

Plant water stress: Associations between ethylene and abscisic acid response

Carolina Salazar¹, Cristián Hernández², and María Teresa Pino^{1*}

Agriculture is severely impacted by water stress due either to excess (hypoxia/anoxia) or deficit of water availability. Hypoxia/anoxia is associated with oxygen (O₂) deficiency or depletion, inducing several anatomical, morphological, physiological, and molecular changes. The majority of these alterations are adaptive mechanisms to cope with low O₂ availability; among them, alterations in shoot length, aerenchyma formation and adventitious roots have been described in several studies. The aim of this review was to address the association between abscisic acid (ABA) and ethylene in function of water availability in plants. The major physiological responses to low O₂ are associated with changes in root respiration, stomatal conductance, photosynthesis, and fermentation pathways in roots. In addition, several changes in gene expression have been associated with pathways that are not present under normal O₂ supply. The expression of ethylene receptor genes is up-regulated by low O₂, and ethylene seems to have a crucial role in anatomical and physiological effects during hypoxia/anoxia. During O₂ depletion, ethylene accumulation down-regulates ABA by inhibiting rate-limiting enzymes in ABA biosynthesis and by activating ABA breakdown to phaseic acid. With regard to water deficit, drought is primarily sensed by the roots, inducing a signal cascade to the shoots via xylem causing physiological and morphological changes. Several genes are regulated up or down with osmotic stress; the majority of these responsive genes can be driven by either an ABA-dependent or ABA-independent pathway. Some studies suggest that ethylene shuts down leaf growth very fast after the plant senses limited water availability. Ethylene accumulation can antagonize the control of gas exchange and leaf growth upon drought and ABA accumulation.

Key words: ABA biosynthesis, anoxia, drought stress, ethylene, hypoxia.

INTRODUCTION

Water stress drives important losses in the crop market. Excess or deficit of water produces a cascade of physiological responses that ends-up in decreased production and reduced crop quality. Numerous factors are involved in plants responses to water stress. Several mechanisms that plants utilize to cope the effects of water stress are mediated by ethylene and abscisic acid (ABA). The independent effects of these molecules have been studied in different species. However, the interaction between these responses has not been specially analyzed.

The interaction between ABA and ethylene in plants under water stress has been studied by different research groups. From these studies it has been concluded that these hormones interact between them, under stress conditions.

Studies of endogenous ABA deficiency have shown that an important role of ABA is to limit ethylene production, and that this interaction is involved in the effects of ABA status on shoot and root growth (Sharp and LeNoble, 2001). Moreover, in horticultural crops and Arabidopsis, restriction of ethylene production can be considered a widespread function of ABA. Therefore, plants subjected to endogenous ABA supplementation may offer functions to maintain rather than inhibit plant growth (Sharp, 2002). This hormonal interaction probably would be more complex, by including effects, e.g., early leaf senescence and leaf, flower, and fruit abscission (Morgan and Drew, 1997).

The knowledge on the physiological, cellular, and molecular responses of plants to drought and waterlogging has already allowed great progress in plant breeding; however, a lot of this effort is still focused on Arabidopsis, ignoring crucial information in plant species with agricultural importance. Thus, understanding the physiological mechanisms associated to ABA and ethylene signaling, gene responses and their interaction is crucial for improving plant water stress tolerance (hypoxia or drought) in fruit tree species. Therefore, the aims of the present review were to address the association between ABA and ethylene in function of water availability in

¹Instituto de Investigaciones Agropecuarias, INIA La Platina, Santa Rosa 11610, La Pintana, Santiago, Chile.

*Corresponding author (mtpino@inia.cl).

²Centro de Estudios Avanzados en Fruticultura (CEAF), Camino Las Parcelas 882, Sector Los Choapinos, Rengo, Chile.

Received: 15 December 2014.

Accepted: 11 May 2015.

doi:10.4067/S0718-58392015000300008

plants and to analyze responses to water stress mediated by ethylene and ABA interaction.

Waterlogging causes anatomical, physiological and molecular alterations in plants

Yield and plant growth are significantly inhibited by a deficiency (hypoxia) or complete absence (anoxia) of oxygen, due to poorly drained soils or water-saturated soils and roots (Sairam et al., 2008). Excess water reduces oxygen (O₂) availability in plant roots, causing a barrier for gas diffusion into plant cells, inhibiting free gas exchange for photosynthesis and respiration and inducing changes in plant water relations (Sanchez-Blanco et al., 1994; Drew, 1997; Amador et al., 2012). Several anatomical, physiological and molecular changes due to flooding have been described, including: epinasty, wilting leaves (Kawase, 1981; Sanchez-Blanco et al., 1994; Dennis et al., 2000), premature leaf senescence, stem deformation, shoot length alteration and leaf area reduction (Aloni and Rosenshtein, 1982; Schaffer et al., 1992; Robbani et al., 2006). Decreased leaf growth is a particularly prompt response to flooding (Else et al., 1995). In avocado trees, O₂ depletion reduces root and shoot growth, leaf expansion, and also causes moderate to severe stem and leaf wilting, leaf abscission, and root necrosis (Gil et al., 2009). One of the major anatomical effects of hypoxia occurs at the root level. Some studies have reported hypertrophic lenticel formation (Jones and Sharitz, 1990; Shimamura et al., 2010), adventitious root development, and parenchymal tissue changes (Aloni and Rosenshtein, 1982; McNamara and Mitchell, 1989; Smith et al., 1990). Several types of tropical and subtropical fruit trees show anatomical or morphological adaptations to flooding stress, such as the development of hypertrophied stem lenticels, adventitious rooting or the formation of porous aerenchyma tissue (Schaffer et al., 2006). Aerenchyma formation in response to low oxygen availability has been reported as an anatomical adaptation to facilitate gas diffusion (like O₂) between hypoxic/anoxic roots and the aerial environment, including *Prunus* rootstocks (Garthwaite et al., 2008; Pistelli et al., 2012). Under hypoxia, aerenchyma formation involves cell death caused by an enhanced rate of ethylene synthesis (Jackson, 1985; He et al., 1994; Gunawardena et al., 2001).

The main physiological responses to low O₂ are associated with changes in root respiration, stomatal conductance, photosynthesis, and fermentation pathways in roots. In leaf gas exchange, the most common effect of flooding stress is a reduction in leaf transpiration and stomatal closure (Blanke and Cooke, 2004; Yetisir et al., 2006; Atkinson et al., 2008; Bai et al., 2013). In avocado trees (*Persea americana* Mill.), hypoxia causes a decline in net photosynthesis, accompanied by decreases in stomatal conductance, transpiration, and the intercellular partial pressure of CO₂ in leaves (Schaffer and Ploetz, 1989; Gil et al., 2009). In 2-yr-old apricot trees (*Prunus*

armeniaca L.) under flooding stress, the midday leaf water potential decreased progressively, and a close relationship was observed between leaf conductance and plant hydraulic conductance (Nicolás et al., 2005).

