




Commentary

Proteomics reveal both photochemical and biochemical limitations involved in salt-induced suppression of photosynthesis in trees

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Salinity, including naturally occurring salt-affected soil but also increasingly secondary soil salinization, is a global ecological problem (Pitman and Läuchli 2002, Hasegawa 2013). Salinity reduces photosynthesis not only in salt-sensitive but also in salt-resistant tree species, such as *Populus euphratica*, *Atriplex centralasiatica* and mangrove species (Ball and Farquhar 1984, Werner and Stelzer 1990, Parida et al. 2003, 2004, Qiu et al. 2003, Wang et al. 2007, Li et al. 2008). Salt-induced stomatal closure, caused by abscisic acid, is thought to be responsible for this decrease in net photosynthetic rates (A_{net}) (Chen et al. 2002, Chang et al. 2006, Munns and Tester 2008). But in addition to stomatal limitations, non-stomatal factors are also involved in decreasing photosynthesis in response to saline conditions (Ball and Farquhar 1984, Ball and Anderson 1986, Seemann and Sharkey 1986, Pérez-López et al. 2012, Oukarroum et al. 2015, Moles et al. 2016, Asrar et al. 2017). However, the relative importance of stomatal and metabolic limitations to the decline of photosynthesis under salt stress is still debated (Flanagan and Jefferies 1989, Brugnoli and Lauteri 1991, Steduto et al. 2000, Centritto et al. 2003, Roussos et al. 2017). By examining the proteome of a mangrove species exposed to saline conditions, Shen et al. (2018) (this issue of *Tree Physiology*) shed new light on the extent to which inhibition of photosynthetic processes is caused by decreased abundance of the proteins involved in the photosynthetic light and dark reactions.

Accumulating evidence suggests that the importance of photochemical and biochemical limitations progressively increase with increasing salinity (Pérez-López et al. 2012, Asrar et al. 2017). With regard to photochemistry, salt inhibits photosystem I and II

(PSI and PSII, respectively) activity, in terms of declines in the maximum quantum efficiency of PSII, actual quantum efficiency of PSII, electron transport rate and energy harvesting by open reaction centers of PSII (Zribi et al. 2009, Khan et al. 2015, Oukarroum et al. 2015). Salt-induced Na^+ accumulation in leaves may decrease the stability of PSII, inhibit photosynthetic electron transport (Muranaka et al. 2002) and reduce the abundance of D1, a key PSII protein (Asrar et al. 2017). Salt stress can also contribute to the inhibition of D1 by lowering the rate of incorporation of [^{35}S]-methionine into proteins of thylakoid membranes (Allakhverdiev and Murata 2004, Nishiyama et al. 2006). Additionally, reactive oxygen species production, which increases under saline conditions, inhibits the repair of PSII by suppressing de novo synthesis of D1 (Allakhverdiev and Murata 2004, Nishiyama et al. 2006, Oukarroum et al. 2015), further reducing the population of functional PSII. However, it is still unknown which proteins other than D1 are inhibited by salt stress, since the synthesis of many other proteins in the thylakoid membranes is completely inhibited by the presence of high NaCl (Allakhverdiev and Murata 2004). By analyzing the leaf proteome of *Avicennia marina*, a pioneer species in the mangrove forest, Shen et al. (2018) showed that salt inhibition of photosynthesis was partly due to the suppressed expression of multiple proteins involved in the light reactions. Salt-stressed *A. marina* had lower levels of photochemical proteins involved in the electron transport chain (e.g., quinine oxidoreductase-like protein isoform 1) and in chloroplastic ATP synthesis (ATPase F1 complex gamma subunit protein) (Shen et al. 2018). Similarly, treatment with NaCl resulted in decreases in the level of ATP synthase CF1 alpha in isolated chloroplasts from *Kandelia candel* (Wang et al. 2015), although

Table 1. Salt-altered photosynthetic proteins characterized by proteomics in tree species

