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Key words: biocontainment, crop–wild gene flow, fitness effects, genetically modified crops, introgression, transgenes.

Letters

Low-decibel ultrasonic acoustic emissions are temperature-induced and probably have no biotic origin

The detection of ultrasonic acoustic emissions (UAEs) in plants is one of the rare methods applicable to field-grown trees without causing any disturbance to the objects investigated. The sensors are weatherproof, are easy to mount, use little energy and produce highly reproducible signals in a range between 20 and 300 kHz (Tyree & Sperry, 1989; Laschimke *et al.*, 2006). In combination with dendrometers and sap flow sensors, UAE sensors allow detailed interpretations of tree water relations, particularly under drought stress. The best-known UAE in plants is caused by cavitation in tree stems (Milburn & Johnson, 1966), which is an abrupt release of tension in the conduit lumen as liquid water at negative pressure is replaced by water vapour very near to vacuum pressure (Sandford & Grace, 1985; Kikuta *et al.*, 2003; Rosner *et al.*, 2006).

However, the information content of UAEs is assumed to be much more diverse than that usually described for signals from cavitation and may have other biological sources. The findings of Zweifel & Zeugin (2008) potentially represented another step towards a better understanding of UAEs. Our

growth chamber study, however, showed that their assumption of detection of a new biologically derived low-decibel (dB) signal was probably wrong. The highly reproducible low-dB signal was not induced by respiration and growth activities in the tree stem, but was probably induced by the temperature sensitivity of the technical devices.

Growth chamber experiments

We tested identical equipment as used by Zweifel & Zeugin (2008) – an acoustic signal conditioner with a peak detector (ASCO-P, APK signal; Vallen System GmbH, Icking, Germany) in combination with a piezoelectric sensor head (VS150-M, 100–300 kHz; Vallen System GmbH) – and measured UAEs in a growth chamber under controlled conditions in three different set-ups.

Expt 1: a temperature sensitivity test of the sensor head in the low-dB range. The sensor head was hung into the empty growth chamber, with dimensions 2 × 1.5 × 2 m (height × width × length), while the other parts of the electronic devices were kept outside the growth chamber.

Expt 2: a temperature sensitivity test of the sensor head including the UAE signal conditioner. The sensor head and the UAE signal conditioner were kept inside the growth chamber, while the logging device was outside the chamber.

Expt 3: a temperature sensitivity test of the UAE equipment in the high-dB range. High-dB signals were mechanically induced to simulate the sound intensity of cavitations. The maximum intensity of this artificial cavitation was *c.* 3–4 dB lower than that reported in the field (Zweifel & Zeugin, 2008).

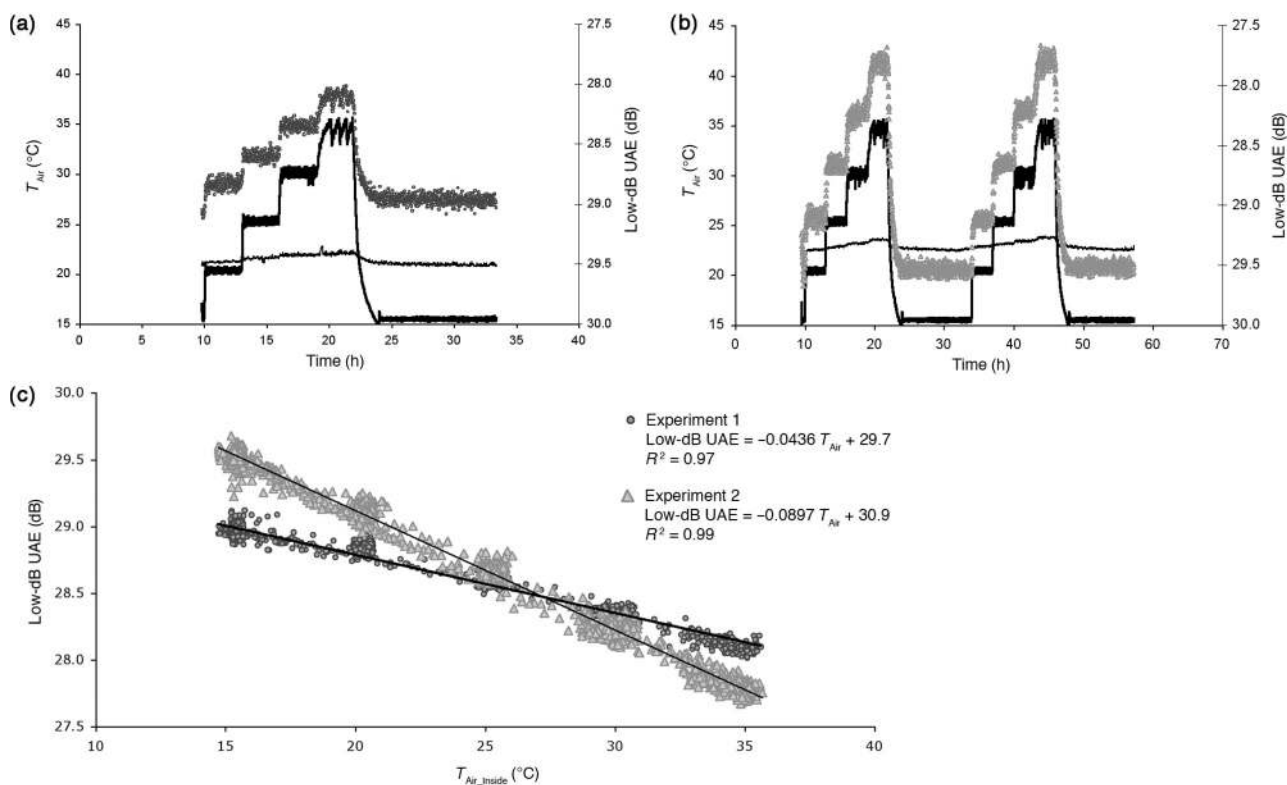


Fig. 1 Temperature sensitivity of ultrasonic acoustic emission (UAE) detection in the low-decibel (dB) range (Expt 1, circles; Expt 2, triangles). (a) Expt 1: the sensor head was exposed to the fluctuating air temperature inside the growth chamber ($T_{Air,inside}$; thick black line, left scale), while the other parts of the technical equipment were exposed to the air temperature outside the growth chamber ($T_{Air,outside}$; thin black line, left scale). (b) Expt 2: the sensor head and the UAE signal conditioner were inside the growth chamber, whereas the logging device was outside. (c) Relationship between air temperature ($T_{Air,inside}$) and low-dB UAE.