In *Prunus salicina* Lindl., hypoxia decreased net photosynthesis by limiting stomatal conductance (Martinazzo et al., 2013), similar to previous studies reported in *Prunus cerasus* L. (Beckman et al., 1992) and *Prunus armeniaca* 'Búlida' (Nicolás et al., 2005). Hypoxia increased the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, a key enzyme in the biosynthesis of ethylene; however, ACC synthase was inhibited under anoxic conditions in maize (He et al., 1994; Sairam et al., 2008), suggesting multiple chemical and molecular responses are involved in hypoxia or anoxia. Several genes with roles at the transcriptional, post-transcriptional, or translational levels have been reported in response to anoxia/hypoxia (Manjunath et al., 1998; Peng et al., 2001; 2005; Liu et al., 2005). Transcription factors (ethylene response factor [ERF]-like) have also been associated to O₂ depletion, but only a small ERF family (*AtERF73/HRE1*) modulates ethylene responses during hypoxia (Yang et al., 2011). The role of regulatory factors on some plant hormones such as abscisic acid (ABA), ethylene (ET), auxin and gibberellins in hypoxic regulation is also interesting but a challenging approach to follow.

Drought stress causes several anatomical, physiological and molecular alterations in plants

Drought is the major abiotic stress factor limiting agriculture. Water deficit not only affects crop and fruit production, it primarily reduces vegetative growth, shoot length and leaf area (Weisz et al., 1994; Deblonde and Ledent, 2001), along with physiological changes such as inhibiting gas exchange (Ekanayake and Midmore, 1992; Dalla Costa et al., 1997; Deblonde and Ledent, 2001; Kiziloglu et al., 2006; Bourtsoukidis et al., 2014). Drought is primarily sensed by roots; then, root-to-leaf signaling through the transpiration stream triggers stomatal closure, which is an important adaptation mechanism to water limitation (Flexas et al., 2002; Anjum et al., 2011). After stomatal closure, decreases in leaf transpiration and CO₂ assimilation occur associated with photosynthesis-related mechanisms such as electron transport, chlorophyll content, and enzymatic processes (Farquhar and Sharkey, 1982). In *P. salicina*, drought stress reduced net photosynthesis by stomatal limitation, while also affecting transpiration (Martinazzo et al., 2013).

Root length and behavior are critical in the drought stress response; in some plant species, root elongation continues even at very low water potentials capable of inhibiting shoot growth completely (Sharp et al., 2004). Some studies have reported that the root/shoot dry weight ratio increases as plant water stress increases due to relative reductions in shoot dry weight (Chazen and Neumann,

1994; Wu and Cosgrove, 2000; Fan and Neumann, 2004; Fan et al., 2006). In addition, roots under water deficit induce a signal cascade to the shoots via xylem causing physiological changes associated with several adaptation mechanisms; abscisic acid (ABA), cytokinins, ethylene, malate, and other unidentified factors have been implicated in root-shoot signaling (Steudle, 2000; Chaves et al., 2003).

Drought also induces several biochemical and molecular changes (Shinozaki and Yamaguchi-Shinozaki, 1997; Yamaguchi-Shinozaki and Shinozaki, 2006). The synthesis of compatible solutes such as proline, soluble sugars, glycine betaine and others seems to have a central role in osmotic adjustment, preventing or reducing the loss of turgor. Several genes are up or down regulated with osmotic stress (Shinozaki and Yamaguchi-Shinozaki, 2007). However, gene expression in response to water deficit is complex and cross linked with responses to other abiotic stresses. The majority of these responsive genes can be driven by either ABA-dependent or ABA-independent pathways (Shinozaki and Yamaguchi-Shinozaki, 2000). There are genes that protect against environmental stresses directly and genes with a role in gene expression regulation and signal transduction (Yamaguchi-Shinozaki and Shinozaki, 2006; Shinozaki and Yamaguchi-Shinozaki, 2007).

Taking flooding and water-deficit together, some plant species have obviously faced episodes subjected to both stresses, and have evolved to show some degree of plasticity and common physiological responses. Some common responses to drought and flooding in plants are changes in root water uptake (Else et al., 2001; Aroca et al., 2012), leaf dehydration (Domingo et al., 2002; Nicolás et al., 2005; Aroca et al., 2012), reductions in leaf transpiration and declines in stomatal conductance regulated by hydraulic and chemical signals (Blanke and Cooke, 2004; Atkinson et al., 2008; Aroca et al., 2012). In Japanese plum (*P. salicina*) grown under either flooding or drought stress conditions, net photosynthesis was reduced due to stomatal limitation under both stresses. However, the photosynthetic performance indexes showed differences between stresses, plum being more susceptible to drought than to flooding (Martinazzo et al., 2013).

Abscisic acid (ABA) seems to play an important role during waterlogging and water deficit

Abscisic acid plays an important role in integrating various stress signals and controlling downstream stress responses, as we will describe for excess water or water deficit (Shinozaki and Yamaguchi-Shinozaki, 2000; Tuteja, 2007; Raghavendra et al., 2010; Ye et al., 2012). ABA modifies root hydraulic properties caused by imbalances between root water uptake and leaf transpiration (Aroca et al., 2012). The main role of ABA seems to be to regulate the plant's water balance, including

under drought (Simonneau et al., 1998; Nan et al., 2002), and flooding stress (Olivella et al., 2000; Nan et al., 2002). For example, in *Triticum aestivum* L. plants, while ABA levels increased in roots and leaves in response to water deficit; ABA briefly increased in roots and leaves but then decreased in response to waterlogging (Nan et al., 2002).

Under waterlogging conditions, some studies have reported changes in ABA concentrations in several species, including alfalfa leaves (*Medicago sativa* L.; Castonguay et al., 1993), tobacco leaves (*Nicotiana tabacum* L.; Hurng et al., 1994), pea leaves (*Pisum sativum* L.; Jackson et al., 1988), tomato (*Solanum lycopersicum* L.; Else et al., 1995), *Gerbera jamesonii* Adlam (Olivella et al., 2000); *Citrus* (Arbona and Gómez-Cadenas, 2008); and *Malus* spp. (Bai et al., 2011). The ABA response to hypoxia may differ between leaves and roots, depending on the plant species and duration of flooding; a study comparing *Malus* species showed that *Malus sieversii* was more responsive to hypoxia stress than *Malus hupehensis*, showing a larger increase in ABA at the leaf and root level (Bai et al., 2011). In *Citrus* seedlings, leaf ABA levels increased after 3 wk flooding, suggesting that stomata closed independently. Also, they found that ABA is produced in old leaves and transported to younger leaves upon flooding, rather than translocation of ABA from roots to shoots (Rodríguez-Gamir et al., 2011). Studies in peas under waterlogging conditions concluded that leaves are not enriched substantially with ABA from roots, suggesting that leaves themselves are the most probable source of this growth regulator (Jackson et al., 1988). Other studies during flooding stress have associated ABA accumulation with an increase in reactive oxygen species (ROS), in *Glycine max* (L.) Merr. roots (Van Toai and Bolles, 1991), *Hordeum vulgare* L. roots and leaves (Kalashnikov et al., 1994), *Zea mays* L. leaves (Yan et al., 1996), and *Triticum aestivum* L. roots (Biemelt et al., 2000), among others. A time course study in *Arabidopsis thaliana* (L.) Heynh. showed that ABA increased with flooding stress, triggering stomatal closure and changes in hydrogen peroxide (H₂O₂) followed by an increase in antioxidant enzyme activities (Liu et al., 2012). In addition, exogenous ABA application increased anoxia tolerance in maize seedlings (Hwang and VanToai, 1991), in *Citrus* (Gómez-Cadenas et al., 1996), in lettuce (*Lactuca sativa* L.; Kato-Noguchi, 2000) and in *Arabidopsis* (Ellis et al., 1999; Dat et al., 2004).