Species and proteomic approach	Salt treatment	Photochemical proteins in response to NaCl		Biochemical proteins in response to NaCl		Reference	
<i>Avicennia marina</i> Leaf MALDI-TOF/TOF MS	NaCl 100 mM (control) and 400 mM (high salt) for 30 days supplemented with or without SNP (100 µM)	Thylakoid lumenal 17.4 kDa protein	NaCl ↑	NaCl+SNP ↓	RuBisCO large subunit (3)	NaCl ↓ NaCl+SNP ↑	Shen et al. (2018)
		ATPase F1 complex gamma subunit protein	↓	↑	Ribulose biphosphate carboxylase large chain RuBisCO large subunit-binding protein subunit alpha isoform 2	↓ ↑ ↑ ↓	
		Quinone oxidoreductase-like protein isoform 1	↓	↑	RuBisCO activase A (2)	↓ ↑/↓	
		Plastocyanin	↑	↓	Ribulose-phosphate 3-epimerase, chloroplastic Carbonic anhydrase (2) Transketolase	↓ ↓/↑ ↓ ↑	
<i>Kandelia candel</i> Isolated chloroplast MALDI-TOF/TOF-MS	NaCl 500 mM 0,3, 6 days	Oxygen evolving enhancer protein 1 precursor	NaCl (3 days) ↑	NaCl (6 days) –	RuBisCO subunit binding-protein beta subunit	NaCl (3 days) ↑ NaCl (6 days) ↓	Wang et al. (2015)
		Photosynthetic water oxidation complex 33 kDa subunit precursor	↑	–	RuBisCO activase (3)	↑ ↑/–	
		Oxygen evolving enhancer protein 2	↑	↑	Phosphoglycerate kinase (3)	↑ ↓/–	
		Chloroplast Rieske-type ion-sulfur protein	↑	–	Sedoheptulose-1,7-bisphosphatase	↑ –	
		Chloroplast manganese stabilizing protein	↑	–	Triosephosphate isomerase (2)	↑ –	
		ATP synthase CF1 alpha subunit (2)	↑	↓			
		ATP synthase beta subunit	↑	–			
<i>Kandelia candel</i> Leaf MALDI-TOF-TOF/MS	NaCl 150 (control), 300, 450 and 600 mM NaCl for 3 days	Chlorophyll a–b binding protein 2	300–450 mM ↑	600 mM ↓	RuBisCO large subunit-binding protein subunit beta	300–450 mM ↑ 600 mM ↑	Wang et al. (2014)
		Chlorophyll a/b binding protein	↑	↓	RuBisCO subunit binding-protein alpha subunit, ruba (2)	↑ ↑	
		Oxygen evolving enhancer protein 2	↑	↓	RuBisCO large subunit (2) Transketolase (3)	↑ ↑ ↑ ↑	

(Continued)

Table 1. (Continued)

