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Field measurements of xylem cavitation: are acoustic emissions useful?

G.E. Jackson[1] and J. Grace

Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, UK

Abstract

Cavitation of water columns within the xylem is deleterious for plant water relations as it results in embolism, so reducing hydraulic conductivity. This cavitation can be detected as it is accompanied by the production of acoustic emissions, which can be detected ultrasonically and logged automatically over periods of days. The acoustic emission technique is useful to determine the threshold water potential at which damage to the water-conducting system of the plant is initiated. It can reveal which environmental variables are deleterious to the plant water relations, and which parts of the plant are most sensitive to cavitation. Species comparisons, and comparisons of the same species in different environments can be made, to obtain indications of drought tolerance. However, acoustic emissions have only a limited use in determining the proportion of embolism in a conducting stem, and other methods are needed to find the percentage reduction in hydraulic conductivity.

Key words: Embolism, hydraulic conductivity, drought stress, vulnerability curves.

Introduction

Since the discovery that plants produce acoustic emissions when water stressed (Milburn and Johnson, 1966) a body of literature has developed interpreting this intriguing feature of plant response to the environment. The present paper examines the phenomenon and its relevance to the water relations of plants. The paper is divided into four sections.

(1) Acoustic emissions are interpreted as the result of cavitation in the water-conducting pathways of plants

(Sandford and Grace, 1985; Borghetti *et al.*, 1989). The physical process of cavitation is therefore briefly reviewed (for extensive reviews see Tyree and Sperry, 1989*a*; Milburn, 1993; Oertli, 1993).

(2) The detection of acoustic emissions from plants requires sensors, amplification and counting equipment. Only one ultrasonic acoustic detection system is currently used by researchers, and the use of that system in practice is examined.

(3) Cavitation leads to blockages or embolisms in the water-conducting pathway. The general methods available for quantifying embolism are reviewed, and the utility of the acoustic emission technique for these determinations is discussed.

(4) Finally, some of the uses of acoustic emission data are detailed, illustrated with examples from our laboratory.

The physical process of cavitation

First of all it is necessary to know the origin and causes of acoustic emissions. They are believed to arise as a result of cavitation of water columns in the vessels and tracheids comprising the water-conducting pathway (the xylem) of plants, but the exact origin of the sound is still unclear (Ritman and Milburn, 1988). The cohesion theory of water transport (Dixon and Joly, 1895) states that water is moved through the soil–plant–atmosphere continuum under a negative pressure, or tension. If this tension increases above a threshold the continuity of the water column can no longer be maintained and it breaks. Pure water can sustain enormous tensions (up to 30 MPa, Briggs, 1950), but the observed tensions at which cavitation occurs are far lower than this because of the mechanism known as 'air seeding'. Tiny air bubbles arise either

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[1] To whom correspondence should be addressed. Fax: +44 131 662 0478. E-mail: G.Jackson@ed.ac.uk

from crevices in the cell wall or through the pit membranes and nucleate the cavitation (Zimmermann, 1983). Tension increases with transpiration rate as a result of friction in the pathway, and so cavitation is expected to be observed in the summer under conditions which favour high transpiration. In the winter, other processes may lead to embolism. During freezing, gas bubbles dissolved in water come out of solution and embolisms may result (Robson and Petty, 1993). Also in the winter tensions may occur when water in the soil or stem is frozen, yet evergreen leaves continue to transpire.

In the xylem cell (composed of only the outer dead cell wall, and termed a conduit) where the water column breakage occurs the previously liquid water becomes water vapour and fills the now non-conducting vessel or tracheid. It is presumed that air diffuses into the cell in subsequent minutes until it reaches atmospheric pressure, at which point it constitutes an embolism or blockage in the conducting tissue. Figure 1 shows a blocked cell surrounded by conducting cells. The air blocking the previously conducting cell arises either out of solution from water in surrounding conducting cells, from intercellular spaces, or from other surrounding embolized cells. One embolized tracheid, as shown here, is not a seriously damaging event since there are many other routes through which water can be drawn and lateral transport is also possible (Greenidge, 1957). However, should many cells become embolized, fewer routes for transport exist and the water potential of distal parts will further decline. It has been postulated that this may lead to 'runaway

cavitation' (Milburn, 1973; Tyree and Sperry, 1988) resulting in the plasmolysis of leaf cells and eventually the death of the entire organ. The occurrence of runaway cavitation has not been demonstrated in the xylem of vascular plants, and may be a rare phenomenon as the pores connecting individual tracheids have a valve-like system designed to resist its occurrence. The pores, or pits, consist of a central torus with a net-like margo connecting it to the overhanging secondary cell wall (Fig. 2). When a cell is embolized the torus is displaced by the difference in pressure on the two sides, and it is sealed against the cell wall which, unless the pressure difference across it increases above a critical level, effectively prevents the passage of any further air or water through it.

