J. Plant Biol. (2019) 62:387-399
DOI 10.1007/s12374-019-0257-1

REVIEW ARTICLE

Response of Carbon and Nitrogen Metabolism and Secondary Metabolites to Drought Stress and Salt Stress in Plants

Gaochang Cui[1,†], Yu Zhang[1,†], Wenjin Zhang[1], Duoyong Lang[3], Xiaojia Zhang[1], Zhixian Li[4] and Xinhui Zhang[1,2,*]

[1]*College of Pharmacy, Ningxia Medical University, Yinchuan 750004, China*
[2]*Ningxia Engineering and Technology Research Center of Hui Medicine Modernization, Ningxia Collaborative Innovation Center of Hui Medicine, Key Laboratory of Hui Ethnic Medicine Modernization, Ministry of Education, Yinchuan 750004, China*
[3]*Laboratory Animal Center, Ningxia Medical University, Yinchuan 750004, China*
[4]*Hunan Provincial Key Laboratory of Coal Resource Clean Utilization and Mine Environmental Protection, Hunan University of Science and Technology, Xiangtan, Hunan 411201, China*

Received: June 25, 2019 / Accepted: July 30, 2019

Abstract Carbon and nitrogen metabolism provide the main energy and basic nutrients for plants. However, environmental stress seriously affects carbon and nitrogen metabolism and thus hinders plant growth, especially drought stress and salt stress. Hence, numerous studies have been conducted to investigate the response of carbon and nitrogen metabolism to drought stress and salt stress by photosynthesis, sucrose and starch metabolism, nitrogen uptake and amino acids. Previous researchers also studied the response of secondary metabolism under both stresses on account of secondary metabolism may confer protection against environmental stresses. Our review highlights the diverse responses of carbon and nitrogen metabolism to drought stress and salt stress and the content changes of three secondary metabolites in plants under stresses.

Keywords: Carbon metabolism, Drought stress, Nitrogen metabolism, Secondary metabolism, Salt stress

Introduction

Plants often encounter a wide range of environmental stress conditions which usually have an adverse effect on plant growth and production (Kiegle 2010; Abdelrahman 2018; Pereira et al. 2018). In these stresses, drought and salt are the two most common stresses and they are the increasingly serious environmental problems worldwide for cultivating agricultural crops (Khalid et al. 2017; Tamburino et al. 2017). Plants are subjected to drought stress and salt stress which adversely affect their growth and development and trigger a series of morphological, physiological, biochemical, and molecular changes (Bhagat 2014). Specifically, drought stress can causes to gross disruption of metabolism and cell structure and eventually to the cessation of enzyme catalyzed reactions (Jaleel et al. 2007), salt stress interferes with plant growth mainly due to it leads to physiological drought and ion toxicity (Huang et al. 2012).

Carbon and nitrogen metabolism are the two most important pathways in plant growth and productivity (Otori et al. 2017), and the carbon and nitrogen metabolism was destroyed due to drought stress and salt stress in various plants (Naya et al. 2007; Manaa et al. 2011; Farhangi-Abriz et al. 2017; Cao et al. 2018). Metabolic processes of carbon including photosynthetic carbon assimilation, sucrose and starch metabolism, carbohydrate transport and utilisation. Plant productivity is determined to a large extent by the rate and efficiency of photosynthesis. And carbon is fixed in leaves (the source) by photosynthesis and is either translocated away as sugar or stored temporarily as sugar, starch or fructan. Later, sugar is resynthesised and translocation from the leaf in the dark. (Leuzinger et al. 2009; McDowell and Sevanto 2010; Sala et al. 2010; zanella et al. 2016). Nitrogen metabolism processes involve, nitrogen uptake, transport, amino acid metabolism reduction, and assimilation (Kusano et al. 2011; Luo et al. 2013). Nitrogen is often considered to be one of the most important factors limiting plant growth in natural ecosystems and in most agricultural soils (Hara 2010). The metabolism of nitrogenous compounds is essential to living processes (Shao 2015). Nitrogen is a major constituent of proteins, nucleotides, chlorophyll (Chl), and numerous other

[†]These authors contributed equally in this work.

*Corresponding author; Xinhui Zhang
Tel : +86-09516880583
E-mail : zhang2013512@163.com

metabolites and cellular components. It is taken up by plants principally in the forms of nitrate (NO_3^-) and ammonium (NH_4^+) (Dai et al. 2015), and through the consecutive action of nitrate reductase (NR) and nitrite reductase (NiR), then yielding glutamine and glutamate as the primary organic nitrogen compounds that distribute nitrogen to all other N-containing metabolites and macromolecules (Nathawat et al. 2005).

Assimilation of nitrogen requires energy, carbon skeletons produced by carbon metabolism. Assimilation of photosynthetic carbon requires a large amount of nitrogen (Nunes-Nesi et al. 2010). The activities of carbon and nitrogen assimilatory processes are closely related to rates of plant growth and development (Fang et al. 2011). The balance of carbon and nitrogen metabolism was disturbed by drought stress and salt stress.

Secondary metabolites are unique sources for food additives, medicinal, flavors and industrially important biochemical (Razavizadeh et al. 2018). Secondary metabolites in plants based on secondary metabolism. Collectively plants synthesise a diverse array of secondary metabolites. For example, phenolic compounds, terpenes and nitrogen-containing compounds. The ability to synthesise particular classes of secondary metabolite is commonly restricted to selected plant groups (Osbourn et al. 2003). Moreover, sucrose and nitrogen influenced the total level of secondary metabolites, and may confer protection against environmental stresses.

Carbon and nitrogen metabolism is directly related to the growth status of plants under drought stress and salt stress, and there is significant changes in secondary metabolites under drought stress and salt stress. In particular, both drought stress and salt stress inhibit photosynthesis by changing leaf morphology, reducing or closing stomata, reducing Chl content and Rubisco activity. Increasing amino acid content such as proline and the content of soluble reducing sugar such as sucrose, increase three kinds of secondary metabolites in most plants which may be related to the response of plants to resist stress. Starch content is decreased under drought stress and increased under salt stress, and the specific reasons need to be further studied. And NH_4^+ generally increased under drought stress, on the contrary, the absorption of NH_4^+ decreased under salt stress in most plants. These differences may be due to water deficiency under drought stress and physiological drought and ion toxicity under salt stress.

The Responses of Carbon Metabolism in Plants to Stress Conditions

The Responses of Photosynthesis in Plants to Stress Conditions

Photosynthesis is the most important process which involves a chain of events where light energy is converted into chemical energy by plants through chemical reactions with water and CO_2. When plants subjected to various stress conditions, it is affected by many factors (Nishiyama et al. 2001; Allakhverdiev and Murata 2004; Murata et al. 2007; Mohanty et al. 2007). Mainly including (1) Stomatal factors, which can affect photosynthesis, stomata control the exchange of water vapour and CO_2 between the leaf interior and the atmosphere, and serve as major gateways for CO_2 influx into plants as well as transpirational water loss from plants (Lawson 2014). Under stress, the decline of photosynthesis was mainly due to the decline of stomatal conductance. (2) The primary function of photosynthetic pigments in plants is photosynthesis. Chl pigments help leaves capture light energy. Chl and carotenoids are central to energy acquisition for green plants (Grotewold 2006). (3) Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), it is the important protein in photosynthesizing plant parts. Rubisco activase is a chloroplast protein which enhances the activation of Rubisco in the presence of ATP and Mg^{2+} (Chakraborty et al. 2014). The causes of decreasing photosynthetic rate under different environmental stresses are still not established. It could be a combination of factors (Cha-Um 2009).

The Responses of Photosynthesis in Plants to Drought Stress

The effects of drought stress in plants are complex, depending on the severity, duration of the stress event, and the plant growth stage. Development of optimal leaf is important to photosynthesis. The decrease of leaf number and area is the visible symptom of drought stress (Taleisnik et al. 2009). In fact, limitation of leaf growth is among the earliest visible impacts of drought stress because leaves are the main photosynthetic organs (Luo et al. 2016). According to Lonbani and Arzani (2011), leaf extensions can be reduced under drought environment in order to get a balance between the water status of plant tissues and the water absorbed by plant roots in triticale and wheat. Similarly, increased the grana thickness and lengths of the palisade cells under moderate drought stress in cucumber (Liu et al. 2018).

More symptoms of plants under drought stress are the invisible such as stomatal closure, Photosystem II (PSII), Rubisco activity and Chl concentration.

Due to the closure of stomata under drought stress, the intake of carbon dioxide (CO_2) is stopped and plants are unable to take CO_2. In particular, the reduction of photosynthesis due to stomatal closure has been reported in grain legumes (Faroog et al. 2016), dry bean (Lanna et al. 2016), cucumber (Liu et al. 2018) and chickpea (Pang et al. 2017) under drought stress. Stomatal closure which limits CO_2 uptake by leaves and prevent the transpirational water loss and suppress particularly photochemical efficiency of PSII by decreasing electron transports (Anjum et al. 2003; Zlatev et al. 2012).