In all three set-ups, the temperature in the growth chamber was varied between 14.7 and 35.7°C, whereas the temperature outside the chamber was minimally disturbed at between 22 and 24°C. The execution interval of the logging device (NI USB-6009; National Instruments, Austin, TX, USA) was 20 Hz. The measurements were averaged and stored every minute in Expts 1 and 2 and every second in Expt 3.

Temperature sensitivity of the UAEs

We found that the patterns of changing low-dB UAEs occurred even without a contact between the sensor head and the plant material. Exposure of either the sensor head alone (Expt 1; $R^2 > 0.97$) or the sensor head together with the corresponding UAE signal conditioner (Expt 2; $R^2 > 0.99$) to the controlled temperature change within the growth chamber revealed a high correlation between the low-dB UAE signal and temperature (Fig. 1). The temperature sensitivity significantly increased when the sensor head and signal conditioner were both exposed to the changing temperature. The sensor head alone induced a decrease in the low-dB signal by -0.0436 dB per °C, whereas the sensor head and the signal conditioner together induced a decrease in the low-dB signal by -0.0897 dB per °C.

Temperature affected not only the low-dB signal but also the high-dB UAE (the UAE associated with cavitation) (Fig. 2). The mechanically induced high-dB UAE (Expt 3) was clearly separated from the low-dB UAE. However, these two UAE signal ranges responded similarly to changes in temperature: UAE signals linearly decreased with increasing temperature.

Consequences for the results in Zweifel & Zeugin (2008)

The temperature sensitivity of the sensor head and the signal conditioner of the UAE equipment explains > 99% of the variance of the low-dB data (Fig. 1). Particularly, the piezoelectronics in the sensor head are very temperature sensitive. The temperature sensitivity is not restricted to the low-dB signal but affects the entire range of UAEs (Fig. 2). Because the temperature sensitivity is linear for the equipment used, it can be corrected by a rate of -0.0858 dB per °C (averaged value of the different experiments).

This temperature correction factor was applied to the original UAE data of Zweifel & Zeugin (2008) and the data were recalculated using a reference temperature of 20°C. This correction led to an almost complete disappearance of the described low-dB dynamics (Fig. 3). The low-dB signal now showed an

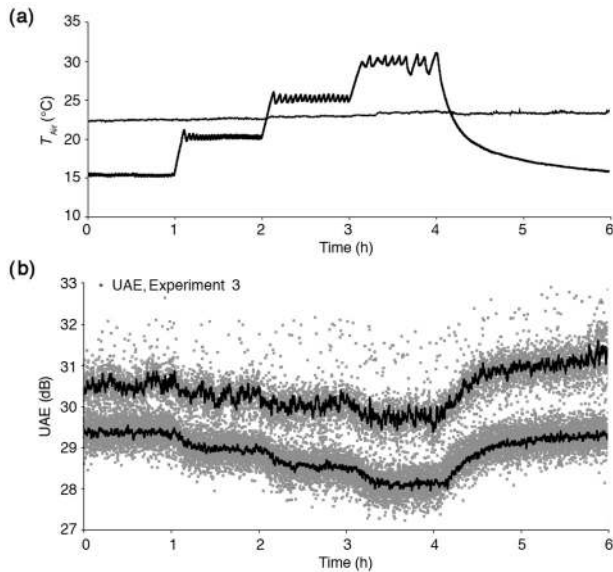


Fig. 2 Temperature sensitivity of the ultrasonic acoustic emissions (UAEs) from low-decibel (dB) to high-dB UAEs (Expt 3). (a) Temperature course inside ($T_{\text{Air, inside}}$; thick line) and outside ($T_{\text{Air, outside}}$; thin line) the growth chamber. (b) Mechanically induced high-dB UAE alternating with the low-dB UAE results in two distinct ranges of UAE (Expt 3). Moving averages of both UAE ranges are indicated by black lines.

almost straight line. The high-dB UAE kept its temporal characteristics; its amplitudes, however, were altered (Fig. 3).

A re-analysis of the results of Zweifel & Zeugin (2008) led to the conclusion that the statements and findings concerning the cavitation-induced UAE are not affected by the temperature artefact. However, the low-dB UAE is probably a temperature

artefact of the measurement equipment and we therefore exclude the possibility of a biological origin of the low-dB pattern shown in Zweifel & Zeugin (2008). The hypotheses concerning the possible origin of the low-dB UAE are therefore obsolete. In particular, the data shown in figs 6 and 7 of Zweifel & Zeugin (2008) lose their significance when temperature-corrected. The answer, therefore, to the question posed in the title of their paper, of whether UAEs are more than signals from cavitation in trees, has to be 'no'. As far as can be determined at present, they are nothing more. Nevertheless, we are convinced that the information content of UAEs is much bigger than what the current knowledge suggests.

General implications for UAE measurements

Use of piezoelectronics in combination with an acoustic signal conditioner to detect UAEs is common in such measurement systems, and we conclude from this investigation that the temperature sensitivity of the equipment may also have been underestimated in other UAE studies. Particularly affected may be investigations where large temperature gradients occur, for example in freeze–thaw experiments. Such experiments with temperature gradients of $> 10^{\circ}\text{C}$ could be substantially affected by an undetected temperature artefact of the measurement equipment.