In *Rumex palustris* Sm., long-term flooding induces shoot elongation, allowing re-establishment of the gas exchange between the atmosphere and submerged plant tissues (Benschop et al., 2005; 2006). This adaptation mechanism in *R. palustris* requires ABA-dependent biosynthesis of gibberellins; basically, ethylene accumulation down regulates ABA levels via inhibiting 9-cis-epoxycarotenoid dioxygenase expression (one of the carotenoid cleavage dioxygenases) and via

activating ABA breakdown to phaseic acid. This decline in endogenous ABA is required in order to stimulate the expression of gibberellin (GA) 3-oxidase, an enzyme that catalyses the conversion to bioactive gibberellin (GA1). Downstream of GA, three sets of genes encode proteins involved in cell wall loosening, in the cell cycle, and in starch breakdown, as well as other genes involved in internode elongation (Benschop et al., 2006). A similar response has been observed in rice (Bailey-Serres and Voesenek, 2008).

Under water deficit, one main function of ABA in plants is regulating the water balance, preventing intracellular water loss (Tuteja, 2007). Drought induces root-to-leaf signaling through the transpiration stream followed by stomatal closure, which is commonly associated with ABA signaling (Wilkinson and Davies, 2002; Tuteja, 2007). ABA promotes the efflux of K⁺ ions from guard cells, leading to a decrease in turgor pressure decrease and subsequently stomata closure (Anjum et al., 2011). A study in *Prunus dulcis* (Mill.) D.A. Webb during a progressive drought stress showed that leaf stomatal conductance depended on the concentration of ABA in the xylem sap (Wartinger et al., 1990). In field-grown *Prunus* trees, ABA concentration in the xylem sap was also associated with drought-induced stomatal closure (Correia et al., 1997). Several studies have shown that ABA is not only synthesized in roots; studies in tomato and sunflower showed that ABA is also synthesized in leaves (Fambrini et al., 1995; Holbrook et al., 2002). In addition, ABA plays an important role in plant growth under drought stress; ABA deficient mutant *Arabidopsis* plants wilt and die under prolonged water stress (Koorneef et al., 1998). ABA also mediates several physiological processes by changes in gene expression. In fact, drought stress responsive genes can be driven by either an ABA-dependent or ABA-independent pathway (Shinozaki and Yamaguchi-Shinozaki, 2000). The ABA-dependent gene response during drought stress is controlled by different classes of transcription factors, such as bZIP (cis-acting basic leucine zipper) AREB1/ABF2, AREB2/ABF4, and ABF3; ABA-responsive protein kinases that activate transcription factors through phosphorylation; and NAC domain proteins (ANAC019, ANAC055, and ANAC072); and MYB/MYC Zinc-finger protein (Bray, 2004; 2007). In addition, water stress responsive genes associated with compatible osmolyte biosynthesis and LEA-like (late embryogenesis abundant) protein are also induced by ABA (Raghavendra et al., 2010; Tuteja, 2007). In addition to the previously described, ABA signaling has been associated with changes in ethylene production due to water deficit; in maize seedlings, for example, ABA signaling has been associated with changes in ethylene production in conjunction with changes in root/shoot elongation under water stress (Sharp and LeNoble, 2002).

Ethylene could play an important role under waterlogging and drought stress

Ethylene production under abiotic stresses such as waterlogging and drought, among others; can reduce photosynthesis (Rajala and Peltonen-Sainio, 2001), inhibit root growth, reduce shoot/leaf expansion (Sharp and LeNoble, 2002; Pierik et al., 2007) and decrease grain yield by grain abortion, among other actions (Wilkinson and Davies, 2010).

Ethylene plays an important role in the plant response to oxygen deficiency, including the induction of gene expression associated with leaf senescence, aerenchyma formation, and glycolysis and fermentation pathways, among other responses. Epinasty, a common response in flooded plants, results from accumulation of the ethylene precursor ACC in roots; basically, ACC is transported through the transpiration stream to the aerial part of the plant, where the presence of oxygen allows it to be converted into ethylene, triggering petiole epinasty (Jackson, 2008; Vidoz et al., 2010). In *Prunus cerasifera* Ehrh., while the wild-type was sensible to flooding, showing epinasty and leaf senescence, the L clone showed an increase in ethylene synthesis (mainly in leaves) and ACC oxidase (ACO) gene expression (Pistelli et al., 2012). In *Citrus*, water-stress induced leaf abscission was associated with ACC expression accompanied by a concomitant increase in ethylene (Gómez-Cadenas et al., 1996). In avocado, long-term hypoxia in the root zone resulted in leaf ethylene accumulation with a significant decrease in stomata conductance and an increase in leaf abscission (Gil et al., 2009).

Under hypoxia, aerenchyma formation is one of the most important morphological responses, and ethylene plays an important role in this. Many authors have reported aerenchyma formation upon hypoxia with a concomitant increase in ethylene in species such as barley (*Hordeum vulgare* L.) (Larsen et al., 1986), maize (Drew et al., 1981; He et al., 1994), wheat (Watkin et al., 1998), soybean (Bacanawmo and Purcell, 1999), *Carex* spp. (Visser et al., 1996), and *Trifolium subterraneum* L. (Aschi-Smiti et al., 2003). In addition, application of exogenous ethylene produced aerenchyma formation in maize roots (Drew et al., 1981). However, in crop species like rice (*Oryza sativa* L.) aerenchyma formation is constitutive and is not inducible by ethylene or the low partial oxygen pressures often observed during flooding (Jackson et al., 1985; Kawai et al., 1998).

Ethylene under water logged conditions is also associated with adventitious root formation (Steffens et al., 2006; Vidoz et al., 2010; Pistelli et al., 2012); adventitious roots are able to maintain plant growth during waterlogging by maintaining nutrient and water uptake (Sairam et al., 2008). In rice, waterlogging induced adventitious root formation mediated by ethylene that also appeared to facilitate aerenchyma formation (Justin and Armstrong, 1991). In tomato,

the development of adventitious roots in the stem has been observed after few days under partial submergence (Vidoz et al., 2010). On the other hand, ethylene can act either alone or in coordination with indole-3-acetic acid (IAA) in stimulating shoot elongation under flooding (Voesenek et al., 2003; Pierik et al., 2007). Likewise, a study in transgenic tomato plants harboring an antisense sequence for ACC oxidase under hypoxia showed similar stomatal conductance as wild-type in young expanded leaves, suggesting that leaf expansion and shoot growth were more closely correlated with endogenous ethylene levels than with xylem sap ABA concentration (Hussain et al., 1999).

