academicJournals

Vol. 6(1), pp. 1-6, January 2014
DOI: 10.5897/IJPPB2013.0199
ISSN 2006- 9871 © 2014 Academic Journals
http://www.academicjournals.org/IJPPB

International Journal of Plant Physiology and Biochemistry

Review

Responses of grapevine rootstocks to drought stress

Dargie Tsegay*, Dor Amsalem, Manuel Almeida and Molly Crandles

International Center for Higher Studies in Agricultural Sciences, Montpellier SupAgro, 2 Place Pierre Viala,
Cedex 2, Montpellier, France.

Accepted 13 January, 2014

Drought response of rootstocks is important for overall viticulture as a result of increase in water scarcity due to climate change and irrigation limitations in winegrowing region. Grapevines are generally well-adapted to arid and semi-arid climates, and they appear to primarily rely on drought avoidance mechanisms in water stress situations. In terms of the response of the grapevine to drought conditions, rootstock can have an impact on the gas exchange and water status. It has been shown that different rootstocks have varying capacities to extract water from the soil and transfer it to the scion. This review addressed several factors that contribute to the drought response of rootstock, including the mechanism of drought tolerance, rootstock anatomy, stomatal regulation, physical and chemical responses.

Key words: Grapevine, rootstock, stress, abscisic acid, stomata.

INTRODUCTION

Grapevines are generally well-adapted to arid and semi-arid climates, and they appear to primarily rely on drought avoidance mechanisms in water stress situations (Chaves et al., 2010). Historically, rootstocks were developed in the early 1900's from American Vitis species in an effort to avoid the damage caused by phylloxera. Therefore, they were selected mainly for their resistance to phylloxera, as well as for other basic requirements such as suitability for grafting. However, the possibility of an increase in water scarcity due to climate change and irrigation limitations makes the search for more drought resistant rootstock an interesting goal (Serra, 2013). Water stress is not exclusively a negative phenomenon for grapevines since mild water-deficit can enhance grape quality for the production of wines (Van Leeuwen, 2009). Genetic variability of grapevine rootstocks will undoubtedly play a fundamental role in the adaptation to future climate changes, especially to drought (Walker, 1992)

Rootstocks have been shown to have an effect on the grapevine which is grafted to them in a number of ways, including having an impact on the vegetative, reproductive and physiological parameters. In terms of the response of the grapevine to drought conditions, it has been shown that the rootstock can have an impact on the gas exchange and water status of the scion (Iacono, 1998). There is an important interaction between rootstock and scion varieties upon grafting. In a study performed by Iacono (1998), it was shown that Muller Thurgau grafted onto hybrid rootstocks used water more efficiently under water stress than the own-rooted scion or rootstock varieties individually. It has been shown that different rootstocks have varying capacities to extract water from the soil and transfer it to the scion (Soar,

---

*Corresponding author. E-mail: tsegadar@yahoo.com.

2006a). There are a number of theories with regards to the mechanism of the relationship between grapevine rootstocks and scions. The efficiency of the transportation of water from the rootstock to the scion is related to the anatomy of the xylem vessels within the rootstock variety, which control the water conductivity (de Herralde, 2006). The rootstock variety also has an impact on the root density and depth of growth, although these factors are influenced by edaphic and environmental conditions as well (Koundouras, 2008). This review will address the question of the drought response of grapevine rootstocks, specifically looking at the mechanism of drought tolerance, the rootstock anatomy, stomatal regulation, physical responses, chemical responses and finally comparing different drought resistant rootstocks.

MECHANISM OF DROUGHT TOLERANCE

Rootstocks can be divided into two types when considering periods of water constraint: the type that tend to induce more vigour and drought tolerance and the type that have lower vigour and less drought tolerance. The first exhibit more rapid root growth later in the season in wetter soil conditions and the second could form more roots in deeper soil layers early in the growing season, no matter what soil moisture conditions prevail (Serra, 2013). When talking about the mechanisms of drought tolerance in rootstocks, one can consider number of factors and responses of the grapevine in order to cope with water deficits. Those mechanisms can be presented as follows: drought escape (involves the ability of the plant to complete the whole life cycle before severe water constraint occurs), drought tolerance with low plant water potential (involves the maintenance of turgor, mainly by osmotic adjustment) and drought tolerance with high plant water potential (avoidance of drought by increasing the uptake of water and decreasing the loss of water).

