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Cavitation and embolism in plants: literature review

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Abstract

Background: The appearance and formation of air bubbles in xylem conducting vessels can drastically reduce the hydraulic capacity of the plants, since this problem is pointed out as one of the main mechanisms that cause the mortality of the woody plants, mainly due to the water deficit and, in smaller degree, due to the freezing-thawing events of the water, during the cold. Plants have mechanisms to minimize the effects of cavitation and embolism, but these vary between plants and even within the same species. **Objective:** In order to better understand the "cavitation and embolism" theme, this research was carried out based on a literature review, in which the articles of higher quality and relevance regarding the theme were selected.

Key words: Cavitation, embolism, Xylem cavitation, Xylem.

INTRODUCTION

The plant tissues involved in the transport of substances at long distances are xylem and phloem. The transport of water and minerals is carried out by the conductive elements of the xylem, from the roots to the leaves. These conductors are tracheids and vessel elements. Through the root cells, the water penetrates the conductors and leaves them, as water vapor, through the surface of the cells of the leaf mesophyll to the extracellular spaces. If the stomata are open, water is lost to the environment in a process called sweating. Thus, one of the key events in water transport is regulation of stomatal opening and closure (RAVEN *et al*., 2001).

Every day, hundreds of gallons of water circulate in the trunk of an adult tree and are lifted up to their canopy tens of meters above the ground. The leaves allow the evapotranspiration of a very large amount of water, while absorbing the carbon dioxide and regulating its surface temperature. The machinery behind the ascending water transport process has to be extremely efficient, since any dysfunction can impair the hydration of the tree and, consequently, its survival (COCHARD, 2006).

The vegetables underwent selective pressures and evolved in relation to the water pumping system, which became extremely efficient and profitable. However, since transport is based on the theory of tension-cohesion and the system operates under great negative pressures, plants live under constant threat (COCHARD, 2004; 2006).

Although plant hydraulic systems are well suited to periods of drought and also to cold periods, plant survival may become threatened when air can enter its conducting vessels, not allowing the circulation of the sap (PIMENTEL, 2004) which causes the rupture of the water column, a process known as cavitation. The consequence of cavitation is embolism, that is, the filling of vessels or tracheids with air bubbles. Thus, cavitation and embolism are detrimental to the tension-cohesion mechanism and consequently to the transport of water via xylem conductors (RAVEN *et al*., 2001; TYREE & SPERRY, 1989; TYREE, 1997).

However, the consequences of xylem cavitation tend to be minimized because air bubbles cannot easily pass through the membrane pores of the spikes. Because capillaries are interconnected, water tends to seek alternative paths, diverting from the blocked point. In addition, the bubbles can be eliminated overnight when the perspiration decreases a lot, the pressure potential (Ψp) of the xylem increases and the gases can re-dissolve in the xylem solution. Another way that causes the gases to dissolve is the positive pressure exerted by the root xylem (root pressure) (TAIZ & ZEIGER, 2004). Thus, bubble formation is considered normal and reversible in many trees (RAVEN *et al*., 2001), and pressure limits supported by xylem, in order to avoid cavitation and embolism, vary widely among species, because of the great diversity and functionality of the vegetables (COCHARD, 2004; 2006).

Despite the existence of these mechanisms to minimize the impact of bubble formation on plants, the system may fail because water conduction by the xylem is constant. As the water tension increases inside the conductors, the tendency for air to be aspirated through microscopic pores of the cell walls increases. Moreover, bubbles can form in the xylem as a consequence of the freezing of the crude sap. After this bubble forms in the column of water under tension, it will tend to expand due to the fact that gases cannot withstand tensile forces (COCHARD, 2006).

Meinzer *et al*. (2000) studying the uptake, transport and loss of water in vegetables, have stated that instead of the embolism being essentially irreversible, it seems that there is a dynamic balance between the formation of air bubbles and the repair throughout the day. The daily release of water from the xylem through cavitation could serve to stabilize the water balance of the leaf, minimizing the temporal imbalance between supply and demand of water, which would challenge and put in check the secular tension-cohesion theory.

Considering the above, we will address in this review, articles that involve in their subjects the cavitation and the embolism in plants, as a consequence of stress, water deficit and freezing and thawing events due to cold.

MATERIAL AND METHODS

This is a bibliographical research. National and mainly international articles, dating starting from the 90's, were selected using the CAPES Portal and Google Scholar databases, using as keywords: "embolism", "cavitation", "xylem cavitation", and "xylem".Then, they were grouped by subject and used in the construction of the literature review. For reasons of teaching and to facilitate reading, we have chosen to divide this review into two sections.The first section reviews the articles whose theme is associated with cavitation and embolism caused by water deficit and the second, those associated with cold, through events of freezing and thawing of water inside the xylem conductors. At the end of this bibliographic survey, 26 articles were effectively used, selected according to quality and relevance with the proposed theme.