Under drought stress, a close relationship between ACC expression and ethylene synthesis has been demonstrated in *Citrus* (Gómez-Cadenas et al., 1996). The ethylene precursor (ACC) moves in the xylem, from root to shoots, showing an association between its expression and ethylene evolution in leaves (Liu et al., 2006; 2007). In maize, leaf ethylene changes were not associated with reductions in leaf elongation under drought (Liu et al., 2007) suggesting that ethylene may play a role in leaf growth inhibition and ACC may be one component of long distance root-sourced signals under drought (Schachtman and Goodger, 2008). A report in wheat showed that after 2 d under drought-stress, plants treated with an ethylene inhibitor (1-MCP) closed their stomata, suggesting chemical but not hydraulic signals controlled stomatal closure (Sharipova et al., 2012).

Association between abscisic acid and ethylene response under water stress

Some studies suggest that ABA and ethylene are antagonists, that ABA accumulation can modulate the influence of ethylene on the processes of shoot and root growth and stomatal conductance and vice versa. Some studies suggest that ethylene prevents ABA accumulation and modulates cellular sensitivity to ABA (Ghassemian et al., 2000; Spollen et al., 2000; Wilkinson and Davies, 2010; Wilkinson et al., 2012).

Studies in plants oxygen depleted by waterlogging often report increased concentrations of ACC, ethylene, and ABA in leaves (Bradford and Yang, 1980; Kozłowski, 1997). In addition, ethylene, ABA, and GA have been associated with shoot elongation upon waterlogging; these three hormones would regulate processes such as apoplastic acidification, cell wall loosening, cell division, and starch breakdown (Schachtman and Goodger, 2008). The same review reported that during oxygen depletion, ethylene accumulation down-regulated ABA by inhibiting the rate-limiting enzymes in ABA biosynthesis and by activating ABA breakdown to phaseic acid (Schachtman and Goodger, 2008). Evidence of cross-response between ABA and ethylene has been associated with flooding stress. A decrease in ABA synthesis occurring soon after roots are flooded could sensitive leaves to the ethylene.

This might enhance epinastic curvature and also unmask ethylene inhibition of leaf expansion (Konings and de Wolf, 1984; Else et al., 1995; Sharp et al., 2000). In maize root seedlings, ABA application prevented aerenchyma formation but without affecting the ethylene concentration (Konings and de Wolf, 1984). In addition, ethylene in combination with hypoxia induced growth due to an increase in GA and a concomitant decrease in ABA (Kende et al., 1998; van der Straeten et al., 2001). A recent study in rice further showed that a rapid decrease in ABA in submerged rice shoots was controlled in part by ethylene-induced expression of the *OsABA8ox1* gene (encoding ABA 80-hydroxylase) and by ethylene-independent suppression of genes involved in the biosynthesis of ABA (Saika et al., 2007).

Some authors have described changes in ethylene production as a consequence of an increased concentration of ABA in drought stressed plants (Elbeltag and Hall, 1974; Wright, 1980; Morgan et al., 1991; Narayana et al., 1991; Morgan and Drew, 1997; Olivella et al., 1998). A study in *G. jamesonii* under drought stress and subsequent re-watering treatment showed that in conjunction with a decrease in transpiration rate and leaf water potential, ABA increased in leaves while ethylene decreased (Olivella et al., 1998). In maize, ABA accumulation maintains primary root elongation at low water potentials by limiting ethylene production (Spollen et al., 2000). Several other studies have suggested that endogenous ABA accumulation may limit ethylene production during water stress, regulating some drought responses in plants such as root and leaf growth (Wright, 1980; Tan and Thimann, 1989; Chaves et al., 2003). In ABA-deficient transgenic maize, leaf ethylene was only increased by a soil water deficit (Voisin et al., 2006). ABA can induce stomatal closure either when produced endogenously or when exogenously supplied; however, ethylene could antagonize the stomatal response to ABA (Wilkinson and Davies, 2009). Leaf abscission induced by ethylene in water-stressed *Citrus* plants required previous root ABA accumulation. Accordingly, some results suggest that the sequence of events upon water stress leading to leaf abscission in *Citrus* is as follows: ABA accumulation in roots followed by ACC accumulation in roots and ACC transport from roots to shoots; then, ACC oxidation to ethylene in leaves inducing eventual leaf abscission. Collectively, ABA is the primary signal to water stress and capable of modulating ethylene, the synthesis of which is the hormonal activator of leaf abscission (Gómez-Cadenas et al., 1996; Wilkinson et al., 2012). A study in *Arabidopsis* showed that an *acs7* mutant with reduced ethylene production showed increased tolerance to salt, heat, and drought stresses associated with higher ABA accumulation and ABA stress signaling modulation (Dong et al., 2011). The final response to water stress would then depend on the ratio between concentrations

of ethylene and ACC and ABA (Acharya and Assmann, 2009; Wilkinson and Davies, 2010; Wilkinson et al., 2012).

CONCLUSIONS

The gathered information here shown that the effects of flooding and water deficit stress present similar responses at the physiological and molecular level. Thus, the major physiological responses to low O₂ are associated with changes in root respiration, stomatal conductance, photosynthesis, and fermentation pathways. On the other hand, water deficit conditions increase ABA concentrations, which induce stomatal closure and a following decay in the photosynthetic rates. The interaction between these hormones takes place under both stresses. During O₂ depletion ethylene accumulation down-regulates ABA by inhibiting rate-limiting enzymes in ABA biosynthesis and by activating ABA breakdown to phaseic acid. Under water deficit, a signaling pathway is induced in roots towards the shoots through the xylem. The majority of the responsive genes involved can be driven by either an ABA-dependent or -independent pathway. Besides, some studies suggest that ethylene shuts down leaf growth very fast after plant senses limited water availability. Ethylene accumulation can antagonize the control of gas exchange and leaf growth upon drought and ABA accumulation.

LITERATURE CITED

Acharya, B.R., and S.M. Assmann. 2009. Hormone interactions in stomatal function. *Plant Molecular Biology* 69:451-462.

Aloni, B., and G. Rosenshtein. 1982. Effects of flooding on tomato cultivars. The relationship between proline accumulation and other morphological and physiological changes. *Physiologia Plantarum* 56:513-517.

Amador, M.L., S. Sancho, B. Bielsa, J. Gomez-Aparisi., and M.J. Rubio-Cabetas. 2012. Physiological and biochemical parameters controlling waterlogging stress tolerance in *Prunus* before and after drainage. *Physiologia Plantarum* 144:357-368.

Anjum, S.A., X.Y. Xie, L.C. Wang, M.F. Saleem, C. Man., and W. Lei. 2011. Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research* 6:2026-2032.

Arbona, V., and A. Gómez-Cadenas. 2008. Hormonal modulation of *Citrus* responses to flooding. *Journal of Plant Growth Regulation* 27:241-250.

Aroca, R., R. Porcel, and J.M. Ruiz-Lozano. 2012. Regulation of root water uptake under abiotic stress conditions. *Journal of Experimental Botany* 63:43-57.