Species and proteomic approach	Salt treatment	Photochemical proteins in response to NaCl			Biochemical proteins in response to NaCl			Reference		
		200 mM	400 mM	600 mM	200 mM	400 mM	600 mM			
<i>Kandelia candel</i> Isolated chloroplast iTRAQ	NaCl 0 (control), 200, 400 or 600 mM for 3 days	Oxygen evolving enhancer protein 1,2	↑	↑	↑	Ribulose bisphosphate carboxylase small chain	–	↓	↓	L.X.Wang et al. (2013)
		Light-harvesting complex II protein Lhcb3,4,6	↑	↑	↑	Ribulose 1,5-bisphosphate carboxylase large subunit (4)	–/↑/↓	–/↓	↓	
		Photosystem II polypeptide 10 kDa	↑	↑	↑	Phosphoglycerate kinase (4)	–/↑	↓	↓	
		Photosystem II 5 kDa protein	–	–	↑	Glyceraldehyde 3-phosphate dehydrogenase	–	–	↓	
		Photosynthetic water oxidation complex 33 kDa subunit	↑	↑	↑	Triosephosphate isomerase	–	↑	↑	
		Chloroplast PsbO4 (2)	↑	↑	↑	Phosphoribulokinase	–	↓	↓	
		33 kDa subunit of oxygen evolving system of photosystem II (2)	↑	↑	↑					
		Chlorophyll a/b binding protein type II	↑	↑	↑					
		Cytochrome b6-f complex iron–sulfur subunit	↑/–	↑	↑					
		Photosystem I reaction center subunit III (2)	↑	↑	↑					
		Photosystem I P700 chlorophyll a apoprotein A1 (2)	↑	↑	↑/–					
		Chlorophyll a/b binding protein	↑	↑	↑					
		ATP synthase subunit beta	↑	↑	↑					
		Ferredoxin-NADP reductase	↑	↑	↑					
		NAD(P)H-quinone oxidoreductase subunit J	↑	↑	↑					
		<i>Robinia pseudoacacia</i> Diploid MALDI-TOF-MS	NaCl 500 mM for 15 days	Photosystem II protein 33 kDa	↑	↑		RuBisCO large subunit (20)	↓/↑	
Polypeptide of the oxygen evolving complex of photosystem II	↓			↓		Ribulose-bisphosphate carboxylase (2)	↓	↓		
ATP synthase CF1 alpha subunit	↑			–		Ribulose-bisphosphate carboxylase oxygenase	↑	↑		
ATP synthase beta subunit	↑			–						
<i>Robinia pseudoacacia</i>	NaCl 500 mM for 15 days	NaCl (5 days)	NaCl (10 days)		NaCl (5 days)	NaCl (10 days)				

(Continued)

Table 1. (Continued)

Species and proteomic approach	Salt treatment	Photochemical proteins in response to NaCl	Biochemical proteins in response to NaCl	Reference
Tetraploid MALDI-TOF-MS		ATP synthase CF1 alpha subunit (2) ↑	RuBisCO large subunit(17) ↑/↓	↑/↓
<i>Bruguiera gymnorhiza</i> ion-trap microelectrospray MS	NaCl concentrations (0, 200 and 500 mM) for 45 days		RuBisCO activase (3) ↑/↓ Phosphoribulokinase ↑ Rubisco subunit binding-protein beta subunit ↓ RuBisCO activase alpha 2 ↑ RuBisCO activase, chloroplast precursor ↑	500 mM ↓ ↓ ↓ ↓ ↓ ↓ ↓

MALDI-TOF/TOF-MS, matrix-assisted laser desorption ionization/time-of-flight/time-of-flight mass spectrometry; iTRAQ, isobaric tagging for relative and absolute quantitation. SNP, sodium nitroprus-

increased levels of this protein have also been seen in chloroplasts (Wang et al. 2015) and *Robinia pseudoacacia* leaves (Z. Wang et al. 2013) (Table 1). Exposure to high levels of NaCl (600 mM) decreased the concentrations of chlorophyll a/b binding proteins and the oxygen evolving enhancer protein, while these proteins increased under a weaker NaCl treatment (300–450 mM) where A_{net} was not greatly reduced (Wang et al. 2014) (Table 1). Taken together, these proteomic profiling results confirm that changes in photosynthesis are associated with changes in the abundance of proteins involved in the light reactions under high salt conditions.

