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Opinion Piece

Populus euphratica: an incompatible host for biotrophic pathogens?

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INTRODUCTION

More than 20 years ago, a group of pioneer studies stressed the importance of high temperature, light and photosynthetic electron flow in plants, demonstrating that exposure to high temperatures offers an advantage for plant acclimation to high light intensity (Havaux, 1993). The balance between light capture and light use in photosynthesis is influenced by environmental fluctuations, and has been suggested to be a key driver of convergent regulatory mechanisms by reactive oxygen species (ROS) and related redox systems in biotic and abiotic interactions between plants and their environment (Foyer and Noctor, 2009).

A plastoquinone (PQ) regulon has been described in Arabidopsis (Mühlenbock *et al.*, 2008) that includes markers for light acclimation, pathogen defence, drought and low-temperature responses, as well as genes regulated by ethylene (ET), ROS, glutathione, salicylic acid (SA), abscisic acid (ABA), sugars and auxin signalling. A putative regulator of RuBisCO has also been found in the PQ regulon, together with other nuclear-encoded chloroplastidial genes regulated by sugars and light signalling. The existence of a PQ regulon represents an integration mechanism for redox homeostasis during disturbances of photophosphorylation reactions.

High temperature modulates photosynthesis, both biochemical and photophosphorylation reactions. The question of which mechanism is the first to sense high-temperature effects and to regulate the other is a matter of debate, but it can be argued that changes in the trans-thylakoid potential and PQ reduction state are strong candidates for the master regulators of high-temperature effects. If high temperature is indeed primarily perceived by the PQ redox state, light reactions would be the first mechanisms to be affected and light acclimation would be mandatory in the short term.

High temperature induces an excess excitation energy (EEE) in photophosphorylation reactions, as it disturbs thylakoid membrane and photosystem stability and induces the expression of genes in the PQ regulon (Mühlenbock *et al.*, 2008). The Arabidopsis response to EEE is regulated by *LSD1* (*LESION SIMULATING DISEASE1*), *PAD4* (*PHYTOALEXIN DEFICIENT4*) and *EDS1* (*ENHANCED DISEASE SUSCEPTIBILITY1*), which have been proposed to represent a ROS/ET homeostatic switch to control acclimatory and pathogen defence mechanisms (Mühlenbock *et al.*, 2008). If a plant is unable to dissipate EEE through the various mechanisms available to it, it initiates programmed cell death (PCD), which is dependent on SA signalling, which, in turn, is positively regulated by *EDS1* and *PAD4*. Within the crosstalk between all of these processes is the redox poise of the PQ pool, which contributes to the EEE response or to the development of PCD.

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POPULUS EUPHRATICA

Populus euphratica Olivier is a woody plant species highly resistant to high temperature, salinity and light intensity, also called Euphrates poplar. The idea that *P. euphratica* is strongly adapted to both abiotic and biotic stress was first proposed more than 10 years ago (Brosché *et al.*, 2005). Despite this proposal, the crosstalk between abiotic and biotic stress responses or signalling remains to be reported in *P. euphratica*, as most studies on this species have focused on abiotic stress.

A comparison between *Picea* and *Populus* has shown a long-term down-regulation of genes related to photophosphorylation reactions, the carbon reduction cycle and pigment synthesis, regardless of the type of biotic stress, with a parallel up-regulation of genes coding for jasmonic acid (JA) biosynthesis and responsive to SA and ET in Populus. This points to a role of photosynthesis genes in the defence response. In the case of *P. euphratica*, a comparison of its response to salt stress with that of another species, *P. tremula*, has shown the constitutive expression of defence genes in *P. euphratica* following abiotic stress, with few changes in overall gene expression. Moreover, with a combination of abiotic stresses, such as heat, salt and drought, most of the expression sequence tags up-regulated in *P. euphratica* are related not only to abiotic, but also biotic stresses. However, this resistance to biotic stress is not applicable to all pathogens, as *P. euphratica* is a compatible host for the necrotrophic fungus *Alternaria alternata* (Osdaghi and Kakavandi, 2015).

The oldest *P. euphratica* trees are found along the Tarim River, which is located in the Taklimakan–Gobi Desert, a typical temperate arid desert. These forests of Euphrates poplar of the Taklimakan–Gobi Desert Biogeographic Province were submitted to a

UNESCO nomination in 2010 for consideration by the World Heritage Convention as being of possible Outstanding Universal Value for Humanity.