In grapevines it is possible to find the two drought tolerance mechanisms (with no drought escape) in the form of drought responses such as stomatal closure, decrease of cell growth and photosynthesis, activation of respiration, and accumulation of osmolytes and proteins (Chaves, 2003; Serra, 2013; Tardieu, 2005). An understanding of drought tolerance is important in order to understand a vineyard's response to soil water availability. It is ideal to minimize changes in shoot water status of the vine so that overall vine health and grape quality is improved under drought stress situations (Chaves et al., 2010).

ROOT ANATOMY, GROWTH AND DEVELOPMENT

The anatomy of grapevines is well adapted to water deficits with xylem characteristics that can influence their capacity to transport water in the grapevine. Grapevines have large xylem vessels in comparison to other plants or to their own stems, allowing the grapevine a quick recovery from water constraints and causing them to be more prone to xylem cavitation, respectively (Serra, 2013). According to Tramontini (2012), the hydraulic system is not just influenced by genetics, but it can also be affected by the soil type that can have an impact on xylem tissue development and thereby the whole-plant hydraulic conductance. As an organ of the grapevine, the root system is dependent on many factors and has large requirements that can be illustrated by the high respiration of the root system: 70-80% of the total carbon losses (Serra, 2013). An efficient root system would be an advantage for the grapevine since it can improve water uptake and is a way of exploiting more effectively the resources available in the soil. Such system would be a well-developed one in terms of depth, the main framework roots, the permanent roots and their diameter. Different factors affect root density and therefore vine quality, such as soil water availability, type of irrigation, canopy manipulation, trellis system and rootstock genotype. The climatic conditions will affect the pattern of new lateral root growth (Serra, 2013). The type of the soil can influence the depth of the roots; number of roots is a factor of more than one variable such as poor water permeability and soil acidity (Morlat, 2003).

Though it was suggested in early studies, done by Pongrácz (1983) and Pouget (1987), that a genetic variability exists regarding rooting depth, more recent studies, done by Swanepoel and Southey (1989), Southey (1992) and Smart (2006), had shown that there is a difference in root density attributed by genetic differences, rather than root depth (Serra, 2013). To understand the effect rootstock has on drought responses it is important to consider the exogenous factors and the genotype-environment interaction (Serra, 2013). It has been shown that the distribution of the root system of a vine depends on the interaction of the rootstock genotype with the soil texture and bulk density, water and nitrogen availability, soil salinity, vine spacing and climatic conditions (Koundouras, 2008). Deep root systems will generally provide a better protection against drought conditions. In addition to that, it was found that drought-tolerant grapevine rootstocks, as compared to drought-sensitive rootstocks, had more new roots in the soil profile during a dry and hot season allowing the grapevine to increase the uptake of water (Serra, 2013).

STOMATAL REGULATION

The regulation of the stomata plays a determinant role in the regulation of the water status by controlling the evapotranspiration rate. Closing the stomata causes an increase in water use efficiency and a decrease in carboxylation efficiency. This is due to the fact that the Rubisco's maximum activity rate is reduced, the fact that there is a parallel decrease of the electron transport rate and photochemical quenching (Iacono, 1998). Stomata regulate transpiration of the plant during drought stress so that leaf water potential does not become too negative, which could cause the xylem to cavitate and destroy the hydraulic system (Schultz, 2003).

A study conducted by Iacono et al. (1998) shows that both a rooted and a grafted *V. vinifera* had the highest rates of net CO_2 assimilation rate under hydric comfort conditions, and after 14 days of experiencing water deficit the grafted *V. vinifera* maintained a high rate of assimilation of net CO_2. A higher rate of photosynthesis resulted from a significant increase in stomatal conductance, water use efficiency and a carboxylation efficiency (Iacono, 1998). The results of this study and several others have indicated that stomatal conductance is a determining factor for drought response. The regulation of stomatal closure has been linked to hydraulic, chemical, physical and even electrical signals (Beis and Patakas, 2010) which will be further discussed in this report.

