species, age of plant, light, temperature and calcium nutrition on exudation. *Plant Soil.* 11: 53-64.
- Sairam RK, Tyagi A (2004). Physiology and molecular biology of salinity stress tolerance in plants. *Curr. Sci.* 86: 407-421.
- Sairam RK, Rao KV, Srivastava GC (2002). Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. *Plant Sci.* 163: 1037-1046.
- Schijlen EGWM, Ric de Vos CH, van Tunen AJ, Bovy AG (2004). Modification of flavonoid biosynthesis in crop plants. *Phytochem.* 65: 2631-2648.
- Scoltzfus RMB, Taber HG, Aiello AS (1998). Effects of increasing root zone temperature on growth and nutrient uptake by 'gold star' muskmelon plants. *J. Plant Nutr.* 21: 321-328.
- Selander CS, Welander NT (1984). Effects of temperature on flowering in *Primula vulgaris*. *Sci. Hortic.* 23:195-200.
- Sethi VP, Sharma SK (2007). Greenhouse heating and cooling using aquifer water. *Energy*, 32: 1414-1421.
- Singh SK, Kakani VG, Brand D, Baldwin B, Reddy KR (2008). Assessment of cold and heat tolerance of winter-grown Canola (*Brassica napus* L.) cultivars by pollen-based Parameters. *J. Agron. Crop Sci.* 194:225-236.
- Stewart DW, Dwyer LM (1983). Stomatal response to plant water deficits. *J. Theor. Biol.* 104:655-666.
- Summerfield RJ, Muehlbauer FJ, Short RW (1989). Controlled environments as an adjunct to field research on Lentils (*Lens culinaris*). IV. Cultivar responses to above- and below-average temperatures during vegetative growth. *Exp. Agric.* 25: 119-134.
- Suzuki N, Mittler R (2006). Reactive oxygen species and temperature stresses: A delicate balance between signalling and destruction. *Physiol. Plant.* 126: 45-51.
- Taulavouri E, Tahkokorpi M, Taulavouri K, Laine K (2004). Anthocyanins and glutathione S-transferase activities in response to low temperature and frost hardening in *Vaccinium myrtillus* (L.). *J. Plant Physiol.* 161: 903-911.
- Taylor AO, Rowley JA (1971). Plants under climatic stress. Low temperature, high light effects on photosynthesis. *Plant Physiol.* 47: 713-718.
- Thakur P, Kumar S, Malik JA, Berger JD, Nayyar H (2010). Cold stress effects on reproductive development in grain crops: An overview. *Environ. Exp. Bot.* 67: 429-443.
- Thomas GW, Kissel DE (1970). Nitrate volatilization from soils. *Soil Sci. Soc. Am. J.* 34: 828-830.
- Tian MS, Woolf AB, Bowen JH, Ferguson IB (1996). Changes in color and chlorophyll fluorescence of broccoli florets following hot water treatment. *J. Am. Soc. Hort. Sci.* 121: 331-313.
- Tromp J (1984). Flower-bud formation in apple affected by air and root temperature, air humidity, light intensity and day length. *Acta Hort.* 149: 39-48.
- Van Der Ploeg A, Heuvelink E (2005). Influence of sub-optimal temperature on tomato growth and yield: a review. *J. Horticul. Sci. Biotechnol.* 80: 652-659.
- Vapaavuori EM, Rikala R, Ryyppö A (1992). Effects of root temperature on growth and photosynthesis in conifer seedlings during shoot elongation. *Tree Physiol.* 10: 217-230.
- Vierling E (1991). The roles of heat shock proteins in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 42: 579-620.
- Vu JVC, Yelenosky G (1987). Photosynthetic characteristics in leaves of 'Valencia' orange (*Citrus sinensis* (L) Osbeck) grown under high and low temperature regimes. *Environ. Exp. Bot.* 27: 279-287.
- Wahid A, Gelani S, Ashraf M, Foolad MR (2007). Heat tolerance in plants: An overview. *Environ. Exp. Bot.* 61:199-223.
- Welander NT (1984). Influence of temperature and day-length on flowering in *Aeschynanthus speciosus*. *Sci. Hortic.* 22: 157-161.
- Went FW (1953). The effect of temperature on plant growth. *Annu. Rev. Plant Physiol.* 4:347-362.
- Williams DG, Black RA (1993). Phenotypic variation in contrasting temperature environment: growth and photosynthesis in *Pennisetum setaceum* from different altitudes in Hawaii. *Funct. Ecol.* 7: 623-633.
- Xu S, Li J, Zhang X, Wei H, Cui L (2006). Effects of heat acclimation pre-treatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two-cool season turfgrass species under heat stress. *Environ. Exp. Bot.* 56: 274-285.
- Yamori W, Noguchi K, Hanba YT, Terashima I (2006). Effects of internal conductance on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. *Plant Cell Physiol.* 47: 1069-1080.
- Yang J, Kong Q, Xiang C (2009). Effects of low night temperature on pigments, chl *a* fluorescence and energy allocation in two bitter melon (*Momordica charantia* L.) genotypes. *Acta Physiol. Plantar.* 31: 285-293.
- Yun JG, Hayashi T, Yazawa S, Katoh T, Yasuda Y (1998). Abrupt and irreversible reduction of chlorophyll fluorescence associated with leaf spot in *Saintpaulia* (African violet). *Sci. Hortic.* 72: 157-169.
- Zhu LH, Borsboom O, Tromp J (1997). The effect of temperature on flower-bud formation in apple including some morphological aspects. *Sci. Hortic.* 70: 1-8.