Once a conduit has embolized can it refill and resume its role in the conducting system? The answer is yes, but only under certain circumstances. If the pressure inside the surrounding conducting vessels and tracheids approaches atmospheric, the torus of the pit membrane between the cells will be released from its position sealed on to the secondary cell wall and, as the air inside the cavitated cell dissolves, water will flow into the embolized cell. However, water in the xylem is usually transported under negative pressure (as a result of the suction generated by evaporation above) and conditions for positive pressures arise only when no transpiration is occurring. A positive root pressure is required if water is to be absorbed in the absence of transpiration, but positive pressures of any magnitude have only ever been demonstrated in angiosperms. For example, Sperry *et al.* (1987) demonstrated a large positive root pressure in embolized wild grape vine, where the air was simply squeezed out of the vessels as the sap rose in the spring. Although various suggestions have been made as to the mechanism of refilling in conifers (Borghetti *et al.*, 1991) the mechan-
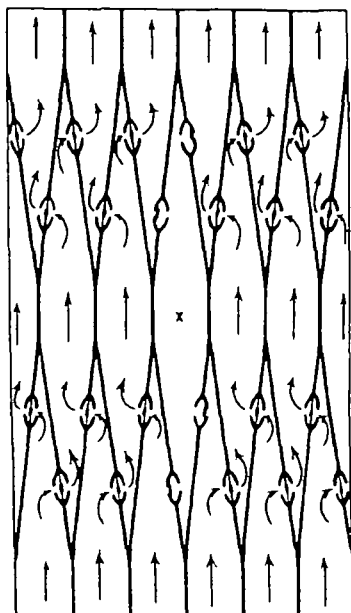

Fig. 1. Tangential section of coniferous wood. The tracheid in the centre (marked X) is vapour-blocked and does not function; water flows around it. (Reproduced with permission from Zimmermann, 1983, *Xylem structure and the ascent of sap*. New York: Springer.)
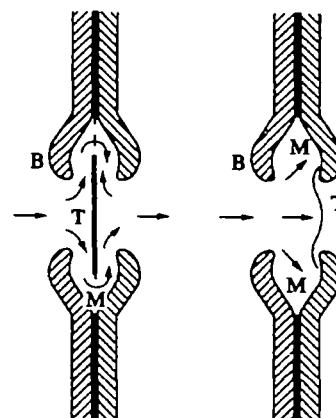

Fig. 2. Cross-section of a bordered pit. (i) Valve open allowing water to pass through it. (ii) Valve closed, following cavitation preventing the flow of water. T, torus; M, pit membrane; B, bordered pit. (Reproduced with permission from Zimmermann, 1983, *Xylem structure and the ascent of sap*. New York: Springer.)

ism still remains unknown. The time elapsed since embolism occurred is probably crucial to the effective refilling of the cell, since tyloses or growths can occur in the embolized cell, which effectively prevents any further conduction (Zimmermann, 1979). The torus of the pit membrane can also become permanently sealed to the surrounding secondary cell wall material so preventing any refilling (Comstock and Coté, 1968).

Detection of acoustic emissions

Milburn and Johnson (1966) were the first to detect acoustic emissions from plants. They were following up the hypothesis that when the water columns inside droughted plants come under sufficient tension they should cavitate, and this should be accompanied by a shock-wave detectable as sound. Cavitation in physical systems, for example, in the water columns of hydraulic pumps, is accompanied by the emission of sound. Their innovative idea was to connect a domestic record player pick-up arm and amplifier to the petiole of a severed leaf. As the leaf dried, the water in the xylem vessels of the petiole would come under tension and would be expected to change state, i.e. cavitate. They were proved correct (Milburn and Johnson, 1966), but the noise generated was naturally less than that in hydraulic pumps. They termed the emissions 'clicks' and noticed that if the leaf was allowed to dehydrate totally, until it produced no more sounds, roughly the same number of clicks were produced as there were conduits within the leaf, in their case around 3000. They also saw that if they added a drop of water to the cut end of the petiole the clicks would slow or stop. These acoustic emissions were recorded in a sound-proof room since any extraneous noise could also be picked up by the record player amplifier. This limited the technique to laboratory investigations. However, in 1983 Tyree and Dixon developed a system to detect acoustic emissions in the ultrasound range. Ultrasound is propagated shorter distances in air and the problem of extraneous noise was therefore minimized, and thus it became possible to use the technique in the natural environment. The original sensors were produced by Bruel and Kjaer (model 8312, DK-2859, Naerum, Denmark) and contained a ceramic material which exploited the piezoelectric effect to convert the small mechanical compression of the ceramic crystal into an electrical signal. Such sensors were originally designed to detect cracking in metallic engineering structures, for example, ships hulls and bridges, and have subsequently been adapted for use with plants.