PSII plays an especially important role in the response of photosynthesis in higher plants to environmental perturbations and stresses (Baker 2010). The quantum yield of PSII was significantly lower in tomato by drought stress in the first few days than control (Zhou et al. 2018). Inversely, M'barki et al. (2018) found that under drought stress, the maximal quantum efficiency of PSII (Fv/Fm) measurements in leaves was significantly improved by 50.70% in olive. But the Fv/Fm and the effective quantum efficiency of PSII photochemistry were not affected by drought stress in the bottle gourd (Mashilo et al. 2018).

Rubisco is the predominant protein in photosynthesizing plant parts and the most abundant proteins on earth (Feller et al. 2007). Drought conditions reduce photosynthesis because a decrease in Rubisco expression and activity, for reasons as yet unclear (Bota et al. 2004; Flexas et al. 2006). Nonetheless, in later years, Medrano et al. (2010) found drought decreased both the initial and the total Rubisco activity per unit area but did not reduce the amount of Rubisco protein per unit leaf area in *subterranean clover*. Thus, suggesting that the active sites were blocked by inhibitors under drought stress. With different, Yue et al. (2018) found higher Rubisco activity under the drought treatment in the *chrysanthemums,* and drought stress did not affect Rubisco activity and Rubisco concentration in Gokce and in rapeseed (Saglam et al. 2014; Chunqian et al. 2017). This may be related to different stress intensity and plants.

Chl concentration has been considered as an index for evaluation of source. Drought stress produced changes in the ratio of Chl a/b and carotenoids (Farooq 2009). During the period of drought treatment the content of Chl, Chl a/b all decreased in rice (Yu 2017). With longer duration of drought stress, Chl a, Chl b, carotenoids content and Chl a/b increased at the beginning and then decreased in *Machilus pingii* seedlings (Jie et al. 2015). This phenomenon may be a response mechanism under drought stress.

In the visible symptoms, the leaf morphology was changed in order to balance water so as to adapt to the new arid environment. However, drought stress has more complex effects on the invisible like stomatal factors, PSII, Rubisco activity and chlorophyll concentration, thus affecting photosynthesis. All the factors have influence on photosynthesis, and stomatal closure impedes photosynthesis is the most widely studied. The response of PSII was different due to different plants under drought stress. Rubisco activity also is imparity in different plants. It can be said explicitly that the reduction of Chl a/b in plants under drought stress was reported in most articles.

The Responses of Photosynthesis in Plants to Salt Stress

Salt stress can cause irreversible damage to the photosynthetic apparatus at any developmental stage of the plant (Wungrampha et al. 2018). Restriction of leaf growth is among the earliest visible effects of salt stress (Taleisnik et al. 2009). Salt stress increased the leaf thickness and destroyed the leaf internal structure in cucumber (Yuan et al. 2015). Salt stress resulted in noticeable anatomical variations such as an increase in thickness of the leaf blade and palisade parenchyma cells in *Borago officinalis L.* (Torabi et al. 2015).

In terms of invisible symptoms, accumulation of NaCl in plant cells, including stomatal guard cells, affects their function. Stomatal closure or decrease is one of the most immediate responses to salt stress (Richardson et al. 2006; Munns and Tester 2008). The increased stomatal limitation was mainly related to the low leaf osmotic potential caused by soil salt stress (Wang et al. 2017). Moreover, the stomatal conductance was a primary limiting factor for the reduction of Pn in soybean under salt stress (He 2016). Up to moderate salt stress, forcible stomatal closure, parallel with a reduction in the net assimilation rate in wheat (Szopkó et al. 2017).

The Fv/Fm decline in chloroplasts from *Pisum sativum L.* and *Vicia faba L.* species was stronger (Percey et al. 2016). In maize, salt stress significantly decreased Fv/Fm, photochemical quenching (qP), and quantum efficiency of PSII photochemistry (ΦPSII), net photosynthetic rate (Pn), and biomass (liu et al. 2016).

Salt stress induces photosynthesis inhibition through the reduction of Rubisco activity in the photosynthetic apparatus (Mittal 2012). The decrease of Rubisco content and activity has been shown to cause low carboxylation efficiency in salt-sensitive soybean (He et al. 2014). Down regulation of the key gene that encodes Rubisco, and thereby decreases enzyme activity and the protein content of Rubisco in *Elaeagnus angustifolia L.* under salt stress (Lin et al. 2018).

Plants resistant to salt stress are related to Chl content (percey et al. 2016). Chloroplasts ability to regulate ion transport across the envelope and thylakoid membranes play a critical role in leaf photosynthetic performance under salt stress. The photosynthesis in maize leaves was reduced under salt stress because of NaCl treatment decreased in Chl and carotenoid content respectively (Jiang et al. 2017; Chen et al. 2018). The same result is confirmed by huang et al. (2015) in *ramie cultivar* (Table 1).

Unlike drought, salt stress destroyed the leaf internal structure. Stomatal closure under salt stress has been well studied. Salt stress affects photosynthesis by reducing the active site of Rubisco or the protein content is not clear. The decrease of Chl decreases the ability of regulating ion transport in membrane and thylakoid membrane under salt stress, which affects photosynthesis. Salt stress and drought stress damage to plants in the same way, but there may be different mechanisms because salt stress damage is irreversible.

Table 1. Influence of drought stress and salt stress on the photosynthesis in plant

Stress	Plant	Response of plants to stress	Influence path	Reference
Drought stress	Triticale and Wheat	Decreased leaf extension	Leaf morphology	Lonbani and Arzani (2011)
	Cucumber	Increased the thickness of grana and the length of the palisade cells Decreased photosynthesis by stomatal closure	Leaf morphology Stomatal factor	Liu et al. (2018)
	Grain legumes	Decreased photosynthesis by stomatal closure	Stomatal factor	Faroog et al. (2016)
	Dry bean	Decreased photosynthesis by stomatal closure	Stomatal factor	Lanna et al. (2016)
	Chickpea	Decreased photosynthesis by stomatal closure	Stomatal factor	Panget al. (2017)
	Tomato	Decreased PSII by quantum yield of PSII	PSII	Zhou et al. (2018)
	Olive	Improved PSII by the maximal quantum efficiency of the PSII	PSII	M'barki et al. (2018)
	Bottle gourd	No effect on PSII	PSII	Mashilo et al. (2018)
	Chrysanthemums	Increased Rubisco activity	Rubisco	Yue et al. (2018)
	Rapeseed	No effect on Rubisco activity	Rubisco	Chunqian et al. (2017)
	Kusmen chickpea	Decreased the activity and content of Rubisco	Rubisco	Saglam et al. (2014)
	Subterranean clover	Decreased the total Rubisco activity	Rubisco	Medrano et al. (2010)
	Rice	Decreased the content of chlorophyll, Chl a/b ratio	Chlorophyll	Meifang (2017)
	Machilus pingii seedlings	Chl a, Chl b, carotenoids content and Chl a/b ratio increased at the beginning and then decreased	Chlorophyll	Jie et al. (2015)
Salt stress	Cucumber	Increased the leaf thickness but destroyed the leaf internal structure	Leaf morphology	Yuan et al. (2015)
	Borago officinalis L.	Increased the leaf thickness and palisade parenchyma cells thickness	Leaf morphology	Torabi et al. (2015)
	Soybean	Decreased photosynthesis by stomatal closure	Stomatal	He (2016)
	Wheat	Decreased photosynthesis by stomatal closure	Stomatal	Szopkó et al. (2017)
	Pisum sativum L.	Decreased the PSII by Fv/Fm,	PSII	Percey et al. (2016)
	Vicia faba L.	Decreased the PSII	PSII	Percey et al. (2016)
	Maize	Decreased the PSII by maximum photochemical efficiency of PSII (Fv/Fm), photochemical quenching (qP), and quantum efficiency of PSII photochemistry (ΦPSII)	PSII	Liu et al. (2016)
	Salt-sensitive soybean	Decreased content and activity of Rubisco	Rubisco	He et al. (2014)
	Elaeagnus angustifolia L.	Down-regulation of the key gene that encodes Rubisco, and decreased enzyme activity and protein content of Rubisco	Rubisco	Lin et al. (2018)
	Maize leaves	Decreased contents of chlorophyll and carotenoid	Chlorophyll	Jiang et al. (2017); Chen et al. (2018)
	Ramie cultivar	Decreased contents of chlorophyll and carotenoid	Chlorophyll	Huang et al. (2015)

The Responses of Sucrose and Starch Metabolism in Plants to Stress Conditions

Sucrose and starch are emerging as key molecules in mediating plant responses to stress. Sucrose is a dominant sugar transported to the sink organs of a plant where it is metabolized to other compounds or stored (Nemati et al. 2018). And sucrose synthase and sucrose phosphate synthase are a key enzyme involved in sucrose metabolism and are closely related to sucrose content (Liu et al. 2018). Sucrose also is channeled into various pathways in different subcellular compartments. And may be used for the production of NADH and ATP, also for the biosynthesis of primary metabolites important for tissue growth and development (Sturm 1999). Starch is a simple molecule composed of glucose residues which are linked to each other by a-1,4-linkages with occasional a-1,6-branches, forming osmotically inert, semi-crystalline and dense granules, and it is the most widespread and abundant storage carbohydrate in plants. We depend upon starch for our nutrition (Zeeman et al. 2010). However, sucrose and starch content are important to plant growth under stress.