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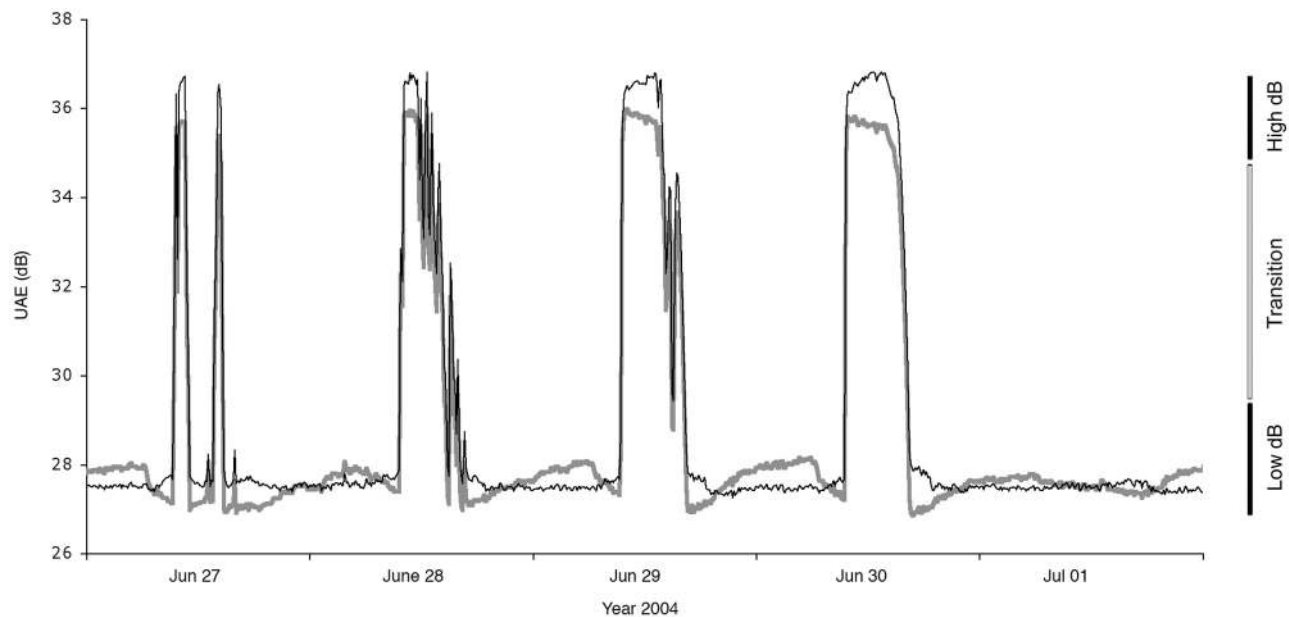


Fig. 3 Original (thick line) and temperature-corrected (thin line) ultrasonic acoustic emission (UAE) data from the field measurements in Valais, Switzerland. The time window corresponds to that of fig. 6(a) in Zweifel & Zeugin (2008).

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Key words: cavitation, embolism, low-dB signal, ultrasonic acoustic emission (UAE).

Meetings

Can Australian fire regimes be managed for carbon benefits?

Fire and Carbon Budgets Workshop, Working Group No. 53, Canberra, Australia, November 2008

Landscape fires affect ecosystem structure and function and mediate interactions between the biosphere and the atmosphere (Bond & Keeley, 2005; Bowman *et al.*, 2009; Flannigan *et al.*, 2009). There is emerging concern about the role of fires as a source of greenhouse gas emissions; future increases in fire activity (via global warming and land use) could exacerbate this problem. A meeting of the Working Group No. 53 ('Fire and Carbon Budgets'; http://www.vegfunction.net/wg/53/53_Fire_Carbon_Budgets.htm), of the Australia/New Zealand Network for Vegetation Function, was convened in Canberra in November 2008 to explore approaches for modelling emission and mitigation scenarios for Australian ecosystems, which are ubiquitously fire-prone.

'Potential for emission abatement in differing ecosystems will depend on a trade-off between "prescribed burning efficacy", on the one hand, and intensity/fuel consumption ("burning efficiency") on the other.'

To what extent will carbon-mitigation benefits accrue under differing regimes of management – particularly the use of prescribed fire to mitigate the impacts of unplanned fire? The potential for major emission abatement via mitigation of wildfire impacts has been discussed for forests in North America (Hurteau *et al.*, 2008) and in Europe (Narayan *et al.*, 2007). In Australia, prescribed fire has been used successfully in northern Australia to achieve greenhouse gas emission abatement (Russell-Smith *et al.*, 2009). A similar prospect has been mooted for southern fire-prone temperate eucalypt forests (Bushfire Cooperative Research Centre, 2006) but systematic analysis to support this proposition is lacking.



Ultrasonic acoustic emissions in drought-stressed trees – more than signals from cavitation?

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Summary

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- Ultrasonic acoustic emission (UAE) in trees is often related to collapsing water columns in the flow path as a result of tensions that are too strong (cavitation). However, in a decibel (dB) range below that associated with cavitation, a close relationship was found between UAE intensities and stem radius changes.
- UAE was continuously recorded on the stems of mature field-grown trees of Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*) at a dry inner-Alpine site in Switzerland over two seasons. The averaged 20-Hz records were related to microclimatic conditions in air and soil, sap-flow rates and stem-radius fluctuations de-trended for growth (ΔW).
- Within a low-dB range (27 ± 1 dB), UAE regularly increased and decreased in a diurnal rhythm in parallel with ΔW on cloudy days and at night. These low-dB emissions were interrupted by UAE abruptly switching between the low-dB range and a high-dB range (36 ± 1 dB) on clear, sunny days, corresponding to the widely supported interpretation of UAE as sound from cavitations.
- It is hypothesized that the low-dB signals in drought-stressed trees are caused by respiration and/or cambial growth as these physiological activities are tissue water-content dependent and have been shown to produce courses of CO₂ efflux similar to our courses of ΔW and low-dB UAE.