The system currently most used by water relations researchers is the 4615 DSM (Drought Stress Monitor) with I15I transducers produced by Physical Acoustic Systems in Princeton, New Jersey. This system was found to have a seven times better signal-to-noise ratio than the

Bruel and Kjaer system (Tyree and Sperry, 1989*b*). It also employs the piezoelectric effect and the electronic system amplifies and records the acoustic emissions. A full system with one transducer can be bought from the British agent in Cambridge for $US 7050 (December, 1995). This price includes software written by MT Tyree for use with a personal computer which can be used to interpret the recorded events. Figure 3 shows an I15I acoustic emission sensor attached to a mature Scots pine tree. It has a band pass filter in the range 100–300 kHz which coincides with the typical cavitation-induced AE which has a strong frequency component in this range (Tyree and Sperry, 1989*b*). This makes it superior to sensors with higher frequency band pass filters which have an increased signal-to-noise ratio. The system allows amplification of the signal of up to 80 dB. Different clamping systems have been designed to attach the sensor to the tree, but it is important to standardize the pressure with which it is attached since this has been shown to affect the number of AEs recorded. In the system shown a calibrated spring is used which, if depressed by 2.54 cm, applies a force of 30 N. A hole is made in the bark, and the phloem and cambium layers beneath are removed so that the sensor is attached directly to the xylem (wood) beneath. A thin layer of petroleum jelly is smeared between the sensor head and the xylem to improve the acoustic contact, and further jelly is placed in the hole surrounding the sensor to prevent local dehydration of the trunk leading to artificially high levels of cavitation. A sensor can be directly attached to the recording system or attached through a multiplexor, in which case any number of sensors can be used and large numbers of plants can be monitored. Data are recorded sequentially and must be analysed later to interpret the events produced by a particular plant. Sensors can be positioned on any part of the plant, including the roots, stems and leaves (Hacke and Sauter, 1995), although stems narrower than 3 mm are difficult to work with. The system can operate in the field continuously, as long as there is space in the memory and the batteries are charged.

Quantification of embolism

Acoustic emission production indicates that the plant is currently developing embolism and the rate of production indicates to what extent the current stress level is affecting the plant. Careful integration of all AEs can give a measure of 'accumulated embolism', however, before looking into how this can be done three other more direct methods of measuring accumulated embolism will be briefly reviewed.

(1) Wood consists of three main components: the woody matrix, air and water. The volume fraction of air (i.e. the accumulated embolism) can be found by difference since the volume fractions of water and woody

Fig. 3. Ultrasound acoustic emission sensor (I15I) operating on a mature Scots pine tree. A hole is made in the bark, and the phloem and cambium layers beneath are removed so that the sensor is attached directly to the xylem (wood) beneath.

matrix can be calculated. The density of many woody tissues can be assumed to be 1.53 g cm^{-3} (Siau, 1971) and the total wood volume found by Archimedes' principle, i.e. displacement in water (Borghetti *et al.*, 1991). The volume fraction of air can be calculated from

$$Vg = 1 - [((W_f - W_d)/V_f) + (W_d/(1.53 V_f))]$$

where Vg is the volume fraction of air, V_f is the fresh volume of the sample, W_f is fresh weight and W_d is dry weight. The density of water is assumed to be 1.00.

The volume fraction of air in whole stem sections can be found, following the removal of the bark, phloem and cambium layers. Alternatively, cores can be taken from mature trees.