The Responses of Sucrose and Starch Metabolism in Plants to Drought Stress

Sucrose stabilizes proteins and protects the cell under drought stress by the formation of an intracellular glass, which prevents cellular collapse. Drought stress decreased starch content but increased sucrose content, higher concentration of sucrose in leaves of drought stressed plants through the regulation of higher sucrose phosphate synthase, sucrose synthase in cotton (Zahoor et al. 2017). Falchi et al. (2019) found a significant and increase of starch in Grapevines exposed to early drought stress, but after early stress, soluble starch degradation product concentration increased showing a inverse relationship with starch content. Contents of reducing sugars and fructans were increased while amylose and amylopectin content decreased in wheat (Bala et al. 2018). Drought stress also resulted in an alteration of differential partitioning between starch and soluble sugars (Pagliarani et al. 2019). Cuellar-Ortiz et al. (2008) reported an interesting result that starch was depleted in broad bean leaves but accumulated in pods in response under drought stress. In the common reed, starch content increased in all vegetative tissues but the amount at the base of the shoot was more than twofold higher than that in the upper part of the shoot (Kanai et al. 2007). Moreover, two sucrose synthase and two invertase genes significantly up-regulated under drought stress, whereas one sucrose transporter gene was down-regulated in the cassava petiole abscission zones under drought stress (Liao 2017). The genes coding for sucrose and pectin synthesis were up-regulated under drought stress in maizi (Yang et al. 2019). The up-regulated genes under drought stress were enriched in starch and sucrose metabolism in *Saccharum spontaneum.L* (Wu et al. 2018).

Drought stress can decrease starch content and increase sucrose content in most plants. But a few studies have shown that starch content increases during drought. There were significant differences in the starch content in different parts of plants under drought stress. In recent years, the study of starch and sucrose gene expression under drought stress has become a trend. And in most studies, sucrose-related genes were up-regulated, but the down-regulation of transporter gene may be one of the reasons for the decrease of biomass.

The Responses of Sucrose and Starch Metabolism in Plants to Salt Stress

Sugars may be adaptive responses for salt stress, or may be ‘injury’ responses resulting from the under-utilization of carbon because of growth cessation, regardless, documenting these changes is necessary for a deeper understanding of salt stress response (Dong 2018). And activation of starch degradation under stress is a common plant response and does contribute to sugar accumulation (Thalmann et al. 2016).

The analysis of starch-metabolizing enzyme activities suggested that the largely improved amylopectin contents contributed to the starch accumulation in cucumber (Yuan et al. 2015). Starch and reducing sugars accumulation were increased with salt stress in clone *L. aequinoctialis (*Morais

Table 2. Influence of drought stress and salt stress on the sucrose and starch metabolism in plant

Stress	Plant	Response of plants to stress	Influence path	Reference
Drought stress	Cotton	Decreased starch content but increased sucrose content	Sucrose and starch metabolism	Zahoor et al. (2017)
	Grapevines	Increased starch exposed to early drought stress, but decreased after early stress	Sucrose and starch metabolism	Falchi et al. (2019)
	Wheat	Increased contents of sugars and fructans but decreased amylose and amylopectin contents	Sucrose and starch metabolism	Bala et al. (2018)
	Broad bean	Starch was depleted in leaves but accumulated in pods	Sucrose and starch metabolism	Cuellar-Ortiz et al. (2008)
	Common reed	Increased starch content The amount at the base of the shoot was more than twofold higher than that in the upper part of the shoot	Sucrose and starch metabolism	Kanai et al. (2007)
	Cassava	Two sucrose synthase and two invertase genes significantly up-regulated, one sucrose transporter gene was down-regulated	Sucrose and starch metabolism	Liao (2017)
	Maizi	The genes coding for sucrose were up-regulated	Sucrose and starch metabolism	Yang et al. (2019)
	Saccharum spontaneum. L	The up-regulated genes were enriched in starch and sucrose metabolis	Sucrose and starch metabolism	Wu et al. (2018)
Salt stress	Cyanobacteria	Sucrose metabolism depends on the expression of a gene cluster	Sucrose and starch metabolism	Kolman et al. (2016)
	Cucumber	The largely improved amylopectin content contributed to the starch accumulation	Sucrose and starch metabolism	Yuan et al. (2015)
	Legumes Cajanas cajan L	Increased both reducing sugar and non-reducing sugar content while decreased the starch content	Sucrose and starch metabolism	Chatterjee et al. (2017)
	Cotton	Decreased carbohydrate content in the main-stem leaf, increased sucrose and starch contents in the subtending leaf	Sucrose and starch metabolism	Peng et al. (2016)

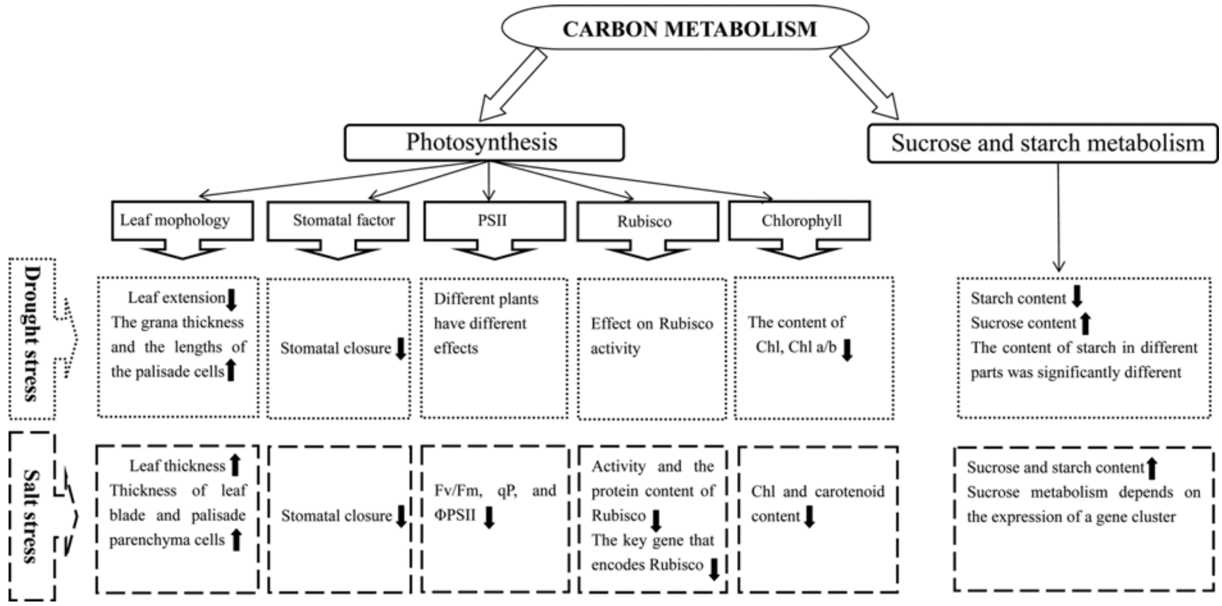

Fig. 1. Response of carbon metabolism to drought stress and salt stress in plants.

et al. 2018). Direct germination on NaCl solution increased both reducing sugar and non-reducing sugar contents while decreased the starch content in *legumes Cajanas cajan L* (Chatterjee et al. 2017). Peng et al. (2016) showed that with increased soil salt stress, carbohydrate contents in the main-stem leaf reduced significantly, while sucrose and starch contents in the subtending leaf increased, as did the activities of sucrose phosphate synthase (SPS) and sucrose synthase (SS) in both the main-stem leaf and subtending leaf in cotton boll (Table 2).

All in all, the content of sucrose in most plants under salt stress is increased. And starch is also increased in some plants cannot be excluded, the reason for the increase of starch remains to be studied (Fig 1).

The Responses of Nitrogen Metabolism to Plants to Stress Conditions

Most plants can use either NO_3^- or NH_4^+ as a source of nitrogen and appropriate levels of NO_3^- can facilitate nitrogen metabolism, thereby benefiting plant growth. NH_4^+ is a central intermediate in this metabolism. The balance within the nitrogen metabolism system is primarily maintained by NR, GS, GOGAT, and GDH. Plants utilize three enzymes (GS, GOGAT, and GDH) for NH_4^+ assimilation. NH_4^+ is rapidly assimilated into organic nitrogen through either the GS/GOGAT cycle or the GDH pathway (Zhang et al. 2017). The GS/GOGAT pathway constitutes in usual conditions the main pathway of NH_4^+ assimilation. When the GS/GOGAT pathway is inhibited by stress. The detoxification of NH_4^+ by GDH might play an important role (Shao et al. 2015). And the lack of N results in changes in root formation, photosynthesis, the production and translocation of photoassimilates, and plant growth rate. Moreover, stress seriously affected nitrogen metabolism (Ding et al. 2005).

The Responses of N Uptake and Amino Acid in Plants to Drought stress

Nitrogen metabolism has important roles in drought tolerance of plant, and higher N uptake can enhance plant drought tolerance in plant (Huan et al. 2017). Drought stress normally presents differential changes in nitrogenous compounds (Liu et al. 2014).