Aschi-Smiti, S., W. Chaïbi, R. Brouquisse, B. Bérénice-Ricard, and P. Saglio. 2003. Assessment of enzyme induction and aerenchyma formation as mechanisms for flooding tolerance in *Trifolium subterraneum* 'Park'. *Annals of Botany* 91:195-204.

Atkinson, C.J., R.S. Harrison-Murray, and J.M. Taylor. 2008. Rapid-flood induced stomatal closure accompanies xylem sap transportation of root-derived acetaldehyde and ethanol in *Forsythia*. *Environmental and Experimental Botany* 64:196-205.

Bacanamwo, M., and L.C. Purcell. 1999. Soybean root morphological and anatomical traits associated with acclimation to flooding. *Crop Science* 39:143-149.

Bai, T., C. Li, D. Liang, and F. Ma. 2013. Contrasting hypoxia tolerance and adaptation in *Malus* species is linked to differences in stomatal behavior and photosynthesis. *Physiologia Plantarum* 147:514-523.

Bai, T., R. Yin, C. Li, F. Ma, Z. Yue, and H. Shu. 2011. Comparative analysis of endogenous hormones in leaves and roots of two contrasting *Malus* species in response to hypoxia stress. *Journal Plant Growth Regulation* 30:119-127.

Bailey-Serres, J., and L.A. Voesenek. 2008. Flooding stress: Acclimations and genetic diversity. *Annual Review of Plant Biology* 59:313-339.

Beckman, C., R.L. Perry, and J.A. Flore. 1992. Short-term flooding affects gas exchange characteristics of containerised sour cherry trees. *HortScience* 27:1297-1301.

Benschop, J.J., J. Bou, A.J.M. Peeters, N. Wagemaker, K. Gühl, et al. 2006. Long-term submergence-induced elongation in *Rumex palustris* requires abscisic acid-dependent biosynthesis of gibberellin. *Plant Physiology* 141:1644-1652.

Benschop, J.J., M.B. Jackson, K. Gühl, R.A.M. Vreeburg, S.J. Croker, et al. 2005. Contrasting interactions between ethylene and abscisic acid in *Rumex* species differing in submergence tolerance. *Plant Journal* 44:756-768.

Biemelt, S., U. Keetman, H.P. Mock, and B. Grimm. 2000. Expression and activity of isoenzymes of superoxide dismutase in wheat roots in response to hypoxia and anoxia. *Plant Cell Environment* 23:135-144.

Blanke, M.M., and D.T. Cooke. 2004. Effects of flooding and drought on stomatal activity, transpiration, photosynthesis, water potential and water channel activity in strawberry stolons and leaves. *Plant Growth Regulation* 42:153-160.

Bourtsoukidis, E., H. Kawaletz, D. Radacki, S. Schütz, H. Hakola, H. Hellén, et al. 2014. Impact of flooding and drought conditions on the emission of volatile organic compounds of *Quercus robur* and *Prunus serotina*. *Trees* 28:193-204.

Bradford, K.J., and S.F. Yang. 1980. Xylem transport of l-aminocyclopropane-l-carboxylic acid, an ethylene precursor, in waterlogged tomato plants. *Plant Physiology* 65:322-326.

Bray, E.A. 2004. Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. *Journal of Experimental Botany* 55:2331-2341.

Bray, E.A. 2007. Plant response to water deficit stress. *Encyclopedia of Life Sciences*. doi:10.1002/9780470015902.a0001298.pub2.

Castonguay, Y., P. Nadeau, and R.R. Simard. 1993. Effects of flooding on carbohydrate and ABA levels in roots and shoots of alfalfa. *Plant, Cell & Environment* 16:695-702.

Chaves, M., J. Maroco, and J. Pereira. 2003. Understanding plant responses to drought from genes to the whole plant. *Functional Plant Biology* 30:239-264.

Chazen, O., and P.M. Neumann. 1994. Hydraulic signals from the roots and rapid cell-wall hardening in growing maize (*Zea mays* L.) leaves are primary responses to polyethylene glycol-induced water deficits. *Plant Physiology* 104:1385-1392.

Correia, M.J., M.L. Rodrigues, M.I. Ferreira, and J.S. Pereira. 1997. Diurnal change in the relationship between stomatal conductance and abscisic acid in the xylem sap of field-grown peach trees. *Journal of Experimental Botany* 48:1727-1736.

Dalla Costa, L., G. Delle Vedove, G. Gianquinto, R. Giovanardi, and A. Peressotti. 1997. Yield, water use efficiency and nitrogen uptake in potato: Influence of drought stress. *Potato Research* 40:19-34.

Dat, J.F., N. Capelli, H. Folzer, P. Bourgeade, and P.M. Badot. 2004. Sensing and signalling during plant flooding. *Plant Physiology Biochemistry* 42:273-282.

Deblonde, P., and J. Ledent. 2001. Effects of moderate drought conditions on green leaf number stem height, leaf length and tuber yield of potato cultivars. *European Journal of Agronomy* 14:31-41.

Dennis, E.S., R. Dolferus, M. Ellis, M. Rahman, Y. Wu, F.U. Hoeren, et al. 2000. Molecular strategies for improving waterlogging tolerance in plants. *Journal of Experimental Botany* 51(342):89-97.