In their natural desert environment and during their active growth season, *P. euphratica* trees show high transpiration rates during the spring and summer, preventing leaf burnout, and develop a positive correlation between photosynthetic rate and irradiation intensity, with a daily double peak of photosynthesis, avoiding the hours of maximum light intensity. At high temperature in natural stands, these trees show a strong decrease in photosynthetic rate, with transpiration maintained through open stomata; the impact of high temperature increases with the depth of the groundwater level, and therefore with drought stress severity (Zhou *et al.*, 2010). It has been shown that, even when submitted to combined heat and drought stresses, *P. euphratica* primarily shows a tolerance to high temperature, increasing transpiration through unequally open stomata, with dissipation of overheating. Drought stress resistance is accomplished afterwards by osmotic adjustment or stomata limitation (Zhou *et al.*, 2010). *Populus euphratica* therefore seems to be adapted to inhibit stomatal closure under mild and moderate drought stress, maintaining a relatively high stomatal conductance whilst adjusting the photosynthetic rate, although severe drought stress leads, ultimately, to stomatal closure (Tang *et al.*, 2013).

How are these events compatible with the fact that *P. euphratica* depends on a high transpiration rate for leaf cooling and photosynthesis adjustment?

REDOX POISE AND PHOTOPHOSPHORYLATION REACTIONS

As the main consequence of high temperature in photosynthesis is oxidative stress, especially in photophosphorylation reactions, it can be argued that the ability to cope with oxidative stress can help to maintain active photosynthesis at high temperature, even when combined with drought stress. High temperature imposes a rate of decrease in photophosphorylation reactions and a redox imbalance caused by EEE in thylakoid membranes. This leads to an over-reduction of the PQ pool into plastoquinol (PQH_2), which can be overcome by mechanisms of EEE dissipation. This is the signal to activate the light-harvesting complex II (LHCII) kinase (STN7) and to initiate state transition, when the linear electron flow (LEF) through photosystem II (PSII) is partially substituted by cyclic electron flow (CEF) through photosystem I (PSI) in grana margins to avoid PSII damage. A strong decrease in the transthylakoid membrane electric potential (ΔpH) also occurs in parallel as a result of electrolyte leakage. ΔpH is a key regulator of photophosphorylation reactions and its decrease leads to difficulties in the maintenance of the electron transport rate, and hence contributes to PQ over-reduction and EEE build-up, which is dissipated by non-photochemical quenching (NPQ) mechanisms.

One of these mechanisms is the xanthophyll cycle, where violaxanthin (VIO) is de-epoxidized to zeaxanthin (ZEA) through the action of VIO de-epoxidase (VDE). The conversion of ZEA back into VIO is catalysed by ZEA epoxidase (ZE), requiring the concomitant oxidation of ascorbate into de-hydroascorbate. Both enzymes are dependent on the thylakoid ΔpH, but the lumenal pH has a large effect on VDE activity, hence resulting in ZEA overaccumulation despite the activity of ZE (Zhang *et al.*, 2011). VIO has been demonstrated recently to be a sufficient source and possibly the major precursor for ABA biosynthesis *in vivo* as a result of its sequential conversion into neoxanthin. However, conditions that increase VDE activity may lead to a decrease in ABA biosynthesis; therefore, ABA biosynthesis implies higher ZE activity and, in contrast, the enhanced VDE activity promoted by high temperatures seems to antagonize ABA accumulation, which most certainly contributes to the influence of ABA on the stomatal aperture. ZEA is generated from β-carotene hydroxylation, which is dependent on the carbon flux through the chloroplastidial methylerythrithol phosphate (MEP) pathway. Therefore, its accumulation is not strictly dependent on VIO; instead, VIO abundance is dependent on ZEA conversion, but, as VDE activity is increased by electrolyte leakage at high temperature, the ZEA pool increases, whereas the VIO pool decreases, leaving less VIO to be ultimately converted into ABA. However, ABA and SA biosynthesis have been found to increase at high temperature in *Pinus radiata* (Escandón *et al.*, 2016), and moderate heat stress has been found to have a positive impact on net photosynthesis and growth. So, how are the xanthophyll cycle, ABA and SA related in acclimation to high temperature?