Key words: cavitation, drought stress, embolism, tree water deficit, ultrasonic acoustic emission (UAE).

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Introduction

Plants emit ultrasonic sounds (ultrasonic acoustic emission (UAE)) that can be detected with adequate sensors (Milburn & Johnson, 1966; Tyree & Sperry, 1989; Kikuta, 2003; Laschimke *et al.*, 2006). A widely accepted theory assumes that the acoustic emissions, which range between 20 and 300 kHz (Tyree & Sperry, 1989; Laschimke *et al.*, 2006), are induced by sounds from the abrupt release of tension in the conduit lumen as liquid water at negative pressure is replaced by water vapour very near to vacuum pressure (Hopwood, 1931; Sandford & Grace, 1985; Rosner *et al.*, 2006). The assumption is based on the cohesion-tension theory (Zimmermann *et al.*,

1995; Milburn, 1996), which states that water transport occurs along water potential gradients in the dead tube-like cells of the xylem, with transpiration, water adhesion to cell walls, and surface tension providing the forces necessary to lift the water against gravity (Koch *et al.*, 2004). If the water potential, equal to the negative of the tension of the water column, exceeds a sapwood-specific threshold, the water column ruptures (cavitation), air enters the flow path and the water column in the affected xylem cell becomes quickly vaporized (embolism). This event causes measurable UAE peaks (Tyree & Sperry, 1989).

The widely accepted interpretation of UAE peaks as sounds from cavitations, however, leaves many questions unanswered.

Zimmermann *et al.* (2004) demonstrated that negative water potentials induced by transpiration are not the only mechanisms by which water moves against gravity in trees. Laschimke *et al.* (2006) hypothesized a bubble system in the conducting xylem elements, which they claim is responsible for water transport and also for acoustic emissions. They maintain that it is the abrupt regrouping of the wall-adherent bubbles that causes the UAE decibel (dB) peaks. Thus, some investigations even question the accuracy of the cohesion-tension theory and its ability to explain water flow and cavitation in plants (Zimmermann *et al.*, 2004; Laschimke *et al.*, 2006). In contrast to these findings, several recent flow and storage models have been able to almost perfectly simulate the water relations of trees according to the cohesion-tension theory (e.g. Steppe *et al.*, 2006; Zweifel *et al.*, 2007).

An even larger question mark about the physical origin of the UAE arises when UAE below the dB range associated with cavitation is included and the focus is no longer on UAE dB peaks only. Most investigations applying UAE detection techniques have filtered out this low-dB range of sound under the assumption that these signals would not be distinguishable from background noise. Interpretations of UAE in trees have consequently almost exclusively focused on the dB peaks. The only exception we found is in Laschimke *et al.* (2006), who included UAE signals > 26 dB. The technical set-up in our investigation allowed the detection of continuous UAE between the high dB intensities (> 35 dB) associated with cavitation and the lowest detectable intensities associated with the background noise of the measurement system (< 25 dB). These signals in the so-called low-dB range (27 ± 1 dB) appeared to have a consistent pattern, which opens up a completely new perspective on the topic. We explored the question of where the signals in the low-dB range originate and how they fit in with the current understanding of UAE peaks.

To investigate UAE, we selected mature, naturally grown Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*) at a site where a wide variety of microclimatic and physiological information was recorded and modelled in parallel. The very dry site at Salgesch in Valais, Switzerland, was equipped with an ecophysiological field station (Zweifel *et al.*, 2005, 2006) that continuously recorded microclimatic profiles in the air and soil, as well as physiological parameters (sap flow, stem radius changes (ΔR), and potential evapotranspiration) of several tree species at 10-min intervals. Of special explanatory value was the so-called tree water deficit (ΔW) (Hinckley & Lassoie, 1981), which is deduced from ΔR by de-trending for growth (Zweifel *et al.*, 2005). The de-trending 'cleans' the original stem radius fluctuations from the fraction of radial growth. What remains is the water-related fraction of ΔR , which is proportional to the stem water content (Steppe & Lemeur, 2007) as long as there is no substantial depletion of the sapwood by cavitation (Zimmermann, 1983; Zweifel *et al.*, 2000). In addition, photosynthesis, transpiration, leaf water potential (Haldimann & Feller, 2004) and hydraulic proper-

ties (Sterck *et al.*, 2008) were manually measured on selected days. Further, the water potential conditions and stomatal regulation of Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*) were accurately simulated with a hydraulic feedback model (Zweifel *et al.*, 2007). The model enabled us to obtain valuable information on the flow and storage dynamics of tree water relations of these two tree species and the underlying species-specific physiological properties that cause them to respond differently to microclimate.

We aimed in this study: to prove the existence of consistent low-dB UAE signals; to relate them to high-dB UAE signals associated with cavitation; to explore the origin of the low-dB UAE; and to propose a potential mechanism to explain the signals of both qualities in the light of current ecophysiological knowledge.

Materials and Methods

Study site and trees

The study site near Salgesch (46° 19' 27" N, 7° 34' 40" E, 975 m asl) is located in Central Valais, Switzerland, an inner-Alpine valley characterized by a dry climate mainly caused by inner-valley shielding. The valley is oriented SE–NW, with the main storm tracks coming from the west and the wet air masses from the south. Mean annual precipitation over the past 20 yr has been *c.* 600 mm yr⁻¹. Annual precipitation at the site was 752 mm in 2001, 899 mm in 2002, 495 mm in 2003, and 500 mm in 2004.

