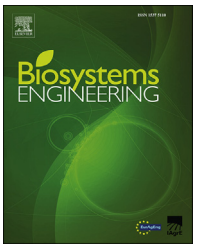
BIOSYSTEMS ENGINEERING XXX (2017) 1–8

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/issn/15375110



Special Issue: Sensing and Control of Crop Water Status

Research Paper

Dormant stem water potential responds to laboratory manipulation of hydration as well as contrasting rainfall field conditions in deciduous tree crops

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ARTICLE INFO

Article history:
Published online xxx

Keywords:
SWP
Pressure chamber
Water stress
Almond
Walnut
Cherry

Pressure chamber measurement of midday stem water potential (SWP) during the growing season has become a practical and widely adopted tool for irrigation management in many woody perennial and some annual crops, but this technique has not been applied to perennial crops during dormancy. The reliability of SWP measurements in dormant trees has in fact been questioned based on concerns that these tissues typically have a low percent of living tissue and/or a high level of embolism. Accurate psychrometer measurements of water potential do not depend on either of these properties, and hence should be useful in evaluating the accuracy of pressure chamber measured SWP in dormant trees. Pressure chamber and in-situ stem psychrometer methods were compared on dormant branches exposed to different levels of hydration in the laboratory. A very highly significant ($Pr < 0.0001$) linear regression was found between the two methods over a wide range of SWP (0 to about −2 MPa) in almond, cherry, and walnut, with r-square values ranging from 0.90 to 0.98. For almond and cherry, the slope of the regression was close to unity. Field measurements showed systematically lower SWP during a dry winter compared to a wet winter, and SWP was found to increase in response to a winter irrigation. This evidence strongly supports the validity of pressure chamber measured SWP as a reliable indicator of dormant tree water status, and hence its use as a tool to evaluate the need for winter irrigation in dormant tree crops.

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http://dx.doi.org/10.1016/j.biosystemseng.2017.09.001
1537-5110/Published by Elsevier Ltd on behalf of IAgrE.

1. Introduction

As California farmers face growing water insecurity, the relevance of winter irrigation applied to dormant tree crops such as almond (*Prunus dulcis*) has become an important issue. The issue arises from the episodic absence of the expected winter precipitation for the Mediterranean climate of California's Central Valley. Historically, this region is characterised by wet, mild winters and dry, hot summers. In the absence of winter precipitation or irrigation, is it possible that the growth and development of the almond tree (*P. dulcis*) may be water limited upon emerging from dormancy in spring? The availability of a reliable plant-based method for measuring water status, such as the pressure chamber, is needed in order to answer this question. In this investigation we determined whether the pressure chamber could be used to measure changes in water potential in response to hydration and desiccation of dormant branches in the laboratory, and whether this method could be used to detect plant responses to irrigation and rainfall during dormancy in the field.

Operationally, the Scholander pressure chamber involves placing freshly excised vascular plant tissue (typically a leaf) into a chamber with the cut end (typically a petiole) protruding through a pressure seal and exposed to atmospheric pressure. The chamber is then slowly pressurised with a gas (typically nitrogen) and the pressure corresponding to the beginning of water exudation from the cut surface is recorded as the 'endpoint' pressure (Scholander, Hemmingsen, Hammel, & Bradstreet, 1964; Scholander, Hammel, Bradstreet & Hemmingsen, 1965). Assuming that the tissue inside the chamber is at water potential equilibrium, the endpoint value represents the static force required to balance the tension on the water in the cell walls (collectively referred to as the 'apoplast') of the leaf, and hence measures the total water potential of the leaf as described by Tyree and Hammel (1972). This principle of operation should apply to any vascular plant tissue, and for covered (non-transpiring) leaves, should measure the water potential in the stem to which the leaf is attached (termed stem water potential, SWP). SWP has been shown to respond sensitively to irrigation treatments (Mccutchan and Shackel, 1992) and has become a practical tool for deficit irrigation management, particularly in perennial tree crops (Shackel, 2011). In these crops, SWP values have been shown to be highly correlated with plant responses to water limited conditions, such as reduced growth and stomatal opening (Shackel, 2011), as well as the degree of embolism in the xylem (Choat et al., 2010).

