

SHORT COMMUNICATION



## Is ABA the exogenous vector of interplant drought cuing?

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### ABSTRACT

We have recently demonstrated that root cuing from drought-stressed plants increased the survival time of neighboring plants under drought, which came at performance costs under benign conditions. The involvement of abscisic acid (ABA) was implicated from additional experiments in which interplant drought cuing was greatly diminished in ABA-deficient plants. Here, we tested the hypothesis that ABA is the exogenous vector of interplant drought cuing. *Pisum sativum* plants were grown in rows of three split-root plants. One of the roots of the first plant was subjected to either drought of benign conditions in one rooting vial, while its other root shared its rooting vial with one of the roots of an unstressed neighbor, which in turn shared its other rooting vial with an additional unstressed neighbor. One hour after subjecting one of the roots of the first plant to drought, ABA concentrations were 106% and 145% higher around its other root and the roots of its unstressed neighbor, compared to their respective unstressed controls; however, the absolute concentrations of ABA found in the rooting media were substantially low. The results may indicate that despite its involvement in interplant drought and the commonly observed exchange of ABA between drought-stressed plants and their rhizospheres, ABA is not directly involved in exogenous interplant drought cuing. However, previous studies have shown that even minute concentrations of ABA in the rhizosphere can prevent ABA leakage from roots and thus to significantly increase endogenous ABA levels. In addition, under drought conditions, plants tend to accumulate ABA, which could markedly increase internal ABA concentrations over time and ABA concentrations in close proximity to the root surface might be significantly greater than estimated from entire rooting volumes. Finally, phaseic acid, an ABA degradation product, is known to activate various ABA receptors, which could enhance plant drought tolerance. It is thus feasible that while the role of ABA is limited, its more stable degradation products could play a significant role in interplant drought cuing. Our preliminary findings call for an extensive investigation into the identity and modes of operation of the exogenous vectors of interplant drought cuing.

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## Introduction

Adaptive plastic responses require the integration of fitness-relevant information.<sup>1,2</sup> While most animals perceive and respond to environmental information using intricate nervous systems, adaptive responsiveness, elaborate decision-making, learning and memory are ubiquitous amongst CNS-less organisms, including archaea,<sup>3</sup> sponges,<sup>4</sup> fungi,<sup>5</sup> bacteria,<sup>6</sup> slime molds,<sup>7</sup> plants,<sup>8–10</sup> and even viruses.<sup>11</sup>

The adaptive value of plastic responses crucially depends on a tight and reliable correlation between the modified phenotype and the conditions under which it is expected to operate. Because plastic responses require time, it must pertain to forthcoming rather than to present conditions, therefore fostering significant advantages to bearers of sensory systems that enable anticipatory responses.<sup>12,13</sup> In plants, preemptive responses are based on the perception of early cues and signals indicatory of forthcoming drought,<sup>14</sup> salinity,<sup>15</sup> nutrient availability,<sup>16,17</sup> competition,<sup>12,18</sup> and neighbor proximity.<sup>19–22</sup> Importantly, early indications of imminent risks and challenges often come from already affected neighboring plants, such as in the cases of herbivory,<sup>23</sup> pathogen attack<sup>24</sup> or drought.<sup>25</sup>

We have previously demonstrated that unstressed plants close their stomata in response to direct or relayed (via additional unstressed plants) cueing from drought-stressed neighbors.<sup>26,27</sup> In a recent study, we found that interplant drought cuing increased the survival of target *Stenotaphrum secundatum* plants under drought, which came at a cost of lowered performance of the communicated plants under benign conditions. Further, we found that interplant drought cuing was greatly reduced in ABA-deficient plants.<sup>25</sup> Our previous findings have demonstrated that interplant drought communication in *Pisum sativum* was attained via root cuing, suggesting that the involved vectors are emitted from the roots of drought-inflicted plants and perceived by the roots of unstressed neighboring plants.<sup>26</sup> Abscisic acid (ABA) is a promising candidate vector that satisfies this mode of communication. It is produced in most plant tissues and is involved in the induction of resistance and tolerance to drought and other stresses.<sup>28</sup> Previous studies have demonstrated that in some legumes and grasses, drought may cause ABA leakage from the roots.<sup>29,30</sup> Additional studies have shown that exogenous ABA can be taken up by roots and elicit stress responses in receiving plants.<sup>31,32</sup> Accordingly, we

hypothesized that ABA is the exogenous vector of interplant drought cuing.