CONTRIBUTION OF THE MEP PATHWAY AT HIGH TEMPERATURE

The MEP flux rate increases with temperature, especially in isoprene-emitting species, such as poplar. Most genes regulating MEP have light-regulated circadian elements with putative heat-shock promoter elements upstream of their transcription start site, highlighting the relationship between light use and temperature modulation. The MEP pathway exerts an important influence over the ability of photosynthetic cells to overcome the oxidative stress imposed by high temperature, whilst maintaining active photosynthesis. Biochemical reactions suffer the impact of energetic constraints, the decrease in RuBisCO activity and the decrease in the Calvin cycle flux rate. The supply of carbon to sink cells becomes dependent on the hydrolysis of stored sucrose, and activated glycolysis regenerates reducing equivalents and increases cytosolic pools of glyceraldehyde-3-phosphate (G3P) and pyruvate (Pyr), which feed MEP at high temperature.

The MEP pathway is dependent on the conversion of G3P and Pyr into 1-deoxy-D-xylulose-5-phosphate (DOXP), and is highly regulated by the feedback inhibition of isopentenyl diphosphate

(IPP) and dimethylallyl diphosphate (DMAPP) pools on DOXP synthase (DXS) activity, as both of these molecules compete with thiamine pyrophosphate (TPP) for DXS binding. Therefore, IPP and DMAPP pools must be kept under tight control, a function possibly performed by isoprene-emitting plant species, such as *Populus* and *Quercus*, when they emit this volatile. Isoprene is synthesized from IPP (obtained from DMAPP) by isoprene synthase (IspS), which is extremely sensitive to pH changes. It has been shown that a small portion of the DMAPP pool, possibly cytosolic, regulates isoprene emission in *Populus*, but DMAPP, together with (*E*)−4-hydroxy-3-methyl-but-2-enyl diphosphate (HMBDP), is also converted into cytokinins (CKs) by isopentenyl transferase (IPT). Isoprenoid CKs are therefore mainly synthesized through MEP, which has an almost exclusive contribution to the synthesis of isopentenyl adenine and its hydroxylated derivative zeatin (Kasahara *et al.*, 2004), the only two active CK forms in plants, although many conjugates can be formed as possible storage compounds.

Although CKs are up-regulated and have a positive effect on photosynthesis under moderate abiotic stress, their exogenous application can increase the stomatal aperture and transpiration in many plants (Pospíšilová *et al.*, 2005), because the increase in active CKs above a certain concentration threshold leads to decreased sensitivity to free ABA. CK abundance levels are down-regulated under more severe stresses, with increasing ABA sensitivity; leaf content and compositional changes of ABA and CKs on abiotic stress, and interactions between ABA and CKs, are species specific (Pospíšilová *et al.*, 2005). The overexpression of IPT in plants, and hence CK biosynthesis, has been correlated with an increased resistance to pathogens, and the modulation of CK levels and their signal transduction has been found to affect both ABA-dependent and ABA-independent pathways, leading to plant adaptation to adverse conditions and to CK use to improve crop fitness (Zalabák *et al.*, 2011).

As it plays a crucial role in *P. euphratica* to keep high-temperature effects under control at the expense of a lower water use efficiency, and with a high transpiration rate, stomatal aperture must be regulated by a balance between CKs and ABA. Moreover, *P. euphratica* is an isoprene-emitting species and therefore the MEP pathway plays a special role in this process. So, what happens?

The effects of moderate heat stress on the leaf proteomes of *P. euphratica* plantlets in hydroponic culture were reported 10 years ago (Ferreira *et al.*, 2006) and, very recently, other authors have replicated some aspects of this experiment with *Pi. radiata*, but with a much diversified and interesting analytical test (Escandón *et al.*, 2016). Although *Pi. radiata* and *P. euphratica* have very different physiologies with regard to secondary metabolism, the basic hormonal regulation of the tree system most certainly applies to both. Moderate heat stress (40 °C) imposed on *Pi. radiata*, with a concomitant absence of drought and light stress, has been shown to induce a short-term transient increase in ABA abundance in parallel with SA abundance. In turn, the long-term acclimation of *Pi. radiata* involves a greater abundance of CK active forms.