RESULTS AND DISCUSSION

3.1 Cavitation and embolism caused by water deficit:

Water transport through the xylem is essential to replace water loss during transpiration, thus avoiding desiccation and allowing photosynthesis. The occurrence of cavitation and embolism due to drought would impair the transport of water, especially to the leaves (LI *et al*., 2009). During periods of drought, due to the lower soil water potential and the high evapotranspiration in the leaves, the probability of embolism is higher, resulting in the death of the plants (BRODRIBB & COCHARD, 2009; BRODERSEN, 2013). According to Choat *et al*. (2012), drought-induced embolism is recognized as one of the main precursors of the death of woody plants.

The vulnerability of xylem to embolism, induced by water deficit, and variation in the natural degree of embolism were measured in lateral roots of four species of trees occurring in neotropical savanna by Domec *et al*., 2006. According to the authors, root embolism varied diurnally and seasonally. At the end of the dry season, the conductivity loss of root xylem reached 80% in the afternoon, when the root water potential (Ψ_{ROOT}) was -2.6 MPa (Megapascal), and this loss of conductivity was recovered in 25 to 40% in the morning, when Ψ_{ROOT} was -1.0 MPa.

Poggi *et al*., (2007) analyzed the relationship between stomatal closure and early cavitation in the genus Citrus, submitted to periods of drought due to suppression of irrigation. The pre-dawn water potential, stomatal conductance, plant transpiration, xylem embolism degree, and xylem vulnerability curves were measured. All the species studied were vulnerable to embolism, but these effects were minimized in some species that were able to regulate the closure of the stomata early, which prevented the occurrence of embolism. This suggests that there is a strong relationship between the closure of the stomata and the onset of cavitation in the xylem vessels. Therefore, according to this study, xylem cavitation is a key process for understanding the Citrus response to drought and can be considered as a promising criterion by which drought tolerant genotypes can be selected in plant breeding programs.

The identification of the hydraulic parameters associated to stoma regulation during water deficit stress as a way to control xylem embolism was also studied in walnut trees (Juglansregia x nigra). Hydraulic sap characteristics were experimentally altered with different methods, altering plant transpiration (E_{PLANT}) and stomatal conductance (g_E). Potted walnuts were exposed to water stress by altering soil water potential (Ψ Soil), soil resistance (R_{SOIL}) and hydraulic resistance of the root (R_{ROOT}). The soil temperature was changed to modify only the R_{ROOT}. An embolus was created on the trunk to increase air resistance. Stomata were closed in response to these tension, maintaining the water pressure in the leaf rake xylem (P_{RAKE}) above - 1.4 MPa and leaf water potential (Ψ_{LEAF}) above - 1.6 MPa. The same dependence of E_{PLANT} and g_E on P_{RAKE} or Ψ_{LEAF} have always been observed, suggesting that stomata were not responding to changes in Ψ_{SOIL}, R_{SOIL} and R_{ROOT}, but rather to their impact on P_{RAKE} and/or Ψ_{LEAF}. The leaf rake was the most vulnerable organ, with a P_{RAKE} threshold for induction of embolism of - 1.4 MPa. The minimum values of Ψ_{LEAF} corresponded to the leaf turgor loss point. This suggests that the stomata are responding to the water status in the leaf as determined by the hydraulic rate of transpiration and that P_{RAKE} may be the physiological parameter regulated by the closure of the stomata during water stress, which would have the effect of preventing extensive developments of cavitation during the dry season. (COCHARD *et al*., 2002a).The studies presented so far demonstrate that the vulnerability of xylem to cavitation differs between species of trees, and even between varieties, according to their resistance to drought. According to Awad *et al*., (2010) these differences are even more evident when comparing xerophilic species with non-xerophilic species. Xerophilousspecies are more resistanttoxylemcavitation.

It is evident that most research on cavitation and embolism has been conducted on woody plants and less attention has been paid to herbaceous plants and to the physiological significance of cavitation for the understanding of water relations in annual crops. In this review, due to the scarcity of papers, only three articles on cavitation and embolism in herbaceous plants were selected. Two of them, with the species *Zea mays* L. (corn) and one with the species *Oryza sativa* (rice).

Cochard (2002b) studied the water relations during drought and the vulnerability of xylem to embolism in four corn genotypes. The water deficit caused a decrease in xylem pressure, leaf water potential and plant transpiration. The transpiration was reduced to a minimum value when the xylem pressures reached -1.6 MPa. The xylem embolism in the leaf veins always remained low, even when the plants exhibited symptoms of clear water stress. This suggests that the closure of the stomata during the drought restricts the xylem embolism to a minimum value. The resistance to cavitation was not related to grain yield, under drought conditions, in none of the four evaluated genotypes. However, it can be speculated that an increase in resistance to cavitation in crops, by genetic selection, for example, may increase maize survival during drought.