- Domingo, R., A. Perez-Pastor, and C. Ruiz-Sanchez. 2002. Physiological responses of apricot plants grafted on two different rootstocks to flooding conditions. *Journal of Plant Physiology* 159:725-732.
- Dong, H., Z. Zhen, J. Peng, L. Chang, Q.Q. Gong, and N.N. Wang. 2011. Loss of ACS7 confers abiotic stress tolerance by modulating ABA sensitivity and accumulation in *Arabidopsis*. *Journal of Experimental Botany* 62:4875-4887.
- Drew, M.C. 1997. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Annual Review of Plant Physiology and Plant Molecular Biology* 48:223-250.
- Drew, M.C., M.B. Jackson, S.C. Giffard, and R. Campbell. 1981. Inhibition by silver ions of gas space (aerenchyma) formation in adventitious roots of *Zea mays* L. subjected to exogenous ethylene or to oxygen deficiency. *Planta* 153:217-224.
- Elbeltag, A., and M.A. Hall. 1974. Effect of water stress upon endogenous ethylene levels in *Vicia faba*. *New Phytologist* 73:47-60.
- Ellis, M.H., E.S. Dennis, and W.J. Peacock. 1999. *Arabidopsis* roots and shoots have different mechanisms for hypoxic stress tolerance. *Plant Physiology* 119:57-64.
- Ekanayake, I.J., and D.J. Midmore. 1992. Genotypic variation for root pulling resistance in potato and its relationship with yield under water-deficit stress. *Euphytica* 61:43-53.
- Else, M.A., D. Coupland, L. Dutton, and M.B. Jackson. 2001. Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure and slows leaf expansion in flooded plants of castor oil (*Ricinus communis*) despite diminished delivery of ABA from the roots to shoots in xylem sap. *Physiologia Plantarum* 111:46-54.
- Else, M.A., K.C. Hall, G.M. Arnold, W.J. Davies, and M.B. Jackson. 1995. Export of abscisic acid, 1-aminocyclopropane-1-carboxylic acid, phosphate, and nitrate from roots to shoots of flooded tomato plants. *Plant Physiology* 107:377-384.
- Fambrini, M., P. Vernieri, M.L. Toncelli, V.D. Rossi, and C. Pugliesi. 1995. Characterization of a wilted sunflower (*Helianthus annuus* L.) mutant III. Phenotypic interaction in reciprocal grafts from wilted mutant and wild-type plants. *Journal of Experimental Botany* 286:525-530.
- Fan, L., R. Linker, S. Gepstein, E. Tanimoto, R. Yamamoto, and P.M. Neumann. 2006. Progressive inhibition by water deficit of cell wall extensibility and growth along the elongation zone of maize roots is related to increased lignin metabolism and progressive stelar accumulation of wall phenolics. *Plant Physiology* 140:603-612.
- Fan, L., and P.M. Neumann. 2004. The spatially variable inhibition by water deficit of maize root growth correlates with altered profiles of proton flux and cell wall pH. *Plant Physiology* 135:2291-2300.
- Farquhar, G.D., and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* 33:317-345.
- Flexas, J., J. Bota, J.M. Escalona, B. Sampol, and H. Medrano. 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Functional Plant Biology* 29:461-471.
- Ghassemian, M., E. Nambara, S. Cutler, H. Kawaide, Y. Kamiya, and P. McCourt. 2000. Regulation of abscisic acid signalling by the ethylene response pathway in *Arabidopsis*. *The Plant Cell* 12:1117-1126.
- Garthwaite, A.J., W. Armstrong, and T.D. Colmer. 2008. Assessment of O₂ diffusivity across the barrier to radial O₂ loss in adventitious roots of *Hordeum marinum*. *New Phytologist* 179:405-416.
- Gil, P.M., L. Gurovich, B. Schaffer, N. Garcia, and R. Iturriaga. 2009. Electrical signaling, stomatal conductance, ABA and ethylene content in avocado trees in response to root hypoxia. *Plant Signaling & Behavior* 4(2):100-108.
- Gómez-Cadenas, A., F.R. Tadeo, M. Talón, and E. Primo Millo. 1996. Leaf abscission induced by ethylene in water-stressed intact seedlings of Cleopatra mandarin requires previous abscisic acid accumulation in roots. *Plant Physiology* 112:401-408.
- Gunawardena, A., D.M. Pearce, M.B. Jackson, C.R. Hawes, and D.E. Evans. 2001. Characterisation of programmed cell death during aerenchyma formation induced by ethylene or hypoxia in roots of maize (*Zea mays* L.). *Planta* 212:205-214.
- He, Ch.-J., M.C. Drew, and P.W. Morgan. 1994. Plant induction of enzymes associated with lysigenous aerenchyma formation in roots of *Zea mays* L. during hypoxia and nitrogen starvation. *Plant Physiology* 105:861-865.
- Holbrook, N.M., V.R., Shashidhar, R.A. James, and R. Munns. 2002. Stomatal control in tomato with ABA deficient roots: response of grafted plants to soil drying. *Journal Experimental Botany* 53:1503-1514.
- Hurng, W.P., H.S. Lur, C-K. Liao, and C.H. Rao. 1994. Role of abscisic acid, ethylene and polyamines in flooding promoted senescence of tobacco leaves. *Plant Physiology* 143:102-105.
- Hussain, A., C.R. Black, I.B. Taylor, and J.A. Roberts. 1999. Soil compaction. A role for ethylene in regulating leaf expansion and shoot growth in tomato? *Plant Physiology* 121:1227-1237.
- Hwang, S-Y., and T.T. VanToai. 1991. Abscisic acid induces anaerobiosis tolerance in corn. *Plant Physiology* 97:593-597.
- Jackson, M.B. 1985. Ethylene and responses of plants to soil waterlogging and submergence. *Annual Review of Plant Physiology* 36:145-174.
- Jackson, M.B. 2008. Ethylene-promoted elongation: An adaptation to submergence stress. *Annals of Botany* 101:229-248.
- Jackson, M.B., T.M. Fenning, and W. Jenkins. 1985. Aerenchyma (gas space) formation in adventitious roots of rice (*Oryza sativa* L.) is not controlled by ethylene or small partial pressures of oxygen. *Journal of Experimental Botany* 36:1566-1572.
- Jackson, M.B., S.F. Young, and K.C. Hall. 1988. Are roots a source of abscisic acid for the shoots of flooded pea plants? *Journal of Experimental Botany* 39(12):1631-1637.
- Jones, R.H., and R.R. Sharitz. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. *Canadian Journal of Forest Research* 20:573-578.
- Justin, S., and W. Armstrong. 1991. Evidence for the involvement of ethene in aerenchyma formation in adventitious roots of rice (*Oryza sativa* L.). *New Phytologist* 118:49-62.
- Kalashnikov, Y.E., T.I. Balakhnina, and D.A. Zakrzhevsky. 1994. Effect of soil hypoxia on activation of oxygen and the system of protection from oxidative destruction in roots and leaves of *Hordeum vulgare*. *Russian Journal of Plant Physiology* 41:583-588.
- Kato-Noguchi, H. 2000. Abscisic acid and hypoxic induction of anoxia tolerance in roots of lettuce seedlings. *Journal of Experimental Botany* 51(352):1939-1944.
- Kawai, M., P.K. Samarajeewa, R.A. Barrero, M. Nishiguchi, and H. Uchimiya. 1998. Cellular dissection of the degradation pattern of cortical cell death during aerenchyma formation of rice roots. *Planta* 204:277-287.
- Kawase, M. 1981. Anatomical and morphological adaptation for plants to waterlogging. *HortScience* 16:30-34.
- Kende, H., E. van der Knaap, and H.T. Cho. 1998. Deepwater rice: A model plant to study stem elongation. *Plant Physiology* 118:1105-1110.
- Kiziloglu, F.M., U. Sahin, T. Tunc, and S. Diler. 2006. The effect of deficit irrigation on potato evapotranspiration and tuber yield under cool season and semiarid climatic condition. *Journal of Agronomy* 5:284-288.
- Konings, H., and A. de Wolf. 1984. Promotion and inhibition by plant growth regulators of aerenchyma formation in seedling roots of *Zea mays*. *Physiologia Plantarum* 60:309-314.
- Koornneef, M., K.M. Leon-Kloosterziel, S. Schwartz, and J.A.D. Hand Zeevaart. 1998. The genetic and molecular dissection of abscisic acid biosynthesis and signal transduction in *Arabidopsis*. *Plant Physiology Biochemistry* 36:83-89.
- Kozłowski, T.T. 1997. Response of woody plants to flooding and salinity. *Tree Physiology Monograph* 1:1-29.
- Larsen, O., H.G. Nilsen, and H. Aarnes. 1986. Response of young barley plants to waterlogging, as related to concentration of ethylene and ethane. *Journal of Plant Physiology* 122:365-372.