CHEMICAL RESPONSES

Chemical signals from roots are important for a grapevine to adapt to water stress, especially during the early stages of water stress (Schachtman, 2008). These signals are transported through the xylem of the plant to the leaves, and allow the plant to regulate water loss and leaf growth. There are many chemical signals that have been shown to have an impact in root to shoot signalling during drought conditions, including abscisic acid (ABA), pH, cytokinins, malate and a precursor of ethylene. Chemical signals are significant during the early stages of drought stress, and therefore have importance in efficient water use and deficit irrigation strategies (Schachtman, 2008).

Abscisic acid

The critical roles ABA plays during plant response to environmental stress won its reputation as a "stress hormone" and as such ABA is central to any discussion of plant adaptation to adverse environmental conditions like drought and salt stresses (Peleg, 2011; Fukaki, 2009). There are some debates on the importance and role of root synthesized ABA, but this may be due to differences in methodology between studies (Schachtman, 2008). Xylem sap ABA is known to have a role in root to shoot chemical signalling of soil moisture deficits, and different rootstocks have different propensities to generate these signals. Better knowledge on grafting scions to selected rootstocks can help in finding good combinations to achieve a better drought resistance (Soar, 2006). Plants have three ways to deal with drought challenges: to reduce water consumption, to increase water uptake and to mitigate the negative impacts of water deficit by closing guard cell stomatal pores upon drought stress through the activation of an array of stress-responsive genes. These changes may occur in root development, phase transition, wax deposition, guard cell patterning and perhaps leaf morphology. ABA, whose level is up-regulated by drought stress, is either required or is involved in all these processes (Jenks*,* 2007). Production of abscisic acid within the roots of a plant and the subsequent transportation to the leaves is thought to be the main mechanism the plant uses to report on the water status of the soil. However, the precise location of ABA production in the roots is not clear, and there is also some ABA synthesis within the leaves that may interact with this communication mechanism (Schachtman, 2008).

Under water-deficit, the root growth rate decreases and the roots synthesize and accumulate ABA. Many findings (Yamaguchi, 2010; Fukaki, 2009; Ober, 2007) reported that, drought-induced accumulation of ABA towards the root apex played a crucial role for the maintenance of elongation in the root apex. One part of this role of endogenous ABA was to limit ethylene production. As a result of this antagonism, ABA accumulation during water stress may often function to maintain rather than inhibit root growth, particularly towards the root apex (Sharp, 2002). In line with this, (Ober, 2003) confirmed that, at low water potential, ABA plays a role in regulating the steady-state membrane potential in root cell elongation zone, and control homeostatic set-points for ion transport processes that shift in response to environmental stresses. De Smet et al. (2006) also concluded that ABA stimulates the elongation of the main root and the emergence of lateral roots in response to drought, and thus favouring developmental plasticity to changes in the soil environment. Therefore, ABA has a significant impact on the final size and architecture of the root system. Conjugated forms of ABA, such as abscisic acid glucose ester may also serve as part of the water stress signal, but the role of these forms are not fully understood (Schachtman, 2008).

It has been shown that while most grapevines are anisohydric, there are some varieties which demonstrate more isohydric (tight stomatal control) characteristics than others. Grenache variety has been shown to be near-isohydric in response to water stress in both the soil and the atmosphere. Shiraz has been shown to be near-anisohydric in both conditions, demonstrating less stomatal control under drought stress (Soar, 2006a). It has also been shown that the difference in the responses of these two varieties is linked to differences in ABA. Grenache showed higher levels of xylem ABA correlating to better stomatal control. There is also likely a physical component that is important for the difference in the drought response for these varieties (Soar, 2006a). These mechanisms are important for understanding the effect of rootstock on the grapevine's response to drought conditions.

pH

It has been observed that during drought stress, there is a change in the pH of xylem sap that may have some importance for chemical root to shoot signals. The pH of the xylem sap may increase by over one pH unit when the plant is under stress (Wilkinson, 1999). This may have an impact on the metabolism of ABA, increasing the concentration of this important chemical, or it may have a direct impact on the leaf water status of the plant. The pH may also impact the ion fluxes through the cell plasma membrane or alter the distribution of ABA within the plant leaves (Schachtman, 2008). The changing pH in the xylem is thought to activate the guard cell ABA receptors and cause the stomata to close (Wilkinson, 1999). The direct mechanism of xylem pH in drought response is not known, and it may involve nitrate availability which is decreased in drought periods (Schachtman, 2008).