Generally, drought stress can increase available N uptake and NR activity, resulting in an increase in NH_4^+ production (Lawlor 2002). NH_4^+ supply alleviated drought stress in rice seedlings, mainly by increasing root NH_4^+ uptake and leaf N metabolism (Cao et al. 2018). The net NH_4^+ influx at the surface of fine roots rose dramatically under drought treatment, while that of nitrate was less changed. Drought stress negatively inhibited the growth of *Malus hupehensis* seedlings and resulted in higher NH_4^+/NO_3^- ratios in their roots and leaves (Huang 2018). The same results were seen in *M. prunifolia* (Meng 2016). Drought stress hardly affected NO_3^- concentration in the leaves of *Fargesia denudata*, although NR activity slightly increased, which was attributed to the NO_3^- supply and transfer rate from the vacuole into cytoplasm (Liu 2014). Grain yield and nitrogen uptake efficiency were decreased, while nitrogen harvest index NHI, NR and protein content were increased after severe drought stress in spring barley (Hoseinlou 2013). Wang et al. (2016) found that drought stress dramatically enhanced the expression levels of nearly all genes involved in N uptake and assimilation in maize roots.

Several aspects of metabolism have been shown to be affected by drought stress, including inhibition of protein synthesis and changes in amino acid metabolism (Shao 2015). Proline, a special amino acid, plays a crucial role in the drought stress response in plants (Zanella et al. 2016). Proline concentration can affect the growth of petunia plants was influenced in the plants (Yamada et al. 2005). García et al. (2015) showed that proline was elevated due to drought stress in potato. The levels of all the nitrogen-assimilating enzymes studied were reduced in *Poterium sanguisorba*. These changes were accompanied by a fall in soluble protein and water content and by an increase in total amino and proline pools (Taylor 2010). Moreover, an important number of genes involved in N metabolism were up-regulated by drought in tomato wild relative *Solanum pennellii* , as *GDH2* and *ASN1*, involved in the synthesis of Glu and Asn respectively (Egea et al. 2018).

All in all, drought stress can affect N uptake and amino acid metabolism. Mainly including: NH_4^+ increased significantly in most plants, while the content of NO_3^- did not change much. And total amino and proline concentrations also increased due to drought. Moreover, genes involved in N uptake and amino acid synthesis were up-regulated by drought stress.

The Responses of N Uptake and Amino Acid in Plants to Salt stress

Uptake N is a key element for plant growth, but generally, salt stress can suppress the uptake of N of plants (Abouelsaad 2016). Numerous studies found that the activities of GDH, GS, GOGAT and NR is reduced due to salt stress in plants. Specifically, Zaghdoud (2016) found reduced NO_3^- or co-provision of NO_3^- and NH_4^+, but increased plant biomass in broccoli under salt stress. Salt stress reduce NH_4^+ production and also might change the pathway of NH_4^+ assimilation in rice plants, weaken GOGAT/GS pathway and elevate GDH pathway (Wang et al. 2012). And salt stress decreased the number of nodules and their weights in the soybean roots, as well as nitrogen content and metabolism decreased in nodules, roots and shoots, while reducing the activities of GDH, GS, GOGAT and NR (Farhangi-Abriz et al. 2017). Similar findings were reported in cucumber seedlings by Shao et al. (2015).

In terms of amino acid metabolism, salt stress increased contents of free proline, asparagine, and glutamine, and increase in salt stress tolerance to rice plants was extended by a higher synthesis of amino acids (Shahzad et al. 2017). More, proline is reported to involve in salt tolerance in various crops. Proline could ameliorate salt stress induced damages in physiochemical attributes against salt stress (Butt

Table 3. Influence of drought stress and salt stress on the N uptake and amino acid in plant

Stress	Plant	Response of plants to stress	Influence path	Reference
Drought stress	Rice seedlings	Increased root NH_4^+ uptake and leaf N metabolism	N uptake	Cao et al. (2018)
	Malus hupehensis	Increased NH_4^+/NO_3^- ratio in their roots and leaves	N uptake	Huang (2018)
	Malus. prunifolia	Inceased NH_4^+/NO_3^- ratio in their roots and leaves	N uptake	Meng (2016)
	Fargesia.denudata	Increased NR activity	N uptake	Liu (2014)
	Spring barley	Decreased grain yield, nitrogen uptake efficiency, increased nitrogen harvest index, nitrogen re-mobilization and protein content	N uptake	Hoseinlou (2013)
	Maize roots	Enhanced the expression levels of nearly all genes involved in N uptake and assimilation	N uptake	Wang et al. (2016)
	petunias	Increased proline content	Amino acid	Yamada et al. (2005)
	Potato	Increased proline content	Amino acid	García et al. (2015)
	Poterium sanguisorba	Increased the total amino and proline content	Amino acid	Taylor (2010)
	Tomato wild relative *Solanum pennellii*	Up-regulated an important number of genes involved in N metabolism as *GDH2* and *ASN1*, involved in the synthesis of Glu and Asn respectively	Amino acid	Egea et al. (2018)
Salt stress	Broccoli	Deceased the activities of GDH, GS, GOGAT and NR, and NO_3^- or co-provision of NO_3^- and NH_4^+	N uptake	Zaghdoud (2016)
	Soybean roots	Decreased nitrogen content and metabolism	N uptake	Farhangi-Abriz et al. (2017)
	Rice	Change the pathway of NH_4^+ assimilation by weaken GOGAT/ GS pathway and elevate GDH pathway	N uptake	Wang et al. (2012)
	Cucumber seedings	Decrease the activities of GDH, GS, GOGAT and NR	N uptake	Shao et al. (2015)
	Cucumber seedings	Increased proline content, and decreased soluble protein content	Amino acid	Shao et al. (2015)
	Kosteletzkya virginica	Up-regulated the expressions of *KvP5CS1*	Amino acid	Wang et al. (2015)

et al. 2016). Shao (2015) showed the salt stress induced growth inhibition in cucumber seedlings was indicated to involve increases in proline contents, and decreased soluble protein contents, which may contribute to osmotic adjustment. And salt stress increased proline concentration in roots, stems and leaves of *Kosteletzkya virginica* seedling, as the key enzyme genes for proline biosynthesis, more, the up-regulated expression of *KvP5CS1* played a more important role under salt stress (Wang et al. 2015) (Table 3).

Different from drought, salt stress reduced NH_4^+ in most plants, it is also found that NH_4^+ may be correlated with biomass. Salt stress reduced the activities of NR, GOGAT/GS pathway, and elevate GDH pathway in some plants, but the cause needs further study. Increased contents of free amino acids for resisting salt stress, especially, proline. Moreover, in recent years, studies on genes associated with key enzymes in amino acid metabolism have frequently been conducted under salt stress (Fig 2).

Relationship between Secondary Metabolism and C/N Metabolism under Drought Stress and Salt Stress

Secondary metabolites (SMs) are unique sources for food additives, medicinal importance, flavors and industrially important biochemical. They also may confer protection against environmental stresses (Razavizadeh et al. 2018). There are three major groups of secondary metabolites in plants based on their biosynthetic pathway. These groups include phenolic compounds, terpenes and nitrogen-containing compounds (Fang et al. 2011). In higher plants a wide variety of secondary metabolites are synthesized from carbohydrates and amino acids (Verma and Shukla 2015). For example, glucosinolates are a group of plant secondary metabolites containing nitrogen and sulfur (Martínez-Ballesta et al. 2015), the biosynthesis of alkaloids is associated with the availability of a few amino acids such as tryptophan, tyrosine, and lysine (Khalil 2017).

Drought stress exerts a considerable influence on the production of secondary metabolites (Piasecka et al. 2017). The rise in endogenous levels of plant SMs in response to drought stress was recorded in plants. In recent years, drought can significantly improve the content of phenols in plants. For instance, drought stress caused increase in phenolics and decrease in plant biomass in *T. ammi* (Azhar et al. 2011). Increase in total flavonoids was found in *Glechoma longituba* grown (Zhang et al. 2012). Enhanced the quantitative and qualitative improvement of phenolic acids, flavonoids in *A. tricolor* (Sarker et al. 2018). Terpenes are involved in protection mechanisms against environmental-induced stresses (Chidawanyika 2015). Imposition of drought stress resulted in improved quality of artemisinin in Artemisia (Verma and Shukla 2015). Interesting research was reported by Nogués et al. (2015) that terpene emission was maintained even when assimilation and stomatal conductance were completely suppressed in *Cistus monspeliensis* under severe drought. Leaves of *Salvia officinalis L.* under moderate drought stress reveal significantly higher concentrations of monoterpenes than those of plants cultivated under well watered conditions (Nowak et al. 2010). Concentrations of terpene compounds and total phenolic concentrations, remained stable regardless of drought stress or plant stress level in *Eucalyptus globulus*