- Liu, P., F. Sun, R. Gao, and H. Dong. 2012. RAP2.6L overexpression delays waterlogging induced premature senescence by increasing stomatal closure more than antioxidant enzyme activity. *Plant Molecular Biology* 79:609-622.
- Liu, H.Y., W.N. Sun, W.A. Su, and Z.C. Tang. 2006. Co-regulation of water channels and potassium channels in rice. *Physiologia Plantarum* 128:58-69.
- Liu, F., L. Vantoi, P.M. Moy, G. Bock, L.D. Linford, and J. Quackenbus. 2005. Global transcription profiling reveals comprehensive insights into hypoxic response in Arabidopsis. *Plant Physiology* 137:1115-1129.
- Liu, H.Y., X. Yu, D.Y. Cui, M.H. Sun, W.N. Sun, et al. 2007. The role of water channel proteins and nitric oxide signaling in rice seed germination. *Cell Research* 17:638-649.
- Manjunath, S., C.H. Lee, P. VanWinkle, and J. Bailey-Serres. 1998. Molecular and biochemical characterization of cytosolic phosphoglucomutase in maize: expression during development and in response to oxygen deprivation. *Plant Physiology* 117:997-1006.
- Martinazzo, E.G., A.T. Perboni, P.V. de Oliveira, V.J. Bianchi, and M.A. Bacarin. 2013. Remove from marked Records Photosynthetic activity in Japanese plum under water deficit and flooding. *Ciência Rural* 43:35-41.
- McNamara, S.T., and C.A. Mitchell. 1989. Differential flood stress resistance of two tomato genotypes. *Journal of the American Society for Horticultural Science* 114:976-980.
- Morgan, P.W., and M.C. Drew. 1997. Ethylene and plant responses to stress. *Physiologia Plantarum* 100:620-630.
- Morgan, P.W., C.J. He, J.A. Degreef, and M.P. Deproft. 1991. Does water deficit stress promote ethylene synthesis by intact plants? *Plant Physiology* 94:1616-1624.
- Nan, R., J.G. Carman, and F.B. Salisbury. 2002. Water stress, CO₂ and photoperiod influence hormone levels in wheat. *Journal of Plant Physiology* 159:307-312.
- Narayana, I., S. Lalonde, and H.S. Saini. 1991. Water-stress-induced ethylene production in wheat - a fact or artifact. *Plant Physiology* 96:406-410.
- Nicolás, E., A. Torrecillas, J. Dell'Amico, and J. Alarcón. 2005. The effect of short-term flooding on the sap flow, gas exchange and hydraulic conductivity of young apricot trees. *Trees-Structure and Function* 19:51-57.
- Olivella, C., C. Biel, M. Vendrell, and R. Save. 2000. Hormonal and physiological responses of *Gerbera jamesonii* to flooding stress. *HortScience* 35:222-225.
- Olivella, C., M. Vendrell, and R. Save. 1998. Abscisic acid and ethylene content in *Gerbera jamesonii* plants submitted to drought and rewatering. *Biologia Plantarum* 41:613-616.
- Peng, H.P., C.S. Chan, M.C. Shih, and S.F. Yang. 2001. Signaling events in the hypoxic induction of alcohol dehydrogenase gene in Arabidopsis. *Plant Physiology* 126:742-749.
- Peng, H.P., T.Y. Lin, N.N. Wang, and M.C. Shih. 2005. Differential expression of genes encoding l-aminocyclopropane-1-carboxylate synthase in Arabidopsis during hypoxia. *Plant Molecular Biology* 58:15-25.
- Pierik, R., R. Sasidharan, and L.A.C.J. Voesenek. 2007. Growth control by ethylene: Adjusting phenotypes to the environment. *Journal of Plant Growth Regulation* 26:188-200.
- Pistelli, L., C. Iacona, D. Miano, M. Cirilli, M.C. Colao, A. Mensuali-Sodi, et al. 2012. Novel *Prunus* rootstock somaclonal variants with divergent ability to tolerate waterlogging. *Tree Physiology* 32:355-368.
- Raghavendra, S., V.K. Gonugunta, A. Christmann, and E. Grill. 2010. ABA perception and signaling. *Trends in Plant Science* 15:395-401.
- Rajala, A., and P. Peltonen-Sainio. 2001. Plant growth regulator effects on spring cereal root and shoot growth. *Agronomy Journal* 93:936-943.
- Robbani, M., K. Banno, and M. Kakegawa. 2006. Differential Flooding tolerance of some dwarfing pear rootstock clones selected from the progenies of *Pyrus betulaefolia* and *P. calleryana*. *Journal of the Japanese Society for Horticultural Science* 75(4):297-305.
- Rodriguez-Gamir, J., G. Ancillo, M.C. Gonzalez-Mas, E. Primo-Millo, D.J. Iglesias, and M.A. Forner-Giner. 2011. Root signalling and modulation of stomatal closure in flooded citrus seedlings. *Plant Physiology and Biochemistry* 49:636-645.
- Saika, H., M. Okamoto, K. Miyoshi, T. Kushihiro, S. Shinoda, et al. 2007. Ethylene promotes submergence-induced expression of *OsABA8ox1*, a gene that encodes ABA 8'-hydroxylase in rice. *Plant Cell Physiology* 48:287-298.
- Sairam, R.K., D. Kumutha, K. Ezhilmathi, P.S. Deshmukh, and G.C. Srivastava. 2008. Physiology and biochemistry of waterlogging tolerance in plants. *Biologia Plantarum* 52:401-412.
- Sanchez-Blanco, M.J., J.J. Alarcon, J. Planes, and A. Torrecillas. 1994. Differential flood stress resistance of two almond cultivars based on survival, growth and water relations as stress indicators. *The Journal of Horticultural Science* 69:947-953.
- Schachtman, D.P., and J.Q.D. Goodger. 2008. Chemical root to shoot signaling under drought. *Trends in Plant Science* 13(6):281-287.
- Schaffer, B., P.C. Andersen, and R.C. Plötz. 1992. Responses of Fruit crops to flooding. *Horticultural Reviews* 13:257-313.
- Schaffer, B., F.S. Davies, and J.H. Crane. 2006. Responses of subtropical and tropical fruit trees to flooding in calcareous soil. *HortScience* 41:549-555.
- Schaffer, B., and R.C. Plötz. 1989. Gas exchange characteristics as indicators of damage thresholds for Phytophthora root rot of flooded and nonflooded avocado trees. *HortScience* 24:653-655.
- Sharipova, G.V., D.S. Veselov, G.R. Kudoyarova, M.D. Timergalin, and S. Wilkinson. 2012. Effect of ethylene perception inhibitor on growth, water relations, and abscisic acid content in wheat plants under water deficit. *Russian Journal of Plant Physiology* 59:573-580.
- Sharp, R.E. 2002. Interaction with ethylene: Changing views on the role of abscisic acid in root and shoot growth responses to water stress. *Plant, Cell & Environment* 25:211-22.
- Sharp, R.E., M.E. LeNoble, M.A. Else, E.T. Thorne, and F. Gherardi. 2000. Endogenous ABA maintains shoot growth in tomato independently of effects on plant water balance: evidence for the involvement of ethylene. *Journal of Experimental Botany* 51:1575-1584.
- Sharp, R.E., and M.E. LeNoble. 2002. ABA, ethylene and the control of shoot and root growth under water stress. *Journal of Experimental Botany* 53(366):33-37.
- Sharp, R.E., V. Poroyko, L.G. Hejlek, W.G. Spollen, G.K. Springer, H.J. Bohnert, et al. 2004. Root growth maintenance during water deficits: Physiology to functional genomics. New directions for a diverse planet. Proceedings for the 4th International Crop Science Congress, Brisbane, Australia. 26 September-1 October. Available at <http://www.cropscience.org.au/icsc2004/> (accessed January 2015).
- Shimamura, S., R. Yamamoto, T. Nakamura, S. Shimada, and S. Komatsu. 2010. Stem hypertrophic lenticels and secondary aerenchyma enable oxygen transport to roots of soybean in flooded soil. *Annals of Botany* 106:277-284.
- Shinozaki, K., and K. Yamaguchi-Shinozaki. 1997. Gene expression and signal transduction in water-stress response. *Plant Physiology* 115:327-334.
- Shinozaki, K., and K. Yamaguchi-Shinozaki. 2000. Molecular responses to dehydration and low temperature: Differences and cross-talk between two stress signaling pathways. *Current Opinion in Plant Biology* 3(3):217-223.
- Shinozaki, K., and K. Yamaguchi-Shinozaki. 2007. Gene networks involved in drought stress response and tolerance. *Journal of Experimental Botany* 58:221-227.
- Simonneau, T., P. Barrieu, and F. Tardieu. 1998. Accumulation rate of ABA in detached maize roots correlates with root water potential regardless of age and branching order. *Plant, Cell and Environment* 21:1113-1122.
- Smith, G.S., M.J. Judd, S.A. Miller, and J.G. Buwalda. 1990. Recovery of kiwifruit vines from transient waterlogging of the root system. *New Phytologist* 115:325-333. doi:10.1111/j.1469-8137.1990.tb00459.x.