An alternative method for measuring water potentials, which can also be used on dormant tissues, is the psychrometer method (Boyer, 1995, pp. 55–59) which is capable of determining the water potential of any kind of sample, because it is based on a state of equilibrium between the sample and the relative humidity around the sample in a closed chamber. Common applications include both plant tissues and soil (Boyer, 1995, pp. 55–59). The psychrometer method measures water potential across a wide range, with Peltier psychrometers using a calibrated wet-bulb depression approach to measure the equilibrium humidity (Dixon & Tyree, 1984).

In order to validate that the pressure chamber and thermocouple psychrometer methods, which have distinctly different procedures for measuring water potential, are in agreement, several studies have used the measures simultaneously, although only a few have made this comparison using non-transpiring leaves (i.e., using SWP). For transpiring leaves, some studies (e.g, Brown & Tanner, 1981; Duniway, 1971; Savage & Cass, 1984) have found a close correlation between the pressure chamber and psychrometer methods whereas others have not (e.g., Hardegree, 1989; Wright, Rahmianna, & Hatfield, 1988). Choat et al. (2010) reported a strong linear relation between isopiestic psychrometer-measured water potential of grapevine (*Vitis vinifera*) stem internode sections and pressure chamber measured SWP of subtending leaves, and Turner, Shackel, and LeCoultre (2000) reported a similarly strong linear relation between pressure chamber and non-damaging leaf-cutter psychrometer-measured SWP. It is generally assumed that the apoplastic fluid of leaves and stems contains few solutes (Tyree & Hammel, 1972), but if apoplastic solutes (AS) are present, then the pressure chamber endpoint will overestimate (more positive) water potential compared to the psychrometer method (Duniway, 1971). This potential error has been assumed to be a fixed value (Duniway, 1971), and based on this assumption should only alter the intercept of a regression between the psychrometer and pressure chamber.

Very few studies have addressed the measurement of dormant twig/stem water potential (SWP) with the pressure chamber technique. Améglio et al. (2000, pp. 109–120) used the pressure chamber to measure the dormant SWP of walnut (*Juglans regia*), finding values in the range of 0 to −0.5 MPa (relatively high), but focused on responses to freezing events not applicable to the current investigation. Two studies have specifically challenged the application of the pressure chamber technique to dormant stems. Pramsohler and Neuner (2013), state that "the formation of embolisms in the conduits and a small portion of living tissues may lead to erroneous results," and list four citations to support this claim, three of which only mention embolism and the fraction of living cells. The only other reference (Beikircher & Mayr, 2013) states "Unfortunately, water potential cannot be determined on leafless shoots during winter due to the small portion of living tissues," but presents no data to support this assertion.

Presumably, a low fraction of living tissue should result in underestimated (more negative) pressure chamber measured SWP values if fewer cells are available to contribute the water needed to fill the apoplast (primarily the vessel lumen) and allow for an observable endpoint at the cut surface. Similarly, xylem embolism would require an additional amount of water to first fill embolised conduits, before water could reach the cut surface, which would also result in erroneously low pressure chamber SWP values. Xylem embolism and a low fraction of living tissue can be thought of as a space and supply balance issue. As proposed by Pramsohler and Neuner (2013), a delay in visualising the endpoint and thus an erroneously underestimated SWP value could result from an inadequate supply (living tissue) to fill the space (embolised vessels) before an endpoint is observed. However, the assertion that water potential cannot be reliably measured during

Please cite this article in press as: Milliron, L. K., et al., Dormant stem water potential responds to laboratory manipulation of hydration as well as contrasting rainfall field conditions in deciduous tree crops, *Biosystems Engineering* (2017), http://dx.doi.org/10.1016/j.biosystemseng.2017.09.001