ABA accumulation in *Pi. radiata* is most probably a result of an increased MEP flux rate, and is simultaneous to SA accumulation and later CK accumulation. When the free ABA concentration increases, it can lead to overall stomatal closure, which is the general consequence of strong drought stress in plants, but the interference of CKs leads to a decrease in ABA sensitivity, leading to a lesser influence on stomatal closure. This may be one of the reasons why *P. euphratica* is able to maintain a high transpiration and photosynthesis rate under high-temperature stress or under combined moderate heat and drought stress, implying a positive effect on the resistance to these abiotic stresses through SA signalling. Moreover, in addition to reducing ABA's sensitivity, CKs suffer inhibition of their activity by SA when the CK abundance reaches a certain level, because of concomitant SA accumulation.

ABA/SA CONTRIBUTIONS TO ABIOTIC AND BIOTIC SIGNALLING CROSSTALK

When ABA levels decrease, ascorbate levels also decrease, with promotion of the conversion of reduced glutathione (GSH) into oxidized glutathione (GSSG) through the ascorbate–glutathione cycle. Therefore, increased ABA abundance contributes to an increased ascorbate pool, and therefore to a greater reducing power, even if ABA does not exert its hormonal influence to a great extent. The balance between ABA anabolism and catabolism is subjected to a fine-tuning regulation of physiologically active ABA levels, and ABA catabolism is accomplished by ABA 8′-hydroxylases, encoded by the *CYP707A* family in Arabidopsis. Their expression increases on salt, osmotic and drought stress, and *CYP707A1* has been found to be highly expressed in *P. euphratica* exposed to drought stress alone, together with protein phosphatase 2C (PP2C), which is considered to be a negative regulator of ABA signalling (Tang *et al.*, 2013). *CYP*s have very low expression in optimal conditions, but they have been suggested to be involved in the control of signalling compounds by modification and conjugation (Foyer and Noctor, 2009). Therefore, on drought stress, the active ABA levels of *P. euphratica* would have a greater influence on stomatal opening. However, a low CK synthesis rate, driven by a low MEP flux rate, cannot decrease ABA's sensitivity and this may be counterbalanced by the activity of ABA 8′-hydroxylases. This fine-tuning of physiologically active ABA does not control ABA abundance, as ABA can be inactivated when binding to sugars. Therefore, active ABA effects are regulated by the plant's sensitivity, mediated by CKs, and by its catabolism through *CYP* expression.

The *CYP*s, encoding ABA 8′-hydroxylases, are true H_2O_2-responsive genes, together with the genes encoding UDP-glucosyl

transferases and glutathione transferases (GSTs). Glutathione reductases play an important role in the maintenance of GSH levels during the light phase. The GSH pool regulates SA involved in the biotic stress response at several levels in Arabidopsis, and increased accumulation of GSH in *Nicotiana tabacum* leads to enhanced expression of *NPR1* (*NON-PATHOGENESIS RELATED1*)-dependent genes, such as *PR1* (*PATHOGENESIS RELATED1*). NPR1 is the only redox-active protein of its type described to date (NUDIX family) and, when reduced by thioredoxins (Trxs) on increased SA, it enters the nucleus and interacts with TGA transcription factors (proteins binding to variants of the palindromic sequence TGAC/GTCA) leading to the expression of PR proteins. The Trxs have been shown to be up-regulated on heat stress in *P. euphratica* (Ferreira *et al.*, 2006), and have been linked to the ability of plant cells to cope with the oxidative stress imposed by heat stress. They are reduced via PSI and via ferredoxin–Trx reductase in illuminated leaves, providing a link between photophosphorylation and enzyme activation on photosynthetic carbon fixation (Kangasjärvi *et al.*, 2012).