(2) The frequent aim in assessing the proportion of embolism in a piece of stem is to quantify how much less the observed hydraulic conductivity is than the theoretical maximum if all the conduits were conducting. This is called the percentage reduction in hydraulic conductivity and can be assessed directly by the so-called 'Sperry technique' (Sperry *et al.*, 1988). A severed stem section (which must be longer than the longest xylem vessels contained within it) is mounted and a suitably prepared perfusing solution allowed to pass through it under a low pressure. The solution is then forced through the same section under a higher pressure, typically 100 kPa, which is intended to refill the embolized conduits. The hydraulic conductivity is defined as the mass flow rate of the solution through the section divided by the pressure gradient across the section. The percentage difference in the two values is the percentage reduction in hydraulic conductivity. This technique can be combined with the

perfusion method (below) by including a dye in the solution passing through the stem section.

(3) Perfusion experiments can be conducted by allowing a dye to flow through a section of stem. The resulting staining pattern of the wood can be analysed; stained cells are assumed to be conducting and unstained cells are assumed to be non-conducting. For example, Greenidge (1957) perfused a variety of mature temperate tree species with acid fuchsin and found, as expected, a layer of conducting sapwood just under the bark, and a larger area of non-conducting heartwood in the centre. Lo Gullo and Salleo (1991) found good agreement when they compared the predicted reduction in hydraulic conductivity on the basis of the proportion of unstained cells (using Safranin dye) with the actual reduction in hydraulic conductivity measured using the Sperry method above.

The above three techniques are all destructive, preventing repeated measurements on the same individual. Non-destructive techniques exist, many of which are based on the attenuation of a beam of radiation, which is attenuated strongly by water and cell walls, and only weakly by air. For example, a collimated beam of gamma rays from an Am^{241} source was passed through a plant stem, and the degree of attenuation could be related to the accumulated number of acoustic emissions (Dixon *et al.*, 1984). Large trees require a more energetic radiation source, and X-rays have also been used (Habermehl, 1982). This basic technique lends itself to imaging techniques developed for use in biomedical applications. Recently, a computer tomograph has been developed (Raschi *et al.*, 1995) which is able sensitively to map areas of embolism within the stem. NMR can also be

used to measure the resonance and relaxation of protons in water molecules and an image produced which indicates the areas within the stem where water lies (Ratkovic and Bacic, 1993).

The above non-destructive techniques are very specialized and require a large investment in equipment. The acoustic emissions technique, as with these techniques, is also non-destructive, and also requires careful interpretation if accurate measures of embolism and estimates of hydraulic conductivity are to be found.

Interpretation of acoustic emission data to estimate hydraulic conductivity

The following points need to be considered before any estimate of the consequences of the number of acoustic emission events can be drawn.

The listening distance

It is necessary to know how far from the sensor acoustic emissions can be detected and, therefore, the volume of wood which is being sampled. Ultrasound is not propagated far and events occurring up to a maximum of between 20 and 30 mm are usual, depending on the species and the environment from which the individual came (Tyree and Sperry, 1989b). The state of hydration, the density of the wood and the orientation of the wood fibres affects the distance the sound is propagated. If the state of hydration changes significantly during the monitoring period recalibration should be undertaken. The water content of wood varies throughout the season (Gibbs, 1958; Jackson *et al.*, 1995a) often with values lower in summer and higher in winter. Higher water contents attenuate the AEs more effectively and the differences in cavitation rates between the seasons could, therefore, be artificially exacerbated. One method to determine the listening distance is to sample sections of fully hydrated stems of various lengths, and to determine the relationship between length and total acoustic emissions during dehydration (Sandford and Grace, 1985). As the sample size increases a greater number of events are recorded, but above a certain size no more events are found, and it is this length which can be assumed to be the extent of the listening distance of the sensor.

The number of conducting cells within that listening distance

Wood of different species and from different environments have vessels and tracheids of different sizes and, therefore, within the same listening distance there can be vastly different numbers of cells. If a million cells can potentially be detected a thousand events may be unimportant, however in less dense wood a thousand events could result in a serious reduction in hydraulic conductivity.

For conifers (which have no vessels) the number of cells can be found by macerating a known volume of tissue in boiling acid and carrying out cell counts (Sobrado *et al.*, 1992). It is a little more difficult to count the number of cells in vessel-bearing species (angiosperms), but from knowledge of the vessel length distribution (Zimmermann, 1983) and cell diameters estimates can be made.

Proportion of non-conducting cells

As well as conducting vessels and tracheids the xylem also contains non-conducting fibre tracheids and living parenchyma cells. Fibre tracheids may cavitate at similar frequencies as the conducting cells, and if there is a high proportion of fibres there will appear to be an artificially high reduction in hydraulic conductivity. The proportion of fibres can be estimated in the macerate used to estimate the total number of cells within the listening distance.