The biochemical limitation of photosynthesis by salt stress has been attributed to reduced efficiencies of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) carboxylation, limited ribulose-1,5-bisphosphate regeneration and decreased triose-phosphate utilization (TPU) (Brugnoli and Lauteri 1991, Pérez-López et al. 2012). Maximum RuBisCO carboxylation rates, potential electron transport rates and TPU can be assessed from the responses of A_{net} to changes in intercellular CO_2 concentrations (C_i), i.e., A/C_i curves (Farquhar et al. 1980, Farquhar and Sharkey 1982, Sharkey et al. 2007). Furthermore, stomatal (L_s) and non-stomatal (L_n) limitations to photosynthesis can also be calculated from the A/C_i curve (Steduto et al. 2000, Erel et al. 2015). However, objections to using A/C_i curve-based calculations of L_n have been raised since patchy stomatal closure under salt stress conditions leads to an overestimation of C_i (Flanagan and Jefferies 1989, Brugnoli and Lauteri 1991). In addition, salt stress may increase cell wall thickness, which reduces CO_2 diffusion to the chloroplast (Delfine et al. 1998). Centritto et al. (2003) suggested that salt stress affects stomatal conductance and mesophyll conductance to CO_2 but not the biochemical capacity to assimilate CO_2 . Recently, studies using SDS-PAGE and immunoblotting techniques have showed molecular evidence for biochemical limitations of photosynthesis under salt stress. High salinity reduced the relative expression of selected chloroplast proteins, i.e., RuBisCO large subunit, the D1 protein of the PSII reaction center complex (PsbA), PSII manganese-stabilizing protein of the oxygen evolving complex (PsbO) and subunit D of the photosynthetic electron transport protein (Cytb₆f complex, PetD) (Asrar et al. 2017). However, it is unclear whether other photosynthetic proteins are inhibited by salinity, besides these selected chloroplast proteins. In contrast to the more targeted approaches described above, the proteomics approach used by Shen et al. (2018) in this issue of *Tree Physiology* can screen broadly for biochemical limitations of photosynthesis in trees exposed to high salt concentrations. High salinity (400 mM for 30 days) decreased the abundance of a number of proteins involved in the Calvin-Benson cycle, including the RuBisCO large subunit, RuBisCO activase and transketolase (Table 1, Shen et al. 2018). The work of Shen et al. (2018) confirms findings from other studies that have looked into particular aspects of the effects of salt exposure on photosynthetic physiology. Reductions in RuBisCO and RuBisCO activase levels have

been found in other woody species treated with different salt treatments, such as *Bruguiera gymnorrhiza* (Zhu et al. 2012) and *R. pseudoacacia* (Z.Wang et al. 2013) (Table 1). In *K. candel*, salt stress caused decreases in RuBisCO concentrations in isolated chloroplasts (Wang et al. 2013, 2015), although these proteins were unchanged or even elevated in analyses of the whole-leaf proteome (Wang et al. 2014) (Table 1). Reductions in these key photosynthetic proteins will lead to decreases in carbon fixation in the salt-stressed trees (Kurek et al. 2007, Lu et al. 2009, Lv et al. 2016). In keeping with this conclusion, the photosynthetic proteome of tetraploid Black Locust is less negatively impacted by salt stress than that of diploid plants, correlating with a smaller inhibition of photosynthesis in the tetraploids (Z.Wang et al. 2013) (Table 1). Indeed, the increase of A_{net} in *B. gymnorrhiza* grown under a 200 mM NaCl treatment might be due to up-regulation of RuBisCO activase levels, which were suppressed by higher NaCl concentrations of 500 mM (Zhu et al. 2012) (Table 1).

A proteomics approach, such as that utilized by Shen et al. (2018), can screen for both photochemical and biochemical limitations that limit photosynthesis in salt-stressed trees supplemented without or with SNP (Table 1). More importantly, proteomic tools can help unravel the relative importance of photochemical and biochemical limitations in suppressing photosynthesis under saline conditions. For example, in *K. candel* leaves, NaCl reduced the levels of chlorophyll a/b binding proteins and an oxygen evolving enhancer protein, but stimulated concentrations of biochemical proteins involved in the Calvin-Benson cycle, (e.g., the RuBisCO large subunit, RuBisCO large subunit-binding proteins, transketolase) (Wang et al. 2014) (Table 1). This suggests that photochemical limitations play a relatively important role in reducing photosynthesis under salt stress. Therefore, proteomic profiling has the potential to discriminate the relative importance of photochemical and biochemical limitations in salinized plants, helping us understand the mechanistic basis for suppressed CO₂ uptake under salt stress, and guiding efforts to generate more salt tolerant plants.

Conflict of interest

None declared.

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