Pubescent oak (*Quercus pubescens* Willd.) and Scots pine (*Pinus sylvestris* L.) are the most abundant tree species, and juniper (*Juniperus communis* L.) is the most abundant woody shrub in the vegetation of the site, which is on a south-exposed slope. Tree age was measured to be between 70 and 110 yr for oak and between 100 and 150 yr for pine at Salgesch (Zweifel *et al.*, 2005). The trees investigated were growing in patches (32 m² in area) surrounded by grass and bare rock. The eight trees included in the measurements had estimated ages of between 50 and 120 yr. The heights of the six selected oaks and the two selected pines ranged from 3.5 to 4.0 m and from 3.5 to 5.0 m, respectively, the stem diameters from 7.2 to 9.5 cm and from 11.9 to 23.2 cm, respectively, and the crown projection area on the ground from 8 to 18 m² for both species. The soil on this steep south-facing slope (-25°) is shallow with a maximum depth of 0.1–0.3 m at the site of measurement. Below the organic material is a mostly solid rock layer.

Climate data

Climate data were collected at the site with a solar-powered logging and steering system (CR10X; Campbell Sci, Shephed, UK). The microclimate was measured in the north- and south-exposed canopies and also outside the patch of trees. The sensor types and installations are described in Zweifel *et al.* (2006).

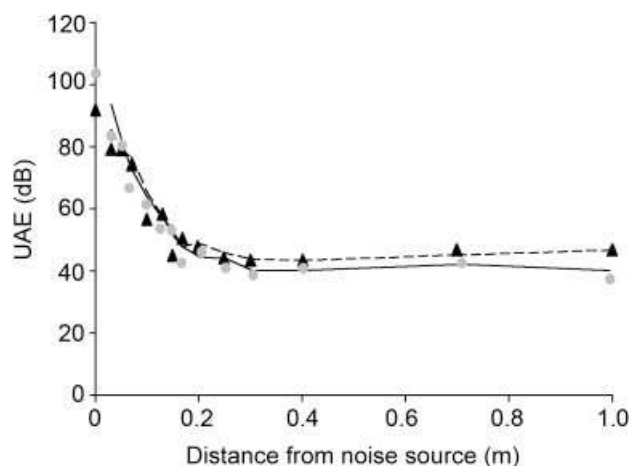


Fig. 1 Ultrasonic acoustic emission (UAE) propagation along the axis of air-dried oak (*Quercus pubescens*, circles) and pine (*Pinus sylvestris*, triangles) branches. The signal was caused by breaking a pencil lead on the branch surface.

Acoustic emission detection

UAEs were detected between 100 and 300 kHz using an acoustic signal conditioner with a peak detector (ASCO-P; Vallen System GmbH, Icking, Germany) in combination with a piezoelectric sensor head (VS150-M; Vallen System GmbH). The analogue signal output represented the UAE peak amplitudes of the respective measurement period. The execution interval of the data logger (CR10X; Campbell Sci.) was 20 Hz. The measurements were averaged and stored every 10 min.

About 2 cm² of bark was removed from the stem 50 cm above-ground and the sensor head was fixed in this hole (1–10 mm deep) to the bare xylem with adhesive tape. About 1 mm of silicon gel was applied between the sensor head and the stem to improve the sound propagation between the wood and the sensor, and to prevent the tissue drying out. The background noise of the measurement system was at 24 ± 1 dB.

The sensitivity of the UAE system was tested by breaking a pencil lead on the surface of air-dried pubescent oak and Scots pine branches and checking whether the system registered noise signal (Fig. 1).

Sap flow measurements

Sap flow was continuously assessed in small north- and south-exposed branches on six oaks and two pines with heat balance gauges (Dynagage; Dynamax, Houston, TX, USA). The distribution of the sap flow gauges within the forest patch is described in detail in Zweifel *et al.* (2006).

Leaf water potential

The water potentials of needles and leaves (Ψ_{leaf}) were measured with a pressure bomb (SKPM 1400; SKYE Instruments,

Powys, UK) according to Scholander *et al.* (1965). Two to five samples were measured per record and then averaged.

Stem radius changes and tree water deficit

Stem radius changes (ΔR) were measured with point dendrometers (ZB01; constructed by the authors) on six oaks and two pines (Zweifel *et al.*, 2006). The dendrometers were mounted 0.5 m above-ground on the north-facing side of each stem (facing up the hill). The electronic part of the dendrometer was mounted on a carbon fibre frame, which was fixed to the stem by three stainless steel threaded rods implanted into the heartwood. The sensing rod was kept pressed gently against the tree stem with a spring. The contact point of the dendrometer head was positioned 1 to 6 mm under the bark surface, but still within the outermost dead layer of the bark. The sensitivity of the dendrometers to temperature and humidity was found to be negligible as a result of the use of a weather-insensitive carbon frame and a temperature-insensitive electronic device (Weggeberpotentiometer LP-10F; Pewatron, Zurich, Switzerland). The resolution of the dendrometers in combination with the data logger used (CR10X; Campbell Sci.) was 0.4 μm .

Stem radius changes have two main components: radial growth and water-related swelling and shrinkage of the stem with water content (Daudet *et al.*, 2005; Zweifel *et al.*, 2005). ΔR de-trended for growth (Zweifel *et al.*, 2005) represents the tree water deficit (ΔW) as introduced by Hinckley & Lassoie (1981). ΔW typically ranges from 0 μm (fully hydrated state) to *c.* 800 μm (extremely dehydrated), and was found to be proportional to the reduction in stem diameter caused by the dehydration of the elastic stem tissues (mainly the phloem cells) (Daudet *et al.*, 2005; Zweifel *et al.*, 2005; Steppe *et al.*, 2006).