The lumen volume, since larger cells conduct more water

The Hagen-Poiseuille equation demonstrates that the conducting ability of a water-conducting pipe with laminar flow increases with the 4th power of its radius, so that a small increase in internal cell diameter leads to a large increase in water conduction. Cavitation of a large cell is, therefore, hydraulically more significant than that of a small cell. The proportion of cells of different radius again can be estimated from the cell macerate.

Whether one acoustic emission corresponds to one conduit cavitating

There is a possibility of overlapping cavitation events. Two or more events may occur simultaneously, or almost simultaneously, and may only be recorded as one event. Alternatively, some emissions may not be recorded because a so-called 'dead time' is built into the electronics which prevents a second event being recorded very shortly after a first one. This is because the signal from an AE sensor, in response to a single event, is actually a series of oscillations, but only one cavitation event must be recorded per acoustic emission. The dead time prevents greater than one oscillation of the same cavitation event being counted. A related problem is that some AEs may occur outside the frequency range detected. It is difficult to estimate the extent of these events since it is still unclear exactly where and how the sound originates within the plant. Whether one acoustic emission corresponds to one conduit cavitating can be calibrated by estimating the number of conducting cells within a fully hydrated sample of wood (within the listening distance of the sensor) and recording the number of events produced as it completely dehydrates (Sandford and Grace, 1985).

The amplification gain of the signal

The gain of the signal can be altered by the user from between 20 to 80 dB, with higher gains producing a larger number of acoustic emissions. However, with a high gain more background noise is detected and so to determine the highest possible gain, consistent with maximizing the number of recorded events, but minimizing the background noise, preliminary trials are needed. The sensor may be attached to a non-cavitating object, such as a dowel, or left hanging freely in air. Any recorded events are therefore background noise. The amplification gain can be set so that, for example, less than one spurious event per minute is produced. In the field situation 74 dB is often found to fulfil this requirement (Jackson *et al.*, 1995*b*), but in growth rooms where there is other electronic equipment the gain may be as low as 70 dB. The gain setting should be noted during sensor listening distance trials since the higher the gain the larger the effective listening distance of the sensor. Since decibels are on a logarithmic scale a difference of one decibel can produce values of a different order of magnitude.

A further problem in interpreting acoustic emission data in terms of a reduction in hydraulic conductivity is that under certain circumstances conduits can refill as well as cavitate, and the extent of refilling can not be easily quantified. For example, a conduit which cavitated by day, could refill at night and subsequently cavitate the following day. Different conduits have different 'vulnerabilities' and the same conduit could cavitate and refill many times. Finally, in order to interpret the acoustic emissions produced by plants, recordings must be undertaken for extended times since day-to-day meteorological variation can greatly affect the number of cavitation events.

Uses of acoustic emission data

From the above consideration it can be seen that interpreting the reduction in hydraulic conductivity from acoustic emission data is not simple (Tyree and Dixon, 1986: Lo Gullo and Salleo, 1991). However, AE data can be used very effectively for particular applications. One frequent application is the construction of 'vulnerability curves'. Figure 4 shows a vulnerability curve for 3-year-old Scots pine saplings. Such plots are of the plant water potential (measured as near as possible to the cavitation measurement site) versus the rate of cavitation and can be constructed for intact plants, or severed plant parts dehydrating on a laboratory bench. In Figure 4 the leaf water potential was measured using a pressure bomb, but the stem water potential could also be found using a psychrometer. The dotted line indicates the threshold below which there was less than one cavitation event per minute. Since the amplification gain was set to the point where less than one event per minute could occur even if
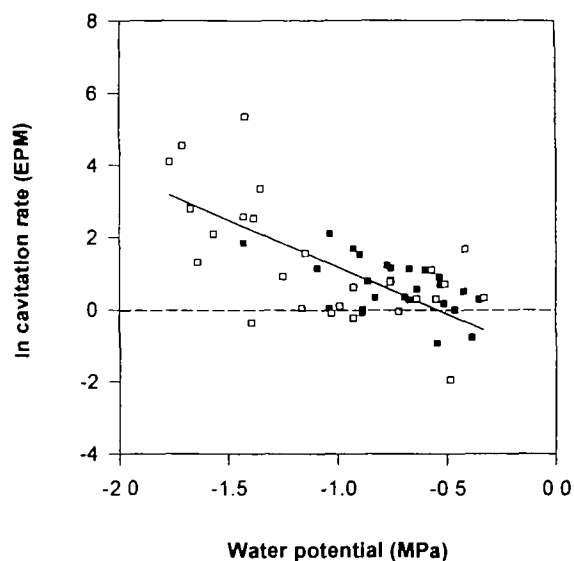