In the present study, we separately analyzed ABA content in the rhizospheres of drought-stressed plants and their unstressed neighbors. Based on previous studies (e.g.<sup>33</sup>), we expected to find higher concentrations of ABA in the rhizosphere of drought-inflicted plants and their unstressed neighbors, compared to unstressed or uncued controls.

## Materials and methods

### Plant material and experimental setup

*Pisum sativum* was chosen as a model plant because of the existing knowledge on the involvement of ABA in its responses to drought stresses, and the ease of its handling under variable growth conditions (e.g.<sup>34</sup>).

ABA concentrations were estimated in root leachates separately collected from either drought-stressed or unstressed plants and their unstressed neighbors. Testing for the effects of drought cuing required that specific induced plants (IND) experience drought or benign conditions, while their neighboring target plants (T1, T2) would only experience root cuing from the IND plants (Figure 1a). This was achieved by using triplets of split-root *P. sativum* cv. Dunn plants planted in rows of four vials (Figure 1a).

The experiment started by growing plants with two equal roots following removal of the tip of the seminal root ('split-root plants'<sup>27</sup>). Three days from germination, the seminal root was severed 2 mm below the hypocotyl and the plants were replanted in damp vermiculite. Seven days from germination, the stump of the seminal root typically regenerated three lateral

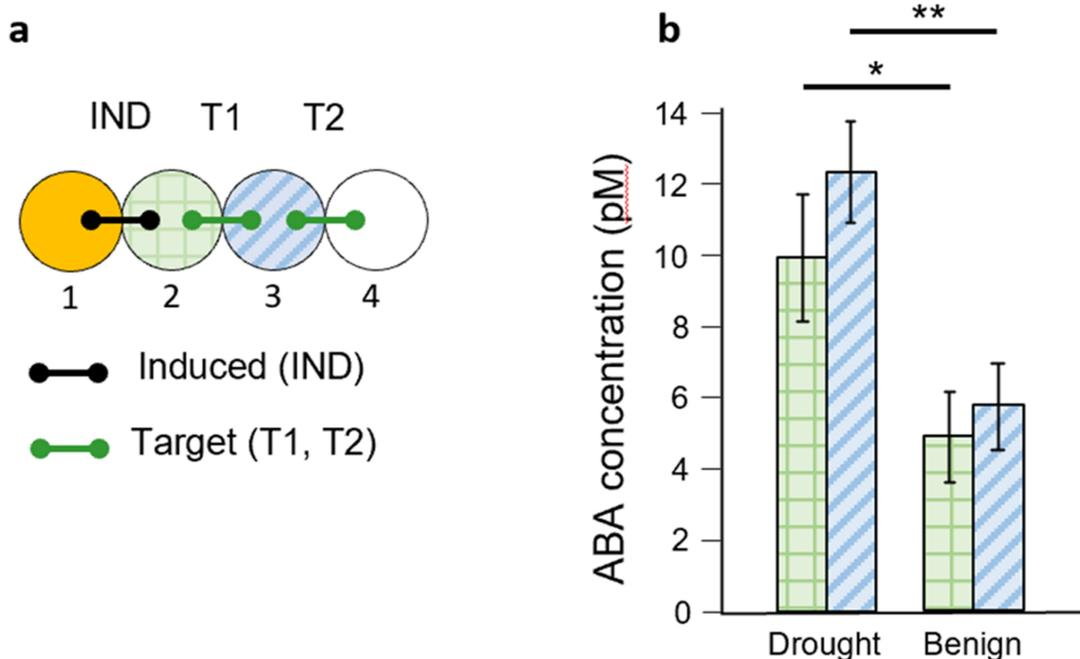
roots. After severing one of the roots, plants with two 25–30 mm long roots were grown in an aqueous medium in 50 ml vials as described in Figure 1a. One of the roots of the IND plant (in vial 1) was subjected to either drought or benign conditions, while its other root shared vial 2 with one of the roots of its nearest unstressed neighbor (T1). The other root of T1 shared vial 3 with one of the roots of an additional unstressed target plant (T2). This configuration permitted T1 to exchange root exudates with both IND and T2 while preventing direct root cuing between IND and T2, and thus allowing to separately study the effects of direct and relayed drought cuing on T1 and T2, respectively<sup>25</sup> (Figure 1a).