Hydraulic plant model to simulate water potentials

A tree–water relations model that includes species-specific hydraulic properties and stomatal regulation was used to simulate plant water potentials. The model is based on the hydraulic principles of a flow and storage system (Steppe *et al.*, 2006), and uses light intensity and feedback signals from the crown water potential, the tree water deficit and the current stomatal aperture to calculate stomatal regulation dynamics. For the model to be run, the potential transpiration of the crown, light intensity, and soil water potential are needed. The systemic feedback structure of the model design does not determine the course of stomatal resistances by a sophisticated mathematical formula, but rather formulates what factors have a (weighted) feedback effect on stomatal regulation. Thus, the model output for stomatal aperture and tree water potentials is the self-regulated response of the virtual model tree to the input factors in the form of the climatic conditions. Pre-set parameters for hydraulic resistances, storage capacities and further species-specific physiological properties determine the potential range of (model tree) responses. Model parameters,

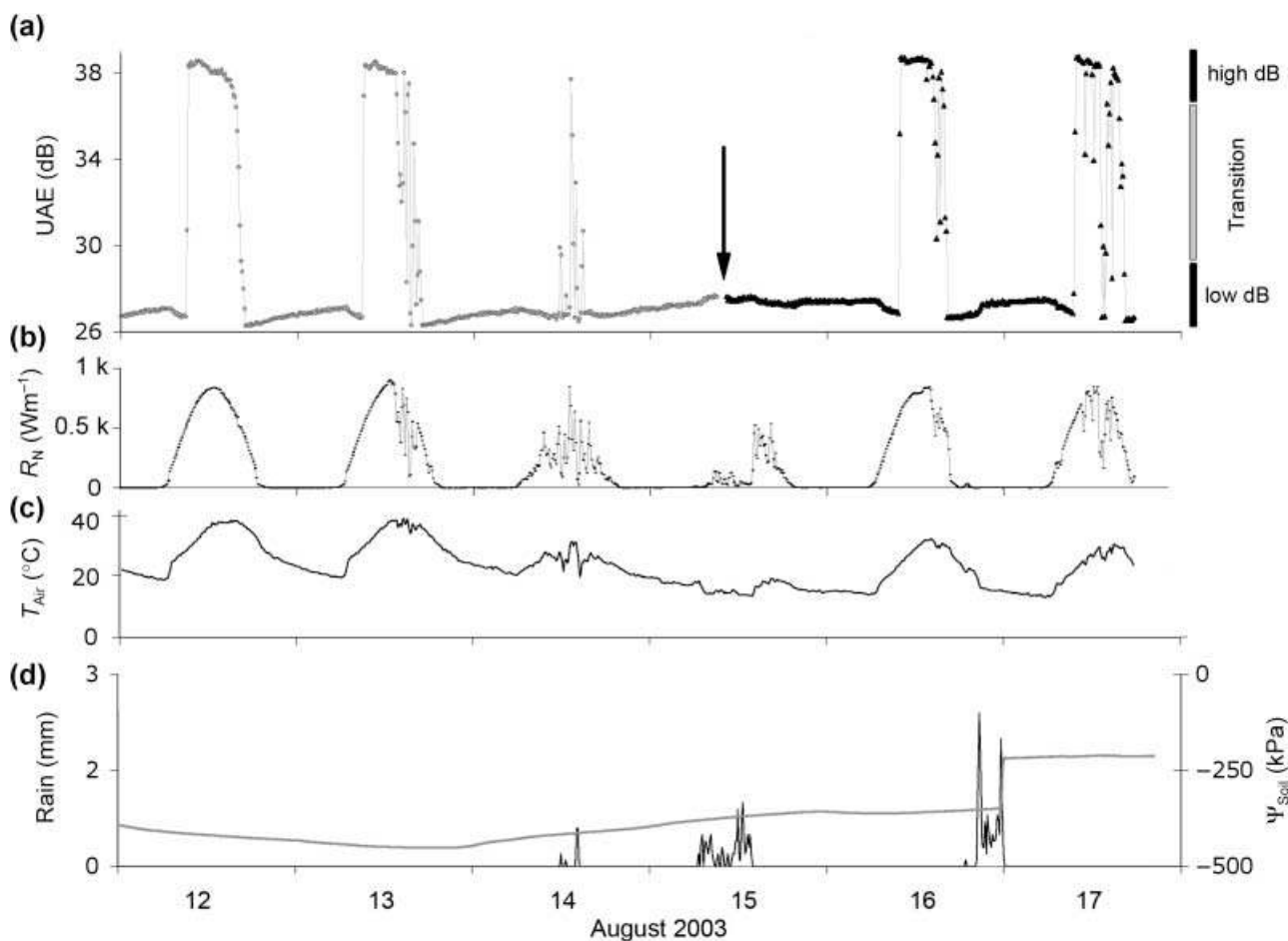


Fig. 2 Representative measurements of (a) ultrasonic acoustic emissions (UAEs) from pubescent oak (*Quercus pubescens*, grey symbols) and Scots pine (*Pinus sylvestris*, black symbols), (b) radiation (R_N), (c) air temperature (T_{Air}), (d) soil water potential (Ψ_{Soil} , grey line), and rain (black line) at Salgesch, Switzerland, in summer 2003. At noon on 15 August, the UAE sensor was moved from oak to pine (arrow). The UAE signals are assigned to the dB ranges 'low dB', 'transition', and 'high dB'.

and the detailed functionality and accuracy of the model, are discussed in Zweifel *et al.* (2007).

Results

Typical UAE patterns

UAE diurnally fluctuated within a low-dB range (27 ± 1 dB) at night and during sunless periods and abruptly increased to a higher-dB range (36 ± 1 dB) on sunny days. The signal remained in the low range all day only on rainy or very cloudy days (e.g. 15 August 2003; Fig. 2). The patterns were similar for the two tree species investigated.

The low-dB range was found to be distinctly above the background noise of the measurement system (23–25 dB). The transition between the low and high-dB ranges was usually very short, so there were few measurement points between the two extremes (Fig. 3). The minimum and maximum peaks of UAE decreased with increasing tree water deficits (Fig. 3).

Characteristics of the high-dB UAE range

The course of UAE signals within the high-dB range was complementary to the course of sap flow rates: as soon as UAE strongly increased, sap flow sharply decreased and vice versa (Fig. 4). An artefact resulting from a technical deficiency can be excluded because UAE and sap flow were measured with independent systems (different sensor types and data loggers).

