From Forest Nursery Notes, Winter 2012

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Holtta, T., Juurola, E., Lindfors, L., and Porcar-Castell, A. Journal of Experimental Botany 63(2):1057-1067. 2012.

Journal of Experimental Botany, Vol. 63, No. 2, pp. 1057–1067, 2012
doi:10.1093/jxb/err349 Advance Access publication 30 October, 2011
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Journal of Experimental Botany
www.jxb.oxfordjournals.org

RESEARCH PAPER

Cavitation induced by a surfactant leads to a transient release of water stress and subsequent 'run away' embolism in Scots pine (*Pinus sylvestris*) seedlings

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Received 5 July 2011; Revised 6 October 2011; Accepted 11 October 2011

Abstract

Cavitation decreases the hydraulic conductance of the xylem and has, therefore, detrimental effects on plant water balance. However, cavitation is also hypothesized to relieve water stress temporarily by releasing water from embolizing conduits to the transpiration stream. Stomatal closure in response to decreasing water potentials in order to avoid excessive cavitation has been well documented in numerous previous studies. However, it has remained unclear whether the stomata sense cavitation events themselves or whether they act in response to a decrease in leaf water potential to a level at which cavitation is initiated. The effects of massive cavitation on leaf water potential, transpiration, and stomatal behaviour were studied by feeding a surfactant into the transpiration stream of Scots pine (*Pinus sylvestris*) seedlings. The stomatal response to cavitation in connection with the capacitive effect was also studied. A major transient increase in leaf water potential was found due to cavitation in the seedlings. As cavitation was induced by lowering the surface tension, the two mechanisms could be uncoupled, as the usual relation between xylem water potential and the onset of cavitation did not hold. Our results indicate that the seedlings responded more to leaf water potential and less to cavitation itself, as stomatal closure was insufficient to prevent the seedlings from being driven to 'run-away' cavitation in a manner of hours.

Key words: Cavitation, leaf gas exchange, stomatal control, water potential, xylem transport.

Introduction

Water columns in the xylem are usually under negative pressure and therefore vulnerable to cavitation (Tyree and Sperry, 1989). Excessive cavitation is unfavourable to plant function as it decreases the hydraulic conductance of the xylem and threatens the supply of water to the leaves. If a plant does not respond by stomatal closure to prevent excess cavitation, it would progressively spread to fill the entire xylem in 'run-away' cavitation and the plant could die of dehydration (Tyree and Sperry, 1988; McDowell *et al.*, 2008). Various tree species have been shown to maintain stomatal conductance and xylem water potential above values that would lead to this excess cycle of xylem cavitation (Sperry and Pockman, 1993; Dang *et al.*, 1997; Borghetti *et al.*, 1998; Irvine *et al.*, 1998; Salleo *et al.*, 2000; Hubbard *et al.*, 2001; Brodribb *et al.*, 2003). Whether the stomata respond to leaf water potentials which correspond to the onset of significant amounts of cavitation or directly to a signal created by cavitation events themselves is not known (Whitehead *et al.*, 1996; Nardini and Salleo, 2000; Salleo *et al.*, 2000; Cochard *et al.*, 2002).

Despite its unfavourable effect on xylem hydraulic conductance, cavitation is hypothesized to relieve water stress temporarily (Meinzer *et al.*, 2001*a*). Following the entry of an air bubble into a conduit, water is quickly sucked out of the embolizing conduits into the surrounding tissue (Hölttä *et al.*, 2007), and the water potential in the plant should be transiently increased (Lo Gullo and Salleo, 1992; Hölttä *et al.*, 2009). Cavitation is therefore hypothesized to act as a water release mechanism. Its importance as a capacitive water release mechanism has been predicted to