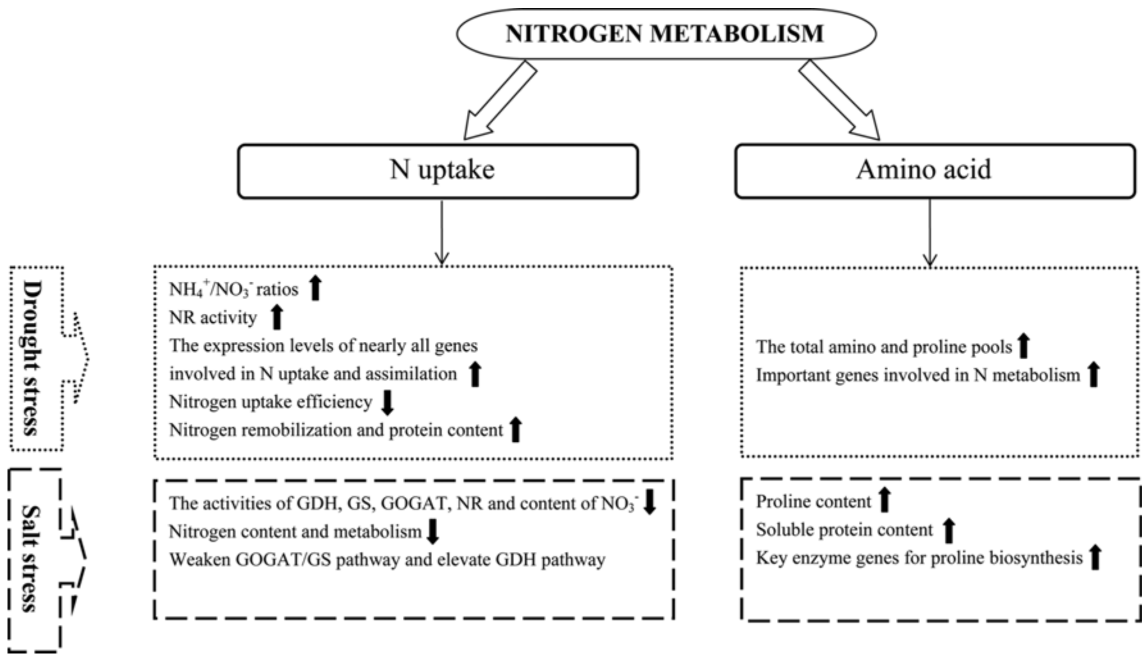

Fig. 2. Response of nitrogen metabolism to drought stress and salt stress in plants.

(Mckiernan et al. 2017). Drought stress increase the polysaccharide, flavonoids, and alkaloids of contents in *Dendrobium moniliforme* (L.) Sw. (Wu et al. 2016). Drought stress increase terpenoid indole alkaloids in *Catharanthus roseus* (Yahyazadeh et al. 2018).

Physiological responses of plant help to increase secondary metabolite accumulation under salt stress (Ashraf et al. 2018). Navarro et al. 2006 showed increased total phenolics content with moderately saline level in red peppers. Salt stress also increased the levels of flavonoids in *Plantago ovata* (Haghighi et al. 2012). Salt stress not affect the growth of safflower seedlings in terms of plant height, root length and plant dry weight, as well as the relative growth rate; however, it did increase the medicine flavonoid content in leaves. (Zhao et al. 2015). Salt stress increased contents of gossypol in cotton by 26.8-51.4%, flavonoids by 22.5-37.6% and tannic by 15.1-24.3% (Wang 2015). Salt stress affected specific major essential oils components causing reductions in α-pinene, β-pinene, and sharp increases in linalool, camphor, and borneol in *Rosmarinus officinallis L.* (El-Esawi et al. 2017). Morever, the qRT-PCR results showed the expression level of terpene synthase 2, terpene synthase 3 and geranylgeranyl diphosphate synthase 4 genes were up-regulated then down-regulated of all lines under salt stress in Maize (Shi et al. 2016). *Catharanthus roseus* and *Rauvolfia tetraphylla* had shown substantial accumulation of vincristine alkaloids and reserpine when exposed to salt stress in the growth medium (Ahl and Omer 2011). A significant rise in alkaloid concentration in *Solanum nigrum* (Verma and Shukla 2015) (Table 4).

Most of phenolic compounds, terpenes and alkaloids in plants increased to adapt to the stress under salt stress and drought stress, the aim may be to protect metabolic balance in plants. The finding was not directly related to biomass. An understanding of secondary metabolism under drought stress and salt stress requires the characterization of enzymes and genes for complete pathways in a broad range of plants.

Conclusion and Future Prospects

It is clear from the literature cited in this chapter that changes

Table 4. Influence of drought stress and salt stress on the secondary metabolism in plant

Stress	Plant	Response of plants to stress	Secondary metabolite type	Reference
Drought stress	*Trachyspermum ammi* L.	Increased phenolics contents	Phenolic compounds	Azhar et al. (2011)
	Amaranthus tricolor	Increased phenolic acids content and flavonoids contents	Phenolic compounds	Sarker et al. (2018)
	Glechoma longituba	Increased total flavonoids contents	Phenolic compounds	Zhang et al. (2012)
	Artemisia	Increased artemisinin content	Terpenoids	Verma and Shukla (2015)
	Cistus monspeliensis	Increased terpene content	Terpenoids	Nogués et al. (2015)
	Salvia officinalis L.	Increased monoterpenes content	Terpenoids	Nowak et al. (2010)
	Eucalyptus globulus	Terpene compounds and total phenolic content remained stable regardless	Terpenoids Phenolic compounds	Mckiernan et al. (2017)
	Dendrobium moniliforme (L.) Sw.	Increased the polysaccharide, flavonoids, and alkaloids contents	Terpenoids Nitrogen-containing compounds	Wu et al. (2016)
	Catharanthus roseus	Increased terpenoid indole alkaloids content	Nitrogen-containing compounds	Yahyazadeh et al. (2018)
Salt stress	Safflower leaves	Increased the medicinal flavonoid content	Phenolic compounds	Zhao et al. (2015)
	Plantago ovata	Increased saponins, flavonoids contents	Phenolic compounds	Haghighi et al. (2012)
	Red peppers	Increased total phenolics contents	Phenolic compounds	Navarro et al. (2006)
	Cotton	Increased gossypol, flavonoids, tannic contents	Phenolic compounds	Wang (2015)
	Rosmarinus officinallis L	Decreased α-pinene, β-pinene contents, and increased linalool, camphor, and borneol contents	Terpenoids	El-Esawi et al. (2017)
	Maize	The expression level of terpene synthase 2, terpene synthase 3 and geranylgeranyl diphosphate synthase 4 genes were up-regulated then down-regulated of all lines	Terpenoids	Shi et al. (2016)
	Catharanthus roseus and Rauvolfia tetraphylla	Increased vincristine alkaloids and reserpine contents	Nitrogen-containing compounds	Said-Al Ahl and Omer (2011)
	Solanum nigrum	Increased alkaloid content	Nitrogen-containing compounds	Verma and Shukla (2015)

of carbon and nitrogen metabolism under both of drought stress and salt stress to that not only influence plant growth but also increase the biosynthesis of secondary metabolism. Plant growth and development are precisely affected by drought stress and salt stress on photosynthesis, sucrose and starch metabolism. N uptake and amino acid documented in the literature. All in all, change of carbon and nitrogen metabolism under drought stress and salt stress is still not fully known. More research is needed to completely understand the regulatory proteins and genes of carbon and nitrogen metabolism such as Rubisco expression, and the relative expression of N uptake related genes, so that these may be manipulated for improving plant tolerance to salt and drought stresses. Sucrose and nitrogen influenced the total level of secondary metabolites (Rühmann et al. 2010). The relationship between secondary metabolism and carbon and nitrogen metabolism under salt and drought stresses is an area that must be studied in detail.

Acknowledgements

The authors are grateful for the financial support provided by the project of the National Natural Science Foundation of China (31860343 and 31460330) and the Key National Research and Development Programs (2017YFC1700706).

Author's Contributions

GC Cui wrote the manuscript; Y Zhang made the figure; WJ Zhang made the table; DY Lang modified the language; XJ Zhang collected the literatures; ZX Li modified the details; XH Zhang provided the ideas. All the authors agreed on the content of the paper and post no conflicting interest.