To analyse the initial conditions triggering the transition of the UAE signal from the low to the high-dB range, time-points were selected when the dB increase was > 5 dB within 20 min. The corresponding physiological and microclimatic conditions of these time-points were then compared with the tree water deficit (Fig. 5). Four main results were derived from the conditions at the time of transition: (1) high-dB signals occurred over almost the entire range of drought intensities; (2) the higher the tree water deficit already was, the more extreme the microclimatic and physiological conditions had to be to induce more high-dB signals: in other words, high-dB

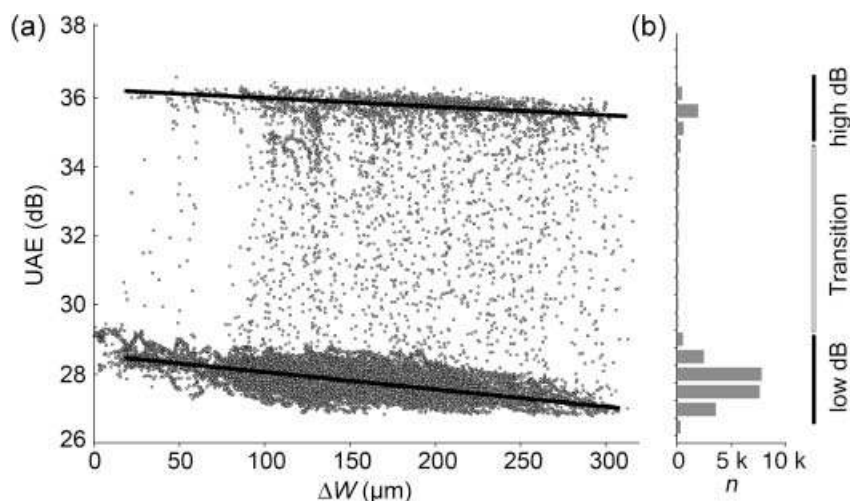


Fig. 3 Range of ultrasonic acoustic emission (UAE) and tree water deficit (ΔW) in pubescent oak (*Quercus pubescens*) in 2004. (a) 10-min values of UAE cluster in low- and high-dB ranges, with a transition range with fewer measurement points between the two extremes. The maximum and minimum UAE values depend on ΔW . Trends are indicated with black lines. (b) Frequency distribution of UAE, n , number of data points.

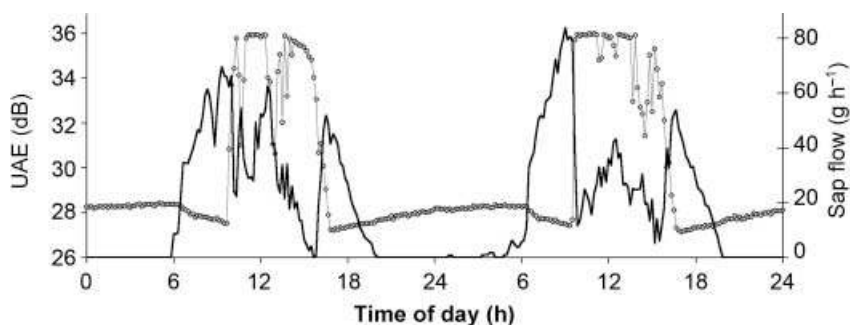


Fig. 4 Typical diurnal courses of ultrasonic acoustic emission (UAE, circles) in relation to branch sap flow rates (line) of pubescent oak (*Quercus pubescens*) at Salgesch from 24 to 25 June 2004.

signals occurred under more moderate conditions when the tree was well watered than when it was already drought-stressed; (3) after rehydration, the transition-initiating conditions returned to the pre-drought values; and (4) vapour pressure deficit (VPD) (Fig. 5a,d) and potential evapotranspiration (ET) (Fig. 5b,e) had good predictive power in combination with the tree water deficit (ΔW) for the occurrence of upward transitions. Soil water potentials (Ψ_{Soil}) had some predictive power for pine, but none for oak (Fig. 5c,f). No such specific patterns were found with other microclimatic variables such as light, wind or temperature (data not shown).

Characteristics of the low-dB range

When we ignored the high-dB range of the UAE signals and instead focused on the fluctuations within the low-dB range only, an unexpectedly close parallelism between the course of UAE and the inverse course of ΔW became apparent. Both courses showed a harmonic diurnal rhythm for pubescent oak as well as for Scots pine (Fig. 6). At night and when it was raining, UAE signals increased in parallel with the rehydration of the tree stems, and during the day, when the trees were transpiring, the signals decreased in parallel with the shrinking of the stems (e.g. 27 June 2004; Fig. 6a). Moreover, the daily

minimum UAE records were closely related to the corresponding mean daily values of ΔW over two seasons (Fig. 7).

Discussion

Two qualities of UAE signals

Ultrasonic acoustic emissions in trees have been measured and described many times in the past 30 yr (Tyree & Sperry, 1989; Perks *et al.*, 2004; Holttä *et al.*, 2005). Yet, such analyses have always focused on the peaks within the measurable UAE range where these peaks have been counted and interpreted as the ultrasonic sound from cavitations (Zimmermann, 1983). In contrast to these studies, we analysed the UAE dynamics within the entire intensity range of measurable UAE and found not only the well-known old pattern but also a new one. This new pattern appeared in the low-dB range only and has, as far as we know, never been described before. The course of the low-dB UAE gradually fluctuates in parallel with the inverse stem radius changes de-trended for growth (ΔW), which in turn represent the tree water status (Hinckley & Lassoie, 1981; Zweifel *et al.*, 2001, 2005). The origin of these low-dB UAEs is unclear but they seem to be closely connected to tree water relations (Fig. 6). In considering