- Spollen, W.G., M.E. LeNoble, T.D. Samuel, N. Bernstein, and R.E. Sharp. 2000. Abscisic acid accumulation maintains maize primary root elongation at low water potentials by restricting ethylene production. *Plant Physiology* 122:967-976.
- Steffens, B., J.X. Wang, and M. Sauter. 2006. Interactions between ethylene, gibberellin and abscisic acid regulate emergence and growth rate of adventitious roots in deepwater rice. *Planta* 223:604-612.
- Stuedle, E. 2000. Root function and adaptation. Water uptake by roots: Effects of water deficit. *Journal of Experimental Botany* 51(350):1531-1542.
- Tan, Z.-Y., and K.V. Thimann. 1989. The roles of carbon dioxide and abscisic acid in the production of ethylene. *Physiologia Plantarum* 75:13-19.
- Tuteja, N. 2007. Review abscisic acid and abiotic stress signaling. *Plant Signaling & Behavior* 2(3):135-138.
- van der Straeten, D., Z.Y. Zhou, E. Prinsen, H.A. van Onckelen, and M.C. van Montagu. 2001. A comparative molecular-physiological study of submergence response in lowland and deepwater rice. *Plant Physiology* 125:955-968.
- Van Toai, T.T., and C.S. Bolles. 1991. Postanoxic injury in soybean (*Glycine max*) seedlings. *Plant Physiology* 97:588-592.
- Vidoz, M.L., E. Loreti, A. Mensuali, A. Alpi, and P. Perata. 2010. Hormonal interplay during adventitious root formation in flooded tomato plants. *Plant Journal* 63:551-562.
- Visser, E.J.W., G.M. Bogemann, C. Blom, and L. Voesenek. 1996. Ethylene accumulation in waterlogged *Rumex* plants promotes formation of adventitious roots. *Journal of Experimental Botany* 47(296):403-410.
- Voesenek, L.A.C.J., J.J. Benschop, J. Bou, M.C.H. Cox, H.W. Groeneveld, F.F. Millenaar, et al. 2003. Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot *Rumex palustris*. *Annals of Botany* 91:205-211.
- Voisin, A.S., B. Reidy, B. Parent, G. Rolland, E. Redondo, D. Gerentes, et al. 2006. Are ABA, ethylene or their interaction involved in the response of leaf growth to soil water deficit? An analysis using naturally occurring variation or genetic transformation of ABA production in maize. *Plant, Cell and Environment* 29:1829-1840.
- Wartinger, A., H. Heilmeyer, W. Hartung, and E.-D. Schulze. 1990. Daily and seasonal courses of leaf conductance and abscisic acid in the xylem sap of almond trees [*Prunus dulcis* (Miller) D.A. Webb] under desert conditions. *New Phytologist* 116:581-587.
- Watkin, E.L.J., C.J. Thomson, and H. Greenway. 1998. Root development and aerenchyma formation in two wheat cultivars and one triticale cultivar grown in stagnant agar and aerated nutrient solution. *Annals of Botany* 81:349-354.
- Weisz, R., K. Kaminski, and Z. Smilowitz. 1994. Water deficit effects on potato leaf growth and transpiration: Utilizing fraction extractable soil water for comparison with other crops. *American Journal of Potato Research* 71:829-840.
- Wilkinson, S., and W.J. Davies. 2002. ABA-Based chemical signalling: The co-ordination of responses to stress in plants. *Plant, Cell & Environment* 25:195-210.
- Wilkinson, S., and W.J. Davies. 2009. Ozone suppresses soil drying- and abscisic acid (ABA)-induced stomatal closure via an ethylene-dependent mechanism. *Plant Cell and Environment* 32(8):949-959.
- Wilkinson, S., and W.J. Davies. 2010. Drought, ozone, ABA and ethylene: new insights from cell to plant to community. *Plant, Cell and Environment* 33:510-525.
- Wilkinson, S., G.R. Kudoyarova, D.S. Veselov, T.N. Arkhipova, and W.J. Davies. 2012. Plant hormone interactions: innovative targets for crop breeding and management. *Journal of Experimental Botany* 63:3499-3509.
- Wright, S.T.C. 1980. The effect of plant-growth regulator treatments on the levels of ethylene emanating from excised turgid and wilted wheat leaves. *Planta* 148(4):381-388.
- Wu, Y., and D.J. Cosgrove. 2000. Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. *Journal of Experimental Botany* 51:1543-1553.
- Yamaguchi-Shinozaki K., and K. Shinozaki. 2006. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology* 57:781-803.
- Yan, B., Q. Da, X. Liu, S. Huang, and Z. Wang. 1996. Flooding-induced membrane damage, lipid oxidation and activated oxygen generation in corn leaves. *Plant Soil* 179:261-268.
- Yang, C., F. Hsu, J. Li, N. Wang, and M. Shih. 2011. The AP2/ERF transcription factor AtERF73/HRE1 modulates ethylene responses during hypoxia in Arabidopsis. *Plant Physiology* 156:202-212.
- Ye, N., L. Jia, and J. Zhang. 2012. ABA signal in rice under stress conditions. *Rice* 5(1):1-9.
- Yetisir, H., M. Caliskan, M. Soyulu, and M. Sakar. 2006. Some physiological and growth responses of watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai) grafted onto *Lagenaria siceraria* to flooding. *Environmental and Experimental Botany* 58(1-3):1-8.