References

Abdelrahman M, Jogaiah S, Burritt DJ, Tran LSP (2018) Legume genetic resources and transcriptome dynamics under abiotic stress conditions. Plant Cell Environ 41:1972–1983

Allakhverdiev SI, Murata N (2004) Environmental stress inhibits the synthesis denovo of proteins involved in the photodamage—repair cycle of photosystem II in Synechocystis sp. PCC 6803. Biochim Biophys Acta 1657:23–32

Anjum F, Yaseen M, Rasul EA, Wahid, Anjum S (2003) Water stress in barley (*Hordeum vulgare* L.). II. Effect on chemical composition and chlorophyll contents. Pak J Agric Biol Sci 40:45–49

Abouelsaad I, Weihrauch D, Renault S (2016) Effects of salt stress on the expression of key genes related to nitrogen assimilation and transport in the roots of the cultivated tomato and its wild salt-tolerant relative. Sci Hortic 211:70–78

Azhar N, Hussain B, Ashraf MY, Abbasi KY (2011) Water stress mediated changes in growth, physiology and secondary metabolites of desi ajwain (*Trachyspermum ammi* L.). Pak J Bot 43:15–19

Ashraf MA, Iqbal M, Rasheed R, Hussain I, Riaz M, Arif MS (2018) Environmental stress and secondary metabolites in plants : an overview. Plant Metabolites & Regulation Under Environmental Stress. Academic Press DOI: org/10.1016/B978-0-12-812689-9.00008-X

Baker NR (2010) A possible role for photosystem II in environmental perturbations of photosynthesis. Physiol Plant 81:563–570

Bota J, Medrano H, Flexas J (2004) Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? New Phytol 162:671–681

Butt M, Ayyub CM, Amjad M, Ahmad R (2016) Proline application enhances growth of chilli by improving physiological and biochemical attributes under salt stress. Pak J Agric Biol Sci 53:43–49

Bala S, Asthir B, Bains NS (2018) Heat and drought stress responses alter grain characteristics by impeding starch precursors of wheat. Indian J Exp Biol 56:565–572

Bhagat KP, Kumar RA, Kumar PR, Kumar S, Bal SK, Agrawal PK (2014) Photosynthesis and Associated Aspects Under Abiotic Stresses Environment. Approaches to Plant Stress and their Management DOI: 10.1007/978-81-322-1620-9-10

Cha-Um S, Charoenpanich A, Roytrakul S, Kirdmanee C (2009) Sugar accumulation, photosynthesis and growth of two indica rice varieties in response to salt stress. Acta Physiol Plant 31:477–486

Chunqian H (2017) Effects of drought and high temperature on photosynthesis and chlorophyll fluorescence characteristics of rapeseed leaves. Chin J Oil Crop Sci 39:342–350 (in Chinese)

Chatterjee P, Biswas S, Biswas AK (2017) Amelioration of salinity stress by NaCl pretreatment with reference to sugar metabolism in *legumes Cajanas cajan* L. and *Vigna mungo* L. Plant Sci Today 4:28–40

Cao X, Zhong C, Zhu C, Zhu L, Zhang J, Wu L (2018) Ammonium uptake and metabolism alleviate peg-induced water stress in rice seedlings. Plant Physiol Biochem 132:128–137

Chakraborty M, Kuriata A, Henderson JN, Salvucci ME, Wachter R, Levitus M (2014) ATP-Mg_2^+ mediated assembly of Rubisco activase investigated using fluorescence correlation spectroscopy. Biophys J 106:40–40

Cuellar-Ortiz SM, De La Paz Arrieta-Montiel M, Acosta-Gallegos J, Covarrubias AA (2008) Relationship between carbohydrate partitioning and drought resistance in common bean. Plant Cell Environ 31:1399–1409

Chidawanyika F (2015) Effects of drought on the production of electrophysiologically active biogenic volatiles important for cereal pest management. Univ Witwatersrand URI: http://hdl.handle.net/10539/18481

Ding L (2005) Effects of nitrogen deficiency on photosynthetic traits of maize hybrids released in different years. Ann Bot 96:925–930

Dong S, Zhang J, Beckles DM (2018) A pivotal role for starch in the reconfiguration of ^{14}C-partitioning and allocation in *Arabidopsis thaliana* under short-term abiotic stress. Sci Rep DOI: 10.1038/s41598-018-27610-y

Dai J, Duan L, Dong H (2015) Comparative effect of nitrogen forms on nitrogen uptake and cotton growth under salinity stress. J Plant Nutr 38:1530–1543

Egea I, Albaladejo I, Meco V, Morales B, Sevilla A, Bolarin MC, Flores FB (2018) The drought-tolerant *Solanum pennellii* regulates leaf water loss and induces genes involved in amino acid and ethylene/jasmonate metabolism under dehydration. Sci Rep DOI: 10.1038/s41598-018-21187-2

El-Esawi MA, Elansary HO, El-Shanhorey NA, Abdel-Hamid AME, Ali HM, Elshikh MS (2017) Salicylic acid-regulated antioxidant mechanisms and gene expression enhance rosemary performance under saline conditions. Front Physiol DOI: 10.3389/fphys.2017.00716

Flexas J, Ribascarbó M, Bota J, Galmés J, Henkle M, Martínezcañellas S

(2010) Decreased Rubisco activity during water stress is not induced by decreased relative water content but related to conditions of low stomatal conductance and chloroplast CO_2 concentration. New Phytol 172:73–82
Feller U, Anders I, Mae T (2007) Rubiscolytics: fate of Rubisco after its enzymatic function in a cell is terminated. J Exp Bot 59:1615–1624
Farhangi-Abriz S, Torabian S (2017) Biochar improved nodulation and nitrogen metabolism of soybean under salt stress. Symbiosis 74:1–9
Fang X, Yang CQ, Wei YK, Ma QX, Yang L, Chen XY (2011) Genomics grand for diversified plant secondary metabolites. Plant Diversity Resour 33:53–64
Farooq M, Gogoi N, Barthakur S, Baroowa B, Bharadwaj N, Alghamdi SS, Siddique KHM (2017) Drought stress in grain legumes during reproduction and grain filling. J Agron Crop Sci 203:81–102
Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. Agron Sustainable Dev 29:153–188
Falchi R, Petrussa E, Zancani M, Casolo V, Beraldo P, Nardini A, Braidot E (2019) Summer drought stress: differential effects on cane anatomy and non-structural carbohydrate content in overwintering *Cabernet Sauvignon* and *Syrah vines*. BIO Web of Conferences DOI: org/10.1051/bioconf/20191303007
García-Pacios J, Garcés P, Del Río D, Maestú F (2015) Bioactive compounds in potatoes: accumulation under drought stress conditions. Funct Foods Health Dis 5:108–116
Grotewold E (2006) The genetics and biochemistry of floral pigments. Annu Rev Plant Biol 57:761–780
Huang CJ, Wei G, Jie YC, Xu JJ, Zhao SY, Wang LC (2015) Responses of gas exchange, chlorophyll synthesis and ros-scavenging systems to salinity stress in two ramie (*Boehmeria nivea* L.) cultivars. Photosynthetica 53:455–463
He Y, Yu C, Zhou L, Chen Y, Liu A, Jin J, Hong J, Qi Y, and Jiang D (2014) Rubisco decrease is involved in chloroplast protrusion and Rubisco-containing body formation in soybean (Glycine max) under salt stress, Plant Physiol Biochem 4:118–124
Huan W, Zongze Y, Yanan Y, Siyu C, Zhang H, Yong W (2017) Drought enhances nitrogen uptake and assimilation in maize roots. Agron J 109:39–46
Huang L, Li M, Yun S, Sun T, Li C, Ma F (2018) Ammonium uptake increases in response to peg-induced drought stress in *Malus hupehensis rehd.* Environ Exp Bot 151:32–42
Hoseinlou SH, Ebadi A, Ghaffari M, Mostafaei E (2013) Nitrogen use efficiency under water deficit condition in spring barley. Int J Agron Plant Prod 4:3681–3687
Haghighi Z, Modarresi M, Mollayi S (2012) Enhancement of compatible solute and secondary metabolites production in *Plantago ovata Forsk*. by salinity stress. J Med Plants Res 6:3495–3500
He Y, Chen Y, Yu CL, Lu KX, Jiang QS, Fu JL (2016) Photosynthesis and yield traits in different soybean lines in response to salt stress. Photosynthetica 54:630–635
Hara S, Tahvanainen T, Hashidoko Y, Gilkes RJ, Prakongkep N (2010) Investigation of nitrogen-fixing potential in soil bacterial microbiota from Lapland boreal forest limit. World Congress of Soil Science: Soil Solutions for A Changing World DOI: 10.1071/FP16135
Huang GT, Ma SL, Bai LP, Zhang L, Ma H, Jia P (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39:969–987
Jaleel CA, Manivannan P, Sankar B, Kishorekumar A, Sankari S, Panneerselvam R (2007) Paclobutrazol enhances photosynthesis and ajmalicine production in *Catharanthus roseus*. Process Biochem 42:1566–1570
Jiang C, Zu C, Lu D, Zheng Q, Shen J, Wang H (2017) Effect of exogenous selenium supply on photosynthesis, Na^+ accumulation and antioxidative capacity of maize (*Zea mays* L.) under salinity stress. Sci Rep DOI: 10.1038/srep42039
Jie L, Guangliang Z, Tingxing HU, Hongling HU, Hong C, Qian W (2015) Effects of drought stress on growth and physiological parameters of *machilus pingii* seedlings. Chin J Appl Environ Biol 21:563–570 (in chinese)
Khalil A (2017) Role of biotechnology in alkaloids production. DOI: 10.1007/978-3-319-51620-2-4
Kusano M, Fukushima A, Redestig H, Saito K (2011) Metabolomic approaches toward understanding nitrogen metabolism in plants. J Exp Bot 62:1439–1453
Kanai M, Higuchi K, Hagihara T, Konishi T, Ishii T, Fujita N, Nakamura Y, Maeda Y, Yoshiba M, Tadano T (2007) Common reed produces starchgranules at the shoot base in response to salt stress. New Phytol 176:572–580
Khalid M, Bilal M, Hassani D, Iqbal HMN, Wang H, Huang D (2017) Mitigation of salt stress in white clover (*Trifolium repens*) by azospirillum brasilense and its inoculation effect. Bot Stud DOI: 10.1186/s40529-016-0160-8
Liu C, Wang Y, Pan K, Zhu T, Li W, Zhang L (2014) Carbon and nitrogen metabolism in leaves and roots of dwarf bamboo (*Fargesia denudatayi*) subjected to drought for two consecutive years during sprouting period. J Plant Growth Regul 33:243–255
Liu YJ, Wang GL, Ma J, Xu ZS, Wang F, Xiong AS (2018) Transcript profiling of sucrose synthase genes involved in sucrose metabolism among four carrot (*Daucus carota* L.) cultivars reveals distinct patterns. BMC Plant Biol DOI: 10.1186/s12870-017-1221-1
Lin J, Li JP, Yuan F, Yang Z, Wang BS, Chen M (2018) Transcriptome profiling of genes involved in photosynthesis in *Elaeagnus angustifolia.* under salt stress. Photosynthetica 56:998–1009
Liao WB, Li YY, Lu C, Peng M (2017) Expression of sucrose metabolism and transport genes in cassava petiole abscission zones in response to water stress. Biol Plant 61:219–226
Liu BB, Li M, Li QM, Cui QQ, Zhang WD, Ai XZ (2018) Combined effects of elevated CO_2, concentration and drought stress on photosynthetic performance and leaf structure of cucumber (*Cucumis sativus* L.) seedlings. Photosynthetica 56:942–952
Liu RQ, Xu XJ, Wang S, Shan CJ (2019) Lanthanum improves salt tolerance of maize seedlings. Photosynthetica 54:148–151
Lanna AC, Mitsuzono ST, Terra TGR, Vianello RP, De Figueiredo Carvalho MA (2016) Physiological characterization of common bean (*Phaseolus vulgaris* L.) 23genotypes, water stress induced with contrasting response towards drought. Aust J Crop Sci 10:1–6
Lawlor DW (2002) Carbon and nitrogen assimilation in relation to yield: mechanisms are the key to understanding production systems. J Exp Bot 53:773–787
Leuzinger S, Bigler C, Wolf A, Körner C (2009) Poor methodology for predicting large-scale tree die-off. Proc Natl Acad Sci USA DOI: 10.1073/pnas.0908053106
Lawson T, Blatt MR (2014) Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiol 164:1556–1570
Lonbani M, Arzani A (2011) Morpho-physiological traits associated with terminal drought-stress tolerance in triticale and wheat. Agron Res 9:315–329
Liu L, Mo Y, Yang X, Li X, Wu M, Zhang X (2014) Reasonable drip irrigation frequency improving watermelon yield and quality under regulated deficit irrigation in plastic greenhouse. Trans Chin Soc Agric Eng 30:95–104 (in chinese)
Luo HH, Zhang YL, Zhang WF (2016) Effect of water stress and rewatering on photosynthesis, root activity, and yield of cotton with drip irrigation under mulch. Photosynthetica 54:65–73
McDowell N, Sevanto S (2010) The mechanisms of carbon starvation: how, when, or does it even occur at all? New Phytol 186:264–