The experiment was conducted in a growth chamber, at 25°C, under continuous 130  $\mu\text{E m}^{-2} \text{sec}^{-1}$  of mixed cool-white fluorescent and incandescent lights.

### Experimental protocol

Drought induction was carried out by carefully pumping the water from Vial 1 (orange; Figure 1a) using a flexible-tip syringe, and filling it with 8 g of either dry or wet mixture of 4:1 mixture of no. 1 vermiculite (Agrekal, Habonim, Israel) and bentonite (Minerco, Netanya, Israel); (VB) for 1 h. To account for handling effects, control (benign) sets were induced by filling vial 1 with a mixture of wet VB (5.5 g VB and 45 mL distilled water). Accordingly, ABA concentration in the rooting media of vials 2 and 3 reflected the effects of drought cuing rather than responses to the physical handling of the plants or the chemical components of VB.

Following the induction period, the contents of the rooting vials of stressed (IND) plants (vial 2) and of their cued unstressed neighbors (vial 3) were analyzed. The experiment



**Figure 1.** The effects of drought cuing on rhizosphere ABA concentrations. Triplets of split-root *P. sativum* plants were grown in rows as described in Figure 1 (a). One of the roots of the IND plant (pot 1, Orange) was subjected to either drought or benign conditions for one hour. ABA concentrations were analyzed in the rhizospheric solution of vial 2 (shared by drought-treated IND and its unstressed T1 neighbor, green) and vial 3 (shared by unstressed T1 and T2 plants, blue). Values are means  $\pm$  SEM of ABA concentrations in vial 2 (green) and vial 3 (blue). Significance values are for Kruskal–Wallis one-way comparisons between drought-cued plants and their controls, \*  $P < .05$ , \*\*\*  $P < .01$ ,  $n = 6$ .

was conducted with 12 biological replications, and leachates were pooled into six 100 mL technical replicates to increase metabolite concentrations in the analyzed samples. The leachate samples were lyophilized, and the dry pellets were analyzed for ABA content at the Instituto de Biología Molecular y Celular de Plantas, CSIC, Universidad Politécnica de Valencia, Spain. Individual samples were macerated in liquid nitrogen with the addition of 1.8 mL of the extraction solution (80% methanol, 1% acetic acid and 19% distilled water), following the addition of the deuterated analogue of ABA (Olchemim Ltd, Olomouc, Czech Republic) to be quantified (30  $\mu$ L of a solution containing ABA). Following, the samples were shaken for 1 h at 4°C and then centrifuged at 10000 g at 4°C for 4 min. The supernatant was removed and conditioned in a 2 mL tube for 24 h at –20°C for precipitation of proteins, and the samples were centrifuged again at 10000 g at 4°C for 4 min; the supernatant was transferred to 5 mL glass tubes, and the samples were concentrated in a rotovapor (Thermo Scientific®) for 3 h. The concentrated samples were finalized with 1 mL of 1% acetic acid, and after a rapid shaking, filtered in Oasis HLB® columns (reverse phase). ABA was recovered by applying 1 mL of 95% methanol, and the samples were dried in the rotavapor and subsequently dissolved with 150  $\mu$ L of 5% acetyl nitrile (ACN) + 1% acetic acid. Readings were retrieved from a spectrometer coupled to a UHPLC and an autosampler (Accucore RP-MS column 2.6  $\mu$ m, 50  $\times$  2.1 mm; ThermoFisher Scientific).<sup>35</sup>

### Statistical analyses

The effects of drought cuing on ABA concentrations in the rooting media of *P. sativum* under drought or drought cuing were analyzed using Kruskal–Wallis one-way ANOVAs. The statistical analyses were conducted using SYSTAT 13 (SPSS).

### Results and discussion

Drought cuing significantly affected ABA concentration in the rhizosphere of both drought-stressed plants and their unstressed neighbors. Sixty minutes following the onset of a drought treatment to one of the roots of the IND plant (vial 1, Figure 1a), ABA concentrations were 106% and 145% higher in vials 2 and 3 of the drought treatments, compared to their respective ‘benign’ controls, with a more pronounced difference in vial 3 (targets 1 and 2) than in vial 2 (IND and target 1; Figure 1b).