Fig. 4. Relationship between the logarithm of the cavitation rate at the time when leaf water potential measurements were carried out. (■) Measurements on watered trees. (□) Measurements on droughted trees. The broken horizontal line corresponds to one cavitation event per minute; the threshold below which the acoustic emissions are deemed indistinguishable from noise.

there was no genuine cavitation these points are indistinguishable from background noise. The cavitation rate increased as the water potential declined, and the threshold water potential at which cavitation was initiated was −0.55 MPa. Using this technique the vulnerability of different plant parts and the vulnerability of different species, or the same species from different environments can be compared. It is a crude indicator of the drought tolerance of the individual.

The cavitation technique is also able to reveal how real-time environmental variability affects plant water relations. A sensitive relationship between micrometeorological environmental changes and changes in cavitation rate is found. Figure 5 shows 48 h of cavitation and simultaneous micrometeorological measurement from midday on day 1 to midday on day 3. Measurement was with mature Scots pine trees in Thetford forest in August 1992, at which time the forest was undergoing a severe drought. The cavitation rate peaks during the day time period and is very low at night. Peaks in *PAR* and *VPD* are associated with peaks in cavitation rate, but there is no relationship with wind speed. The maximum cavitation rate is about 70 events per minute. Using this technique the importance of variability in particular variables or combination of variables for initiating cavitation can be found.

Since cavitation sensors can be placed at any point on the plant the comparative vulnerability of the different plant parts can be found. For example, the distal branches may cavitate before the main stem, and may be lost first. This may be an adaptive strategy to release water to the
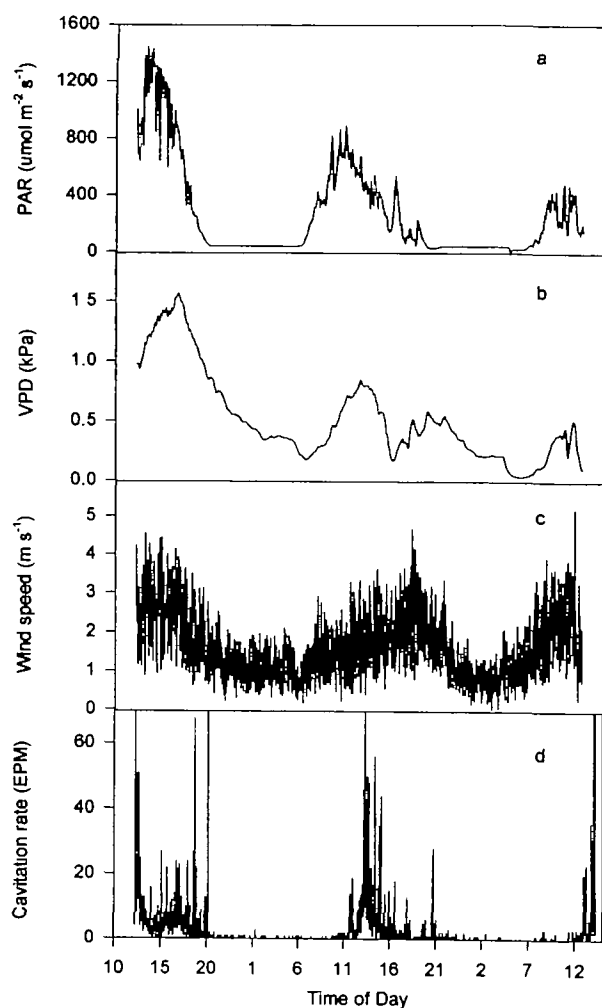
Fig. 5. The relationship between cavitation rate and meteorological variables of mature Scots pine trees in Thetford forest. (a) Photosynthetically active radiation, (b) vapour pressure deficit, (c) wind speed, and (d) cavitation rate per minute.

main stem, or due simply to the lower water potential of parts closer to the transpiring surfaces.

Acoustic emissions have also been used practically in horticultural systems, and there is great potential for these applications. In California AEs were used to control irrigation systems for grape vines. When the cavitation rate reached a predetermined threshold rate irrigation was initiated, but this was not at the first sign of cavitation, since it was found that the wine had an improved flavour if the vines experienced some degree of water stress. A second system was employed in Japan where a particular cavitation rate initiated sun screens to reduce evapotranspiration and, in turn, prevent an increase in water stress.

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