266

Mashilo J, Odindo AO, Shimelis HA, Musenge P, Tesfay SZ, Magwaza LS (2018) Photosynthetic response of bottle gourd [*Lagenaria siceraria* (Molina) Standl.] to drought stress: relationship between cucurbitacins accumulation and drought tolerance. Sci Hortic 231:133–143

Mittal S, Kumari N, Sharma V (2012) Differential response of salt stress on Brassica juncea: photosynthetic performance, pigment, proline, D1 and antioxidant enzymes. Plant Physiol Biochem 54:17–26

M'barki, Naouraz, Chehab H, Aissaoui F, Dabbaghi O, Attia F, Mahjoub Z (2018) Effects of mycorrhizal fungi inoculation and soil amendment with hydrogel on leaf anatomy, growth and physiology performance of olive plantlets under two contrasting water regimes. Acta Physiol Plant DOI:10.1007/s11738-018-2692-x

Yu MF (2017) Effect of drought stress at tillering stage on photosynthetic characteristics and yield formation of cold-region rice. J Nucl Agric Sci 31:1794–1802

Meng S, Zhang C, Li S, Li Y, Zhao Z (2016) Nitrogen uptake and metabolism of *populus simonii* in response to peg-induced drought stress. Environ Exp Bot 123:78–87

Murata N, Takahashi S, Nishiyama Y, Allakhverdiev S (2007) Photoinhibition of photosystem II under environmental stress. Biochim Biophys Acta 1767:414–421

Mohanty P, Allakhverdiev SI, Murata N (2007) Application of low temperature during photoinhibition allows characterization of individual steps in photodamage and repair of photosystem II. Photosynth Res 94:217–234

Medrano H, Parry MAJ, Socias X, Lawlor DW (2010) Long term water stress inactivates Rubisco in *subterranean clover*. Ann Appl Biol 131:491–501

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Martínez-Ballesta Mcarmen, Moreno-Fernández Diego A, Castejón Diego, Cristina, O, Morandini, PA, Micaela C (2015) The impact of the absence of aliphatic glucosinolates on water transport under salt stress in *Arabidopsis thaliana*. Front Recent Dev Plant Sci DOI: 10.3389/fpls.2015.00524

Mckiernan AB, Potts BM, Hovenden MJ, Brodribb TJ, Davies NW, Rodemann T (2017) A water availability gradient reveals the deficit level required to affect traits in potted juvenile eucalyptus globulus. Ann Bot 119:1043-1052

Morais MBD, Neto AGB, Willadino L, Cláudia Ulisses, Tercílio Calsa Junior (2018) Salt stress induces increase in starch accumulation in duckweed (*lemna aequinoctialis, lemnaceae*): biochemical and physiological aspects. J Plant Growth Regul DOI: 10.1007/s00344-018-9882-z

Manaa A, Ahmed HB, Valot B, Bouchet JP, Aschismiti S, Causse M, (2011) Salt and genotype impact on plant physiology and root proteome variations in tomato. J Exp Bot 62:2797–2813

Naya L, Ladrera R, Ramos J, González EM, Arrese-Igor C, Minchin, FR (2007) The response of carbon metabolism and antioxidant defenses of alfalfa nodules to drought stress and to the subsequent recovery of plants. Plant Physiol 144:1104–1114

Nishiyama Y, Yamamoto H, Allakhverdiev SI, Inaba M, Yokota A, Murata N (2001) Oxidative stress inhibits the repair of photodamage to the photosynthetic machinery. EMBO J 20:5587–5594

Nemati F, Ghanati F, Ahmadi Gavlighi H, Sharifi M (2018) Comparison of sucrose metabolism in wheat seedlings during drought stress and subsequent recovery. Biol Plant 62:595–599

Nunes-Nesi A, Fernie AR, Stitt M (2010) Metabolic and signaling aspects underpinning the regulation of plant carbon nitrogen interactions. Mol Plant 3:973–996

Nathawat NS, Kuhad MS, Goswami CL, Patel AL, Kumar R (2005) Nitrogen-metabolizing enzymes: effect of nitrogen sources and saline irrigation. J Plant Nutr 28:1089–1101

Nogués I, Medori M, Calfapietra C (2015) Limitations of monoterpene emissions and their antioxidant role in *cistus sp*. under mild and severe treatments of drought and warming. Environ Exp Bot 119:76–86

Nowak M, Kleinwaechter M, Manderscheid R, Weigel HJ, Selmar D (2010) Drought stress increases the accumulation of monoterpenes in sage (*Salvia officinalis*), an effect that is compensated by elevated carbon dioxide concentration. J Appl Bot Food Qual 83:133–136

Navarro JM, Flores P, Garrido C, Martinez V (2006) Changes in the contents of antioxidant compounds in pepper fruits at different ripening stages, as affected by salinity. Food Chem 96:66–73

Osbourn AE, Qi X, Townsend B, Qin B (2003) Dissecting plant secondary metabolism - constitutive chemical defences in cereals. New Phytol 159:101–108

Otori K, Tanabe N, Maruyama T, Sato S, Yanagisawa S, Tamoi M (2017) Enhanced photosynthetic capacity increases nitrogen metabolism through the coordinated regulation of carbon and nitrogen assimilation in *Arabidopsis thaliana.* J Plant Res 130:909–927

Percey WJ, Mcminn A, Bose J, Breadmore MC, Guijt RM, Shabala S (2016) Salinity effects on chloroplast PSII performance in glycophytes and halophytes. Funct Plant Biol 43:1003–1015

Pagliarani C, Casolo V, Ashofteh Beiragi M, Cavalletto S, Siciliano I, Schubert A, Lodovica Gullino M, Maciej A, Zwieniecki & Secchi F (2019) Priming xylem for stress recovery depends on coordinated activity of sugar metabolic pathways and changes in xylem sap pH. Plant Cell Environ 42:1775–1787

Pang J, Turner NC, Khan T, Du YL, Xiong JL, Colmer TD (2017) Response of chickpea (*Cicer arietinum* L.) to terminal drought: leaf stomatal conductance, pod abscisic acid concentration, and seed set. J Exp Bot 68:1973–1985

Piasecka A, Sawikowska A, Anetta K, Ogrodowicz P, Krzysztof M, Krystkowiak K (2017) Drought-related secondary metabolites of barley (*Hordeum vulgare* L.) leaves and their metabolomic quantitative trait loci. Plant J 89:898–913