Cytokinins and other chemical responses

Cytokinins may have a role in the root to shoot signalling in plants under water stress, especially since they are produced in the roots. These chemicals are involved in nutrient deprivation responses, and may be linked to drought stress responses as well. It was shown that there was a large reduction in cytokinins zeatin and zeatin riboside in vines that were subjected to partial root drying. The ratio of ABA : cytokinin in the xylem of the plant may play an important role in stress signalling (Schachtman, 2008). The relationship between cytokinins and ABA has been described as an antagonist one in terms of stomatal closure (Serra, 2013).

There are many other compounds found within plant xylem that may play an important role in stress signalling which deserve further investigation: peptides, hormones, amino acids, sugars and organic acids. Malate has been connected with stomatal closure in certain plant species, but has not yet been fully investigated in grapevines. Ethylene and ethylene precursors- specifically 1-aminocyclopropane-1-carboxyllic acid- have been shown to be transported from the roots to the shoots of a plant, but their importance in rootstock drought response for grapevines is not well reported (Schachtman, 2008).

PHYSICAL RESPONSES

Chemical signals are important during the early stages of stress, while physical signals such as hydraulics and aquaporins have been shown to have more significance during severe drought conditions (Schachtman, 2008).

Hydraulic responses

It has been indicated that hydraulic signals trigger ABA production in leaves during severe drought stress (Schachtman, 2008). It has also been shown that Grenache (a near-isohydric variety) had a much larger hydraulic conductance than Syrah (an anisohydric variety) in the leaf petioles and that this was linked to stomatal conductance. This is important because it indicates that the differences in the hydraulic architecture in the petioles of the two varieties are related to stomatal closure for both isohydric and anisohydric varieties (Schultz, 2003). Higher hydraulic conductance is linked to more drought-tolerant rootstocks. In those rootstocks, the development of xylem is improved and there is a lower vessel embolization; those properties can relay to the high conductance (Serra, 2013).

Aquaporins

Aquaporins are integral membrane proteins from a larger family of major intrinsic proteins that form pores in the membrane of biological cells. Aquaporins play a major role in transcellular water movement by facilitating the transport of water through cell membranes therefore they significantly control root hydraulic conductivity. Aquaporins are part of the major membrane intrinsic protein family, and are subdivided into several subfamilies (Vandeleur, 2009). Certain plasma membrane intrinsic proteins- specifically PIP2s- have been shown to have high water permeability and have been linked to water stress responses. The role of VvPOP1;1 and VvPIP2;2 have been studied, and it has been shown that these aquaporins are found in the root tip of grapevine roots. VvPIP1;1 seems to regulate water transportation across roots to match transpirational demand with root water transport capacity as a response to water stress. This has been shown for Grenache and Chardonnay own-rooted vines; more rootstock-specific investigations are necessary (Vandeleur, 2009). In terms of function, the aquaporin proteins are involved in the movement of water across the plasma membranes in the cell-to-cell pathway.

Molecular studies on eight identified putative aquaporin were made in 110 Richter, a drought-tolerant rootstock. The study results show differences in the expression of the genes responsible for those proteins in the leaves and roots: a decrease in the leaves that can be explained as a way to limit water loss, and an increase in the roots, that helps in water uptake at water deficits times (Serra, 2013).

COMPARISON OF ROOTSTOCKS AND THEIR DROUGHT TOLERANCE

Rootstocks have been proven to play an important role in the drought tolerance of the grapevines, doing so by controlling and adjusting the water supply to the demand of transpiration of the shoots (Tramontini, 2013). The study of the rootstock-scion relationships became important due to the demand of certain genotypic characteristics that are very desirable, such as water tolerance, salinity tolerance and resistance to soil pests. An appropriate choice of rootstock for a given scion variety can improve transpiration efficiency, and thus the water use (Soar, 2006). The classification of rootstocks has been conducted without a standardized methodology, so there may be different rankings for the same rootstock due to differences in soil properties, climate, intensity and duration of water deficit between the studies. It is important to consider the interaction between scion and rootstock when measuring drought resistance in the plant: yield values may give an indication of drought tolerance, but other more accurate measurements such as leaf water potential are important (Serra, 2013).