The role of SA signalling in plants is not limited to light acclimation and the regulation of redox homeostasis, but also influences defence against pathogens (Mateo *et al.*, 2006). On the one hand, abiotic stress resistance is built up at the expense of the positive effects exerted by SA over PSII stability and the RuBisCO activation state during heat stress, which is reached rapidly in SA-pre-treated plants. Local tissue abiotic resistance signals may be accompanied by whole-plant signalling (systemic acquired acclimation) and can even influence neighbouring plants through plant-to-plant SA signalling. On the other hand, the catabolism of ABA and glutathione transferase (GT) expression respond to oxidative stress and regulate the involvement of SA signalling, through NPR1 activity, in pathogen defence, as mentioned above. More recently, Arabidopsis hybrids with increased expression of key SA biosynthesis-related genes prior to pathogen exposure have been found to present increased resistance against the biotrophic pathogen *Pseudomonas syringae* pv. *tomato* DC3000 (Yang *et al.*, 2015). SA biosynthesis was the sole factor contributing to the heterosis with regard to biotrophic defence, as hybrids expressed SA biosynthesis-related genes more quickly and at higher levels, showing increased acetylation of histone 3 (H3) in their promoter regions. Although the mechanisms of gene priming are not well understood, this H3 acetylation could work as a memory of the primary treatment, which would amplify the expression of these genes in subsequent stress exposures (Yang *et al.*, 2015). The treatment of Arabidopsis with high levels of CKs has been shown to prime SA-dependent defence responses, whereas low levels of CKs led to susceptibility to a biotrophic virulent oomycete (Argueso *et al.*, 2012). The effect of high CK concentration was largely dependent on SA biosynthesis, suggesting that CKs act upstream of SA during the activation of defences. Therefore, the hormone concentration during the responses of plants to pathogens seems to be an important aspect to be considered. Hormonal balance might depend on a modulation resulting from the acclimation of plants to abiotic factors.

PATHOGEN MANIPULATION OF PLANT CELL PHYSIOLOGY

Several plant pathogens aim to manipulate plant physiology to allow the completion of their life cycles. The plant-driven down-regulation of photosynthesis, and the shift to non-assimilatory metabolism, is the plant response to infection by several types of pathogen (Kangasjärvi *et al.*, 2012, and references therein). Biotrophic and hemibiotrophic pathogens, in particular, prefer to maintain plant cells alive in order to drain their resources, by enhancing cell endurance (Seifi *et al.*, 2013). Therefore, they secrete protein effectors that aim to control chloroplast metabolism in order to inhibit transcriptional retrograde signalling: *Pseudomonas syringae* destroys thylakoid stacking and inhibits SA biosynthesis; *P. syringae* pv. *syringae* secretes syringolin A that interferes with proteasome activity and inhibits NPR1 reduction by Trxs and consequent signalling towards SA biosynthesis; and *Xanthomonas campestris* secretes XopJ that functions in the same way as syringolin A (Seifi *et al.*, 2013).

Pathogens induce a reprogramming of plant cell metabolism towards the activation of photorespiration (Kangasjärvi *et al.*, 2012), and hence to nitrogen reutilization [via the glutamine synthetase (GS) and glutamine-oxoglutarate aminotransferase (GOGAT) cycle], ROS scavenging and tricarboxylic acid (TCA) cycle replenishment (Seifi *et al.*, 2013). As amino acids are generally used as nutritional sources by pathogens, especially fungi, a source of amino acids is important to support the initial stages of pathogen nutrition on infection. Photorespiration offers a good source of glycine, serine, glutamate and glutamine. In addition to having been more recently described as the SA receptor in plant cells, NPR1 has also been associated with the negative regulation of photorespiratory gene expression, as the Arabidopsis *npr1* mutant, with a dysfunctional NPR1, is hypersusceptible to *Pseudomonas* infection and, in parallel, shows a photorespiratory gene expression higher than that of the wild-type, which is maintained during pathogen infection (Sørhagen *et al.*, 2013).

Several studies have demonstrated the importance of photorespiration to pathogen defence (Kangasjärvi *et al.*, 2012, and references therein), showing that higher temperatures favour an increased photorespiratory rate even when the irradiance remains constant. This could be one of the reasons why high temperature generally increases plant susceptibility to pathogen attack. However, plant acclimation to high temperatures could increase their ability to better cope with new heat stress events and decrease their susceptibility to pathogen attack, namely to biotrophic and hemibiotrophic pathogens.

CONCLUSION

Populus euphratica is a member of the Salicaceae family and its bark is rich in SA, most probably conjugated with glucose. This constitutive large pool of SA in *P. euphratica* tissues could allow dominant and fine-tuned SA signalling, which has been described in *Populus* sp., involving a reprogramming of carbon partitioning during stress, compatible with constitutive chemical defence and sustained growth.

Studies on plant–pathogen interactions could benefit from the identification of pathogen compatibility factors and/or host determinants of defence, as these should add important mechanistic insights to these interactions. Therefore, *P. euphratica*, and even its closest Western relative *Salix*, should receive greater attention in the future as they are most probably incompatible hosts to most, if not all, biotrophic pathogens. This could be a result of their continuous and successful resistance to the oxidative stress imposed by several abiotic stresses and to which these species seem to be extensively acclimated.

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