Peng J, Liu J, Zhang L, Luo J, Dong H, Ma Y, Meng Y (2016) Effects of soil salinity on sucrose metabolism in cotton leaves. PloS one DOI: 10.1371/journal.pone.0156241

Pereira DT, Simioni C, Ouriques LC, Ramlov F, Maraschin M, Steiner N (2018) Comparative study of the effects of salinity and uv radiation on metabolism and morphology of the red macroalga acanthophora spicifera (*Rhodophyta, ceramiales*). Photosynthetica 56:799–810

Richardson A, Wojciechowski T, Schreiber L, Veselov D (2006) The short-termgrowth response to salt of the developing barley leaf. J Exp Bot 57:1079–1095

Razavizadeh R, Komatsu S (2018) Changes in essential oil and physiological parameters of callus and seedlings of *Carum copticum* L. under in vitro drought stress. J Food Meas Charact 12:1581–1592

Rühmann S, Leser C, Bannert M, Treutter D (2010) Relationship between growth, secondary metabolism, and resistance of apple. Plant Biol 4:137–143

Sala A, Piper F, Hoch G 2010 Physiological mechanisms of drought induced tree mortality are far from being resolved. New Phytol 186:274–281

Sturm A, Tang GQ (1999) The sucrose-cleaving enzymes of plants are crucial for development, growth and carbon partitioning. Trends Plant Sci 4:401–407

Shao QS, Shu S, Du J, Xing WW, Guo SR, Sun J (2015) Effects of nacl stress on nitrogen metabolism of cucumber seedlings. Russ J Plant Physiol 62:595–603

Szopkó D, Molnár I, Kruppa K, Háló B, Vojtkó A, Molnár-Láng M (2017). Photosynthetic responses of a wheat (Asakaze)–barley (Manas) 7h addition line to salt stress. Photosynthetica 55:317–

328.

Shahzad R, Khan AL, Bilal S, Waqas M, Kang SM, Lee IJ (2017) Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa.* L. Environ Exp Bot 136:68–77

Sarker U, Oba S (2018) Drought stress enhances nutritional and bioactive compounds, phenolic acids and antioxidant capacity of amaranthus leafy vegetable. BMC Plant Biol DOI: 10.1186/s12870-018-1484-1

Saglam A, Terzi R, Demiralay M (2014) Effect of polyethylene glycol induced drought stress on photosynthesis in two chickpea genotypes with different drought tolerance. Acta Biol Hung 65:178–188

Shi LP, Jing JI, Wang G, Jin C, Xie C, Du XL (2016) The expression and analysis of terpene synthesis related genes in maize under the condition of salt stress. China Biotechnol 36:31–37

Ahl Said-Al H, Omer E (2011) Medicinal and aromatic plants production under salt stress. A review. Herba Polonica 57:72–87

Taleisnik E, Rodriguez AA, Bustos D, Erdei L, Ortega L, Senn ME, 2009. Leaf expansion in grasses under salt stress. J Plant Physiol 166:1123–1140

Thalmann M, Pazmino D, Seung D, Horrer D, Nigro A, Meier T, Kölling K, Pfeifhofer WH, Zeeman SC, Santelia D. 2016. Regulation of leaf starch degradation by abscisic acid is important for osmotic stress tolerance in plants. J Exp Bot 28:1860–1878

Tamburino R, Vitale M, Ruggiero A, Sassi M, Sannino L, Arena S (2017) Chloroplast proteome response to drought stress and recovery in tomato (*Solanum lycopersicum* L.). BMC Plant Biol DOI: 10.1186/s12870-017-0971-0

Torabi F, Majd A, Enteshari S (2015. The effect of silicon on alleviation of salt stress in borage (*Borago officinalis* L.). Soil Sci Plant Nutr 61:1–11

Taylor, AA, De-Felice J, Havill DC (2010) Nitrogen metabolism in *Poterium sanguisorba* during water stress. New Phytol 90:19–25

Verma N, Shukla S (2015) Impact of various factors responsible for fluctuation in plant secondary metabolites. J Appl Res Med Aroma DOI: 10.1016/j.jarmap.2015.09.002

Wang H, Yang Z, Yu Y, Chen S, Zhang H, Yong W (2016) Drought enhances nitrogen uptake and assimilation in maize roots. Agron J DOI: 10.2134/agronj2016.01.0030

Wang H, Tang X, Wang H, Shao HB (2015) Proline accumulation and metabolism-related genes expression profiles in *Kosteletzkya virginica* seedlings under salt stress. Front Plant Sci DOI: 10.3389/fpls.2015.00792

Wang H, Zhang M, Guo R, Shi D, Liu B, Lin X (2012) Effects of salt stress on ion balance and nitrogen metabolism of old and young leaves in rice (*Oryza sativa* L.). BMC Plant Biol 12:194–194

Wang X, Wang W, Huang J, Peng S, Xiong D (2017) Diffusional conductance to CO_2 is the key limitation to photosynthesis in salt-stressed leaves of rice (*Oryza sativa* L.). Physol Plantarum 163:45–48

Wu KC, Wei LP, Huang CM, Wei YW, Cao HQ, Xu L (2018) Transcriptome reveals differentially expressed genes in Saccharum spontaneum L. leaf under drought stress. Sugar Tech DOI: 10.1007/s12355-018-0608-0

Wang Q, Eneji AE, Kong X, Wang K, Dong H (2015) Salt stress effects on secondary metabolites of cotton in relation to gene expression responsible for aphid development. Plos One DOI: 10.1371/journal.pone.0129541

Wungrampha S, Joshi R, Singla-Pareek SL, Pareek A (2018) Photosynthesis and salinity: are these mutually exclusive? Photosynthetica 56:366–381

Wang H, Yang Z, Yu Y, Chen S, Zhang H, Yong W (2016) Drought enhances nitrogen uptake and assimilation in maize roots. Agron J DOI:10.2134/agronj2016.01.0030

Wu X, Yuan J, Luo A, Chen Y, Fan Y (2016) Drought stress and re-watering increase secondary metabolites and enzyme activity in *Dendrobium moniliforme.* Ind Crop Prod 94:385–393

Yue C, Xianzhi S, Chengshu Z, Sheng Z, Jinghui Y (2018) Grafting onto artemisia annua improves drought tolerance in chrysanthemum by enhancing photosynthetic capacity. Hortic Plant J 4:33–41

Yuan Y, Min Z, Sheng S, Du N, He L, Yuan L (2015) Effects of exogenous putrescine on leaf anatomy and carbohydrate metabolism in cucumber (*Cucumis sativus* L.) under salt stress. J Plant Growth Regul 34:451–464

Yang M, Geng M, Shen P, Chen X, Li Y, Wen X (2019) Effect of post-silking drought stress on the expression profiles of genes involved in carbon and nitrogen metabolism during leaf senescence in maize (*Zea mays* L.). Plant Physiol Biochem135:304–309

Yamada M, Morishita H, Urano K, Shiozaki N, Yamaguchi-Shinozaki K, Shinozaki K (2005) Effects of free proline accumulation in petunias under drought stress. J Exp Bot 56:1975–1981

Yahyazadeh M, Meinen R, HNsch R, Abouzeid S, Selmar D (2018) Impact of drought and salt stress on the biosynthesis of alkaloids in *Chelidonium majus* L. Phytochemistry 152:204–212

Zlatev Z, Lidon FC (2012) An overview on drought induced changes in plant growth, water relations and photosynthesis. Emir J Food Agr 24:520–524

Zhou R, Kong L, Wu Z, Rosenqvist E, Wang Y, Zhao L (2018) Physiological response of tomatoes at drought, heat and their combination followed by recovery. Physiol Plantarum 164:144–154

Zeeman SC, Kossmann J, Smith AM (2010) Starch: its metabolism, evolution, and biotechnological modifification in plants. Annu Rev Plant Biol 61:209–234

Zanella M, Borghi GL, PironeC, Thalmann M, Pazmino D, Costa A (2016) β-amylase 1 (bam1) degrades transitory starch to sustain proline biosynthesis during drought stress. J Exp Bot 67:1819–1826

Zahoor R, Dong H, Abid M, Zhao W, Wang Y, Zhou Z (2017) Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and carbohydrate metabolism. Environ Exp Bot 137:73–83

Zhang R, Sun Y, Liu Z, Jin W, Sun Y (2017) Effects of melatonin on seedling growth, mineral nutrition, and nitrogen metabolism in cucumber under nitrate stress. J Pineal Res DOI: 10.1111/jpi.12403

Zaghdoud C, Carvajal M, Ferchichi A, Del CMM (2016) Water balance and N-metabolism in broccoli (*Brassica oleracea* L.var. Italica) plants depending on nitrogen source under salt stress and elevated CO_2. Sci Total Environ 571:763–771

Zhang L, Wang Q, Guo Q, Chang Q, Zhu Z, Liu L, Xu H (2012) Growth, physiological characteristics and total flavonoid content of *Glechoma longituba* in response to water stress. J Int Med Res 6:1015–1024

Zhao G, Yu H, Xing S, Li S, Shi Q, Wang C (2015) Salinity stress increases secondary metabolites and enzyme activity in safflower. Ind Crop Prod 64:175–181