Two rootstocks grafted with Cabernet Sauvignon were studied under three different irrigation levels. It was found that the SO4 rootstock was better adapted to fertile regions where there was no drought stress while the 1103P rootstock showed more efficient use of soil water and was therefore more adaptable to areas with water limitation (Koundouras, 2008). Pavlousek (2010) conducted an experiment comparing 4 existing rootstocks along with 20 new hybrids in terms of resistance to drought conditions based on shoot growth. Results showed *Vitis cinerea* species have a suitable genotype for breeding drought-resistant rootstocks. Through the evaluation of growth intensity of annual shoots, CCI (chlorophyll content index) and visual characteristics of plants, Pavlousek (2010) confirmed that rootstock hybrids that contain *Vitis berlandieri*, *Vitis riparia* and *V. cinerea* in their pedigree show better drought resistance as compared to hybrids with *Vitis rupestris* and *Vitis amurensis* which show a medium tolerance to these conditions.

It has been shown by Soar (2006) that the general response of different rootstock-scion combinations is easily evidenced when subjected to water stress conditions. Soar (2006) experiment puts together Shiraz scions grafted to seven different rootstocks along with a ungrafted control unit and were monitored for two seasons (2001/2002 and 2002/2003). Through the observation of certain physiological factors (leaf gas exchange, water relations, canopy growth and yield and sap ABA analysis) it was possible to understand the effect of water stress on the different combinations of scion-rootstock. This study determined that rootstocks such as 420-A and K51-40 are well adapted to regions that require only supplemental irrigation because of their less susceptibility to experience excessive vigour under high water availability. Oppositely, Ramsey rootstock has high vigour which makes it suitable in regions experiencing high irrigation requirements (Soar, 2006).

CONCLUSION

The drought response of rootstocks is important for overall viticulture, especially when temperature continues to increase in winegrowing region. Rootstock response to water stress conditions has been widely investigated for full understanding of the mechanism of drought response. This knowledge would allow rootstocks to be used efficiently in areas that are susceptible to drought in order to avoid permanent drought damage to vineyards. It has been shown that there are several factors that contribute to the drought response of rootstock, including root anatomy, growth patterns, and chemical and physical signals related to stomatal regulation. These factors can be influenced by both the genotype of the rootstock as well as the environment. It has been shown that it is not only one factor that contributes to rootstock drought response, but likely, a combination of all of these factors are important when a rootstock is subjected to drought conditions.

REFERENCES

Beis A, Patakas A (2010). Differences in stomatal responses and root to shoot signalling between two grapevine varieties subjected to drought. Funct. Plant Biol. 37:139-146.

Chaves MM, Maroco JP, Pereira JS (2003). Understanding plant responses to drought from genes to the whole plant. Funct. Plant Biol. 30:239-264.

Chaves MM, Zarrouk O, Francisco R, Costa M J, Santos T, Regalado P A, Rodrigues LM, Lopes MC (2010). Grapevine under deficit irrigation: hints from physiological and molecular data. Annals Appl. Biol. 105:661-676.

De Herralde F, del Mar Alsina M, Aranda X, Save R, Beil C (2006). Effects of rootstock and irrigation regime on hydraulic architecture of *Vitis vinifera* L. cv Tempranillo. Int. J. Sci. Wine Vine. 40: pp.133-139.

De Smet I, Zhang H, Inzé D, Beeckman T (2006). A novel role for abscisic acid emerges from underground. J. Trends Plant Sci. 11:434-439.

Fukaki H, Tasaka M (2009). Hormone interactions during lateral root formation. J. Plant Mol. Biol. 69: pp.437-449.

Iacono F, Buccella A, Peterlunger E (1998). Water stress and rootstock influence on leaf gas exchange of grafted and ungrafted grapevines. Sci. Horticult. 75:27-39.

Jenks AM, Hasegawa MP, Jain MS (2007). Advanced in molecular breeding toward drought and salt tolerant trops. Springer, Dordrecht, The Netherlands.

Koundouras S, Tsialtas I, Zioziou E, Nikolaou N (2008). Rootstock effects on the adaptive strategies of grapevine (*Vitis vinifera* L. cv. Cabernet Sauvignon) under contrasting water status: Leaf physiological and structural responses. Agric. Ecosyst. Environ. 128:86-96.

