

## DOCTORAL THESIS

### Xylem-carried abscisic acid (ABA) in plant responses to soil-drying

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# **Xylem-Carried Abscisic Acid (ABA) in Plant Responses to Soil-Drying**

by

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## Abstract

Plants have evolved several mechanisms to cope with soil drying. One of the mechanisms, which has recently received much more attention, is that when plants are subjected to soil drying, shoot physiology is largely regulated by a root-derived chemical signal. The properties and function of this signal have been studied over one decade and accumulated evidence has shown that abscisic acid (ABA) is the most possible candidate of such a signal. In this study, the sources, metabolism, transport pathway, fate of the root-derived ABA and its relations to shoot physiological processes when plants are subjected to water deficit have been extensively investigated.

First of all, the method to collect xylem sap was explored. When an intact root system in a pot was pressurized at a pressure numerically equal to the absolute value of leaf water potential, the xylem flow rate at such a pressure was found to be similar to the transpiration flow rate of the whole plant. The total solute concentration (measured as osmolality) in the xylem sap was negatively related to volume flow rate, but the xylem-carried ABA concentration kept relatively stable with a range of volume flow rates. ABA concentration in the xylem sap sequentially collected from detached shoots (leaves or twigs) decreased, but not in the xylem sap collected from detopped roots, suggesting that the method developed in the present study to collect xylem sap, that is, collection of xylem sap under a pressure in magnitude equal to the value of leaf water potential, is reliable.

The role of roots in controlling xylem-carried ABA concentration of plants in response to soil drying was of great interest and investigated. The xylem-carried ABA concentration was nearly linearly related to the root ABA content and both were substantially stimulated by soil drying. When  $^3\text{H}$ -ABA was loaded into roots and monitored for its disappearance, it was found that the capability of roots to catabolize ABA was much lower than that reported in leaves, with a half-life of 1.15 h and considerable amount (46%) of fed  $^3\text{H}$ -ABA remaining unmodified during 21 h of incubation. A previous soil drying significantly reduced such a capability of catabolism and extended the half-life of fed  $^3\text{H}$ -ABA and the amount left unmodified. The xylem-carried ABA concentration was markedly reduced by treatments such as light shedding, defoliation and girdling, of which all either reduced or blocked the downward transport of shoot-derived ABA, especially under soil drying condition. It was estimated that about 25 to 30% of xylem-carried ABA might come from shoot when plants were under soil drying.

A decline in stomatal conductance and a rapid and substantial increase of xylem-carried ABA concentration resulting from either soil drying and/or soil compaction took place much earlier than that of leaf water potential. A tight relationship between stomatal conductance and the xylem-carried ABA concentration was observed in several tropical tree species and this relationship could be mimicked by artificially feeding ABA solution to excised leaves, implying that xylem-carried ABA may act as a chemical signal controlling stomatal conductance.

A split-root system and consecutive soil drying cycles were also applied to study the effects of leaf water status and the drying history on the sensitivity of stomata to xylem-carried ABA. Both whole-root drying and half-root drying treatment caused a significant increase of xylem-carried ABA concentration of *Acacia confusa* and *Leucaena leucocephala* plants and a substantial decrease of stomatal conductance, even though the leaf water potential of half-root drying plants was comparable to that of well-watered plants. However, the response of stomata to the increase of xylem-carried ABA concentration of half-root drying plants was much less than that of whole-root drying plants. When *Acacia confusa* plants were subjected to three consecutive soil drying cycles, the linear relation between predawn leaf water potential and xylem-carried ABA concentration was observed and no obvious changes of such a relation occurred throughout the soil drying cycles. However, an increased response of stomata to xylem-carried ABA and a decreased response to predawn leaf water potential were observed as soil drying cycle progressed.

Stomatal recovery from water stress was observed after rewatering, but the degree and the rate of recovery were affected significantly by the degree of water stress the plants were exposed to. The severer the water stress, the slower the stomata recovered. Upon rewatering the water-stressed plants, the leaf water potential and the xylem-carried ABA concentration rapidly returned to pre-stress levels, but the recovery of stomatal conductance was much more slowly, suggesting that stomatal recovery can not be explained by the decrease of the xylem-carried ABA concentration. The results also showed that the recovery of stomatal conductance was influenced by the leaf water status during the period of water stress. Stomatal conductance of half-root dried plants, of which the leaf water potential was comparable to that of well-watered plants, recovered more rapidly than that of whole-root dried plants, suggesting that the leaf water status during the period of soil drying may play an important role. Furthermore, stomatal recovery varied greatly among plant species and it was observed that the stomatal recovery of *A. confusa* was much more fast than that of *L. leucocephala*. results from incubation of isolated epidermes from pre-stressed *Commelina communis* and *Vicia faba* plants suggested that some physiological and/or morphological processes in the guard cells are related to recovery processes.

The rate of photosynthesis of *A. confusa* and *L. leucocephala* was inhibited substantially when subjected to either whole root or half-root drying treatment, but photochemical efficiency, measured as a ratio of variable fluorescence to a peak fluorescence emission of a dark-adapted leaf ( $F_v/F_m$ ), was not affected except in the whole root-dried *L. leucocephala* plants where leaf water potential was reduced to -2.5 MPa. In all cases where photosynthesis was inhibited, there was a concomitant reduction of both leaf conductance and calculated internal CO<sub>2</sub> concentration as well as an increase of xylem-carried ABA concentration, suggesting that drought-induced decline of photosynthesis was a result of the stomatal factor caused by the increase of xylem-carried ABA concentration. Non-stomatal factors were species-specific and were brought about only at very low water potential.

It is concluded that xylem-carried ABA concentration acts as a root-derived chemical signal and plays a crucial role in the control over stomatal conductance. The

concentration of xylem-carried ABA, which is a good measure of soil water status around the root system, is determined by the amount of shoot-derived ABA as well as the capabilities to synthesize and catabolize ABA in the roots. The sensitivity of stomata to xylem-carried ABA is by no means a fixed characteristic and is affected by leaf water status and drying history and varies greatly among plant species.

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