Stiller *et al*. (2003), investigated the role of xylem cavitation, plant hydraulic conductance and root pressure in response to gas stress changes in rice (*Oryza sativa*). Field and laboratory results indicate that xylem cavitation plays an important role in reducing the hydraulic conductivity of plants during drought and that rice can easily reverse cavitation, possibly aided by nocturnal root pressure.

Although cavitation recharge cycles became common events in plants, it was not known whether these cycles weakened the resistance to cavitation of the xylem. Hacke *et al*. (2001) demonstrated in their experiments two responses: Resilient xylem (*Acer negundo* and *Alnus incana*) that showed no change in resistance to cavitation after a cavitation recharge cycle. In contrast, weakened xylem (*Populus angustifolia, P. tremuloides*, *Helianthus annuus* and *Aesculus hippocastanum*) showed a considerable reduction in resistance to cavitation. The weakening was observed when cavitation was induced by centrifugation. Observations in *H. annuus* show that the weakening of the xylem cavitation resistance was proportional to the stress-induced embolism.

In another study, Ladjal *et al*. (2005) related the effects of drought on hydraulic conductivity and the vulnerability of xylem to embolism with the diameter of tracheids in several species of Mediterranean cedars. The hydraulic characteristics of young plants of the following cedar species were studied: *Cedrus atlantica* (Endl.) G. Manetti ex Carrière (Luberon, France), *C. brevifolia* (Hook. F.) Henry (Cyprus), *C. libani* A. Rich (Hadeth El Jebbe, Lebanon) and *C. libani* (Armut Alani, Turkey). With an ideal water supply, no great differences were observed between the species in relation to hydraulic conductivity (KS) or specific conductivity of the leaf (KF). Under moderate soil drought for 10 weeks, accentuated acclimatization was induced by a reduction of KS, particularly in the two Lebanese cedar species (*C. libani*), and a decrease in the lumen size of tracheids of all species. *Cedrus atlantica*, was the species with the lowest tracheids (diameter), being the most vulnerable to embolism: a loss of 50% in hydraulic conductivity (Ψ_{PLC50}) occurred at a water potential of -4.4 MPa in well-watered treatment and of - 6.0 MPa in the treatment of moderate drought. Therefore, in this case, the smaller diameter of tracheids increased the vulnerability of xylem to embolism in drought conditions, different from that observed by Pittermann & John (2003), where the narrowing of the tracheid diameter protects against embolism by freezing in cold climates, will be seen in the next section.

3.2 Cavitation and embolism caused by freeze-thaw events:

Freezing and thawing events during the winter can cause embolism within the conducting vessels of the xylem, reducing hydraulic conductivity, especially in temperate plants. According to classical theory, air bubbles are formed during freezing and expansion during thawing (AMÉGLIO, *et al*., 2001; MAYR *et al*., 2007).

Studies with conifers, which are predominant in cold and temperate climates, have shown that these trees are very resistant to embolism when subjected to induced freezing-thawing. The analysis was performed using ultrasound electronic microscopy techniques. Twigs of the species conifer *Piceasabies* L. Karst. were subjected to up to 120 freeze-thaw cycles during which ultrasonic sonic emissions, xylem temperature and diameter variations were recorded. The embolism increased with the number of freeze-thaw events in previously dehydrated branches at a water potential of 22.8 MPa. Saturated branches had low acoustic activity and totally dehydrated branches did not show any. Acoustic emissions were detected only during the freezing process. This means that the embolism was formed during freezing, which is in contradiction to the classical freezing and thawing theory of induced embolism. The air bubbles in the tracheids are small and dissolve again during thawing. However, the increase in embolism rates in consecutive freezing and thawing events cannot be explained by the classical theory (MAYR *et al*., 2006).

According to Améglio *et al*. (2001) during the winter, freezing and thawing events can induce embolism and reduce the hydraulic conductivity of temperate woody plants such as walnut. In barefoot plants the amount of stored carbohydrates is lower, which increases freezing problems due to lower osmolarity. Simulating the conditions that walnut plants are exposed to in winter (total leaf loss and freeze-thaw events) have depleted potted plants and compare them with non-defoliated (control) plants. They concluded that in the defoliated plants the osmotic pressure of the xylem was 0.4MPa whereas in the control this value was 0.21MPa (both kept at 1,5 °C). This study explains that the fall of the leaves, by reducing the concentration of carbohydrates, tends to increase the problems with the embolism in the winter.