Morlat R (2003). Grapevine root system and soil characteristics in a vineyard maintained long-term with or without interrow sward. The Am. Soc. Enol. Viticult. 54:1.

Ober ES, Sharp RE (2003). Electrophysiological responses of maize roots to low water potentials: relationship to growth and ABA accumulation. J. Exp. Bot. 54.813-824.

Ober ES, Sharp RE (2007). Regulation of root growth responses to water deficit. In: Advances in molecular breeding toward drought and salt tolerant crops. pp. 33-53. Springer, Dordrecht, The Netherlands.

Pavlousek P (2010). Evaluation of drought tolerance of new grapevine rootstock hybrids. J. Environ. Biol. 32:543-549.

Peleg Z, Blumwald E (2011). Hormone balance and abiotic stress tolerance in crop plants. J. Current Opinion Plant Biol. 14:290-295.

Pongrácz DP (1983). Rootstocks for grapevines. David Philip Publisher, Cape Town, South Africa.

Pouget R (1987) Usefulness of rootstocks for controlling vine vigour and improving wine quality. Acta Horticult. 206:109-118.

Schachtman DP, Goodger JQ (2008). Chemical root to shoot signalling under drought. Trends Plant Sci. 13:281-287.

Schultz H (2003). Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. Plant Cell Environ. 26:1393-1405.

Serra I, Strever A, Myburgh P, Deloire A (2013). Review: the interaction between rootstocks and cultivars (*Vitis vinifera* L.) to enhance drought tolerance in grapevine. Austr. J. Grape Wine Res. doi: 10.1111/ajgw.12054.

Sharp RE, LeNoble ME (2002). ABA, ethylene and the control of shoot and root growth under water stress. J. Exp. Bot. 53.33-37.

Smart DR, Schwass E, Lakso A, Morano L (2006) Grapevine rooting patterns: a comprehensive analysis and a review. Am. J. Enol. Viticult. 57.89-104.

Soar CS (2006). Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz: Mediation of rootstock effects via xylem sap ABA. Austr. J. .Grape Wine Res. 12.82-96.

Soar CS (2006a). Grape Vine Varieties Shiraz and Grenache Differ in Their Stomatal Response to VPD: Apparent Links with ABA Physiology and Gene Expression in Leaf Tissue. Austr. J. Grape Wine Res.12:2-12.

Southey JM (1992). Root distribution of different grapevine rootstocks on a relatively saline soil. South Afr. J. Enol. Viticult.13:1-9.

Swanepoel J, Southey M (1989). The influence of rootstock on the rooting pattern of the grapevine. Viticultural and Oenological Research Institute (VORI), Stellenbosch, South Africa.

Tardieu F (2005). Plant tolerance to water deficit: physical limits and possibilities for progress. Comptes Rendus Geosciences. 337:57-67.

Tramontini S, van Leeuwen C, Domec JC, Destrac-Irvine A, Basteau C, Vitali M, Mosbach-Schulz O, Lovisolo C (2012). Impact of soil texture and water availability on the hydraulic control of plant and grapeberry development. Plant and Soil 368:215-230.

Tramontinia S, Vitali M, Centioni L, Schubert A, Lovisolo C (2013). Rootstock control of scion response to water stress in grapevine. Environ. Exp. Bot. 93:20-26.

Van Leeuwen C, Tregoat O, Choné X, Bois B, Pernet D, Gaudillere P (2009). Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. Int. J. Sci. Wine Vine. 43:121-134.

Vandeleur KR, Mayo G, Shelden CM, Gilliham M, Kaiser NB, Tyerman DS (2009). The role of plasma membrane intrinsic protein aquaporins in water transport through roots: Diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. Plant Physiol. 149:445-460.

Walker MA (1992). Future Directions for Rootstock Breeding. In: Rootstock seminar: a worldwide perspective (eds J.A. Wolpert, M.A., Walker and E. Weber). pp. 60-68.

Wilkinson S (1999). pH as a stress signal. Plant Growth Regulation. 29:87-99.

Yamaguchi M, Sharp R. (2010). Complexity and coordination of root growth at low water potentials: recent advances from transcriptomic and proteomic analyses. J. Plant Cell Environ. 33:590-603.