Under drought, plants adaptively change the amount and composition of their volatile emissions (e.g.<sup>36</sup>) and root exudates,<sup>37–39</sup> with increased concentrations of various organic acids, sugars, alkaloids and terpenoids, among others.<sup>40–42</sup> Increased root exudation has been demonstrated to help plants alleviate drought and osmotic stresses and manipulate the abundance and composition of mycorrhizal fungi and soil bacteria, some of which help plants tolerate drought and accelerate post-drought regeneration.<sup>37,41,43</sup>

In some plants, drought may also cause increased exudation of ABA from the roots.<sup>30,44,45</sup> As roots readily uptake exogenous ABA, which in turn can elicit adaptive stress responses in receiving plants,<sup>31,32</sup> our results (Figure 1b) could seemingly

support the hypothesis that ABA is the exogenous vector of interplant drought cuing. However, although both stressed IND plants and their unstressed target neighbors substantially increased ABA exudation compared to their unstressed controls, the absolute concentrations of ABA found in their rooting media were exceedingly low, ca. three orders of magnitude below the known affinity of ABA receptors.<sup>46</sup>

We have previously demonstrated that 1 h of drought stress elicited stomatal closure in both stressed *P. sativum* plants and, via a chain root cuing, in multiple neighboring plants.<sup>26,27</sup> Additionally, a recent study clearly demonstrated the involvement of ABA in interplant drought cuing.<sup>25</sup> Thus, how can we interpret the extremely low ABA concentrations found in the rooting media of the stressed plants and their unstressed neighbors (Figure 1b)? A simple sobering possibility could be that despite its involvement in interplant drought cuing and the exchange of ABA with the rhizosphere, ABA might not participate in exogenous root cuing in the studied plants and further efforts should be allocated to alternative candidate metabolites, the presence<sup>47</sup> or the exudation of which is increased under drought.<sup>45</sup> However, we posit that our preliminary findings do not negate the possibility that ABA might be directly involved in exogenous belowground interplant drought cuing for the following reasons:

- (a) Minute ABA concentrations can play a role: roots uptake and accumulate ABA over time and thus internal ABA concentrations can substantially increase over time.<sup>48</sup> In addition, even extremely low and otherwise negligible ABA concentrations (1 nM) were demonstrated to effectively prevent ABA leakage from roots and thus to significantly increase endogenous ABA levels and their adaptive effects on plant drought tolerance and resistance.<sup>49,50</sup>
- (b) Local versus mean ABA concentrations: the balance between root exudation and diffusion typically generates a radial downhill gradient of exudates around the root.<sup>51</sup> However, the analysis of exudate concentrations in entire rooting vials, as done here, necessarily reflects the mean concentration of ABA in the entire rooting volume rather than the effective ABA concentration near the root surface. Theoretically, more accurate concentrations can be mathematically modeled, but estimating the precise exudate concentrations and their functional effectiveness in multiple spatial and temporal (4D) coordinates in large rooting volumes and a vast variety of root distances and states is expected to be overwhelmingly challenging, if at all possible.
- (c) The possible role of ABA degradation products: large amounts of ABA and its catabolism products are constantly emitted into the soil following the decomposition of dead plant matter.<sup>52</sup> Interestingly, both plants and bacteria metabolize ABA to phaseic acid, dihydrophaseic acid, fulvic acids, and other metabolites, which

could take part in interplant drought cuing<sup>47</sup> Specifically, phaseic acid is known to activate various ABA receptors, which in turn could enhance plant drought tolerance.<sup>53</sup> Accordingly, it is feasible that at least under some circumstances, direct ABA cuing is limited, but ABA's degradation products could play a significant role in interplant drought cuing.

As a follow-up to this preliminary study, it would be interesting to further investigate the potential roles of ABA and its decomposition products in interplant drought cuing; however, although these metabolites seem to be suitable candidates, it is undeniably feasible that additional or totally different metabolites as well as various soil microbes are involved in the newly discovered inter-root drought cuing.

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No potential conflict of interest was reported by the author(s).

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## Author contributions

O.F. conducted the experiment, A.N. conceived the project, designed the experiment, analyzed the results and wrote the paper. Both authors read and approved the final version of the manuscript.

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