Vessels of xylem *Prunus persica* Batsch (peach) and *Juglans regia* L. (walnut) are also vulnerable to cold, inducing embolism. Améglio *et al*. (2002) carried out studies with these two species and observed that in peach, xylem embolism progressively increased during the winter, reaching a maximum of 85% in Hydraulic Conductivity Loss (HCL) in early March. In the walnut tree, HCL was close to 100%, but the degree of xylem embolism varied, which reflects the walnut's ability to generate positive xylem pressures in winter and spring, different from the peach. Controlled freeze-thaw experiments have shown that frost alone is insufficient to increase embolism in peach trees, and that conditions favorable to evaporation during thawing are also necessary. In the opening of the buds, there was complete recovery of the embolism in walnut, but the HCL remained high in the peach tree. Three mechanisms responsible for restoring the hydraulic conductivity of walnut branches were identified: development of stem pressure, development of root pressure and formation of a new functional xylem ring, whereas only one mechanism was observed in peach trees, formation of a new functional ring. However, when both species were protected from frost, HCL was zero.

It is also possible to observe the vulnerability of the xylem to the embolism by cycles of freezing and thawing, in the work of Sperry & Sullivan (1992). Conifers such as *Abies lasiocarpa* Nutt., And *Juniperus scopulorum* Sarg. showed little vulnerability of the xylem to embolism by freezing, even for repeated cycles. The oak species *Quercusgambeii* presented an embolism superior to 90% and the species *Betula populus* (birch) an intermediate embolism in response to the same freezing patterns. The study shows how conifers are well adapted to natural freeze-thaw conditions.

Davis *et al*. (1999) found a strong correlation between freezing cavitation and the mean diameter of the conducting vessels. In their experiments angiosperms with vessels of small diameter (mean diameter, 30 mm) did not show cavitation induced by freezing under moderate water stress (xylem pressure 5 20.5 MPa), while species with larger vessels (mean .40 mm) were almost completely cavitated under the same conditions. However, species with intermediate mean diameters (30-40 mm) showed partial cavitation by freezing.

Still on the above-cited article it is thus possible to observe that the results shown are consistent for species with a critical diameter of 44 mm or above, from which cavitation may possibly occur through a freeze-thaw cycle at 20.5 MPa. Cochard & Tyree (1990) with different species but also of larger diameter observed the same result. At the end of the study, they correlated the vulnerability to freezing cavitation with hydraulic conductivity per cross-sectional area, which was also confirmed in other studies.

In a study by Utsumi *et al*. (1999), they analyzed the changes in the amount and distribution of water in the lumen of the initial wood vessels of the *Fraxinus mandshurica* species of the current year during the course of the freezing and thawing process. At the end of the experiments they concluded that the cavitation of the initial wood vessels of the current year is not produced during freezing but progresses during reheating after freezing.

Conclusion:

At the end of the review on cavitation and embolism, caused by water deficit, from the literature presented here, we highlight the following relevant points: a) the conductivity of the xylem is directly proportional to the water potential of the root (Ψ_{ROOT}), that is, how much smaller (more negative) Ψ_{ROOT} lower the conductivity in the conducting vessels and vice versa; b) cavitation is a hydraulic signaling mechanism that allows the stomata to close while maintaining the integrity of the stomatal conductance, ie, the faster the plant perceives cavitation, and consequently to close its stomata, the less damage caused by embolism. This stomatal sensitivity seems to be perceived by the pressure in the leaf rake; c) species of the cerrado (xerophilous), operate well apart from the point of catastrophic dysfunction for cavitation, when compared with non-xerophilous plants, which reflects the morphophysiological adaptations of these plants the frequent drought conditions; d) the embolism of stems and branches is markedly larger than that recorded in the leaves, which would explain the efficiency of the mechanisms used to minimize cavitation and embolism; e) it is not conclusive that the smaller diameter of tracheids increases the susceptibility and vulnerability of xylem to embolism under dry conditions; f) the reason why research has placed more emphasis on investigating this issue in woody plants is due to the fact that these are more susceptible to the threats of embolism due to the great distances that water travels in the conductors of large trees. However, understanding the mechanisms of cavitation in herbaceous plants, especially in economically important annual crops, would be crucial for the selection of varieties resistant to drought.

On cavitation and embolism caused by the freezing of the xylem sap, we leave the following considerations: a) it is remarkable that the probability of embolism depends more on the dynamics of the sap in the freezing, than the characteristics of the xylem; b) although the smaller diameter of the conductors seems to decrease the cavitation, under freezing conditions, we must consider that the water in smaller vessels freezes before in vessels of larger diameter, which would increase the embolism; c) the lower amount of stored carbohydrate increases the freezing problems due to the lower osmolarity; d) when the xylem sap freezes, air bubbles arise, as a result of the difference between the solubility of air in water and ice; e) when the ice melts the air bubbles are retained and expand, then the tensile forces are generated in the vascular system.

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