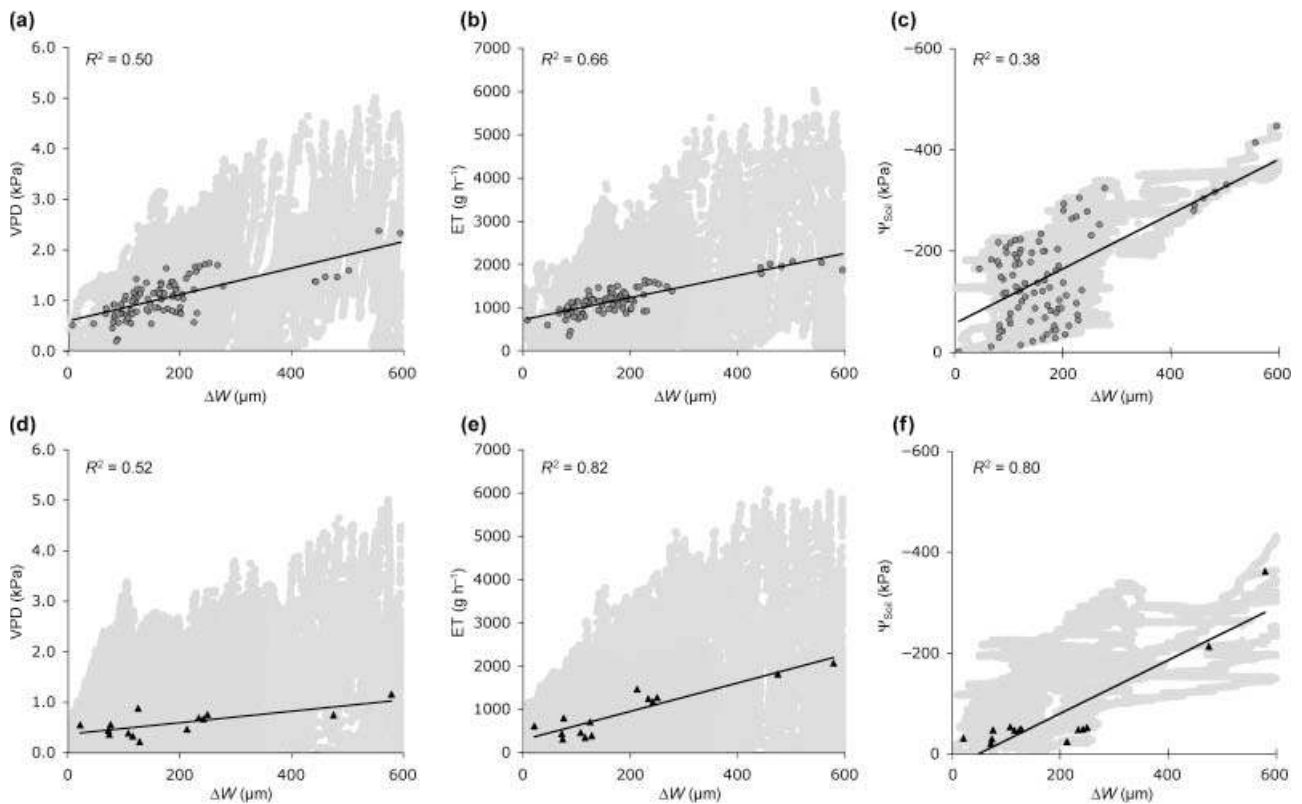


Fig. 5 Physiological and microclimatic conditions at the time when ultrasonic acoustic emissions (UAEs) initially increase from the low-dB range to the high-dB range on the morning of a sunny day (bold symbols). Light grey symbols represent the entire set of data. (a, d) Vapour pressure deficit (VPD) in relation to the tree water deficit (ΔW), (b, e) the potential evapotranspiration (ET) in relation to ΔW , and (c, f) the soil water potential (Ψ_{Soil}) in relation to ΔW . Data are for (a–c) pubescent oak (*Quercus pubescens*) and (d–f) Scots pine (*Pinus sylvestris*) at Salgesch, Switzerland.

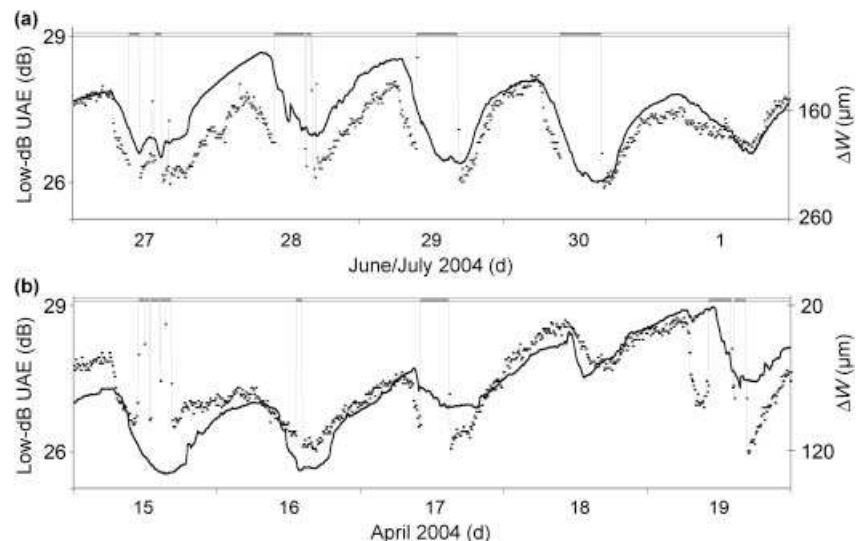


Fig. 6 Diurnal courses of ultrasonic acoustic emissions (UAEs, circles) in the low-dB range compared with the tree water deficit (ΔW , line) for (a) pubescent oak (*Quercus pubescens*) and (b) Scots pine (*Pinus sylvestris*) at Salgesch. Periods of high-dB UAE are indicated by a grey bar. Data are shown with a 10-min resolution.

possible mechanisms, we first discuss the characteristics of the two different UAE signals in relation to each other and the respective tree water relations. Secondly, we focus on the question of whether the changing stem water content might

explain the attenuation of a stable sound source, and thirdly we discuss possible origins of the low-dB UAE. Finally, we suggest a possible mechanism to describe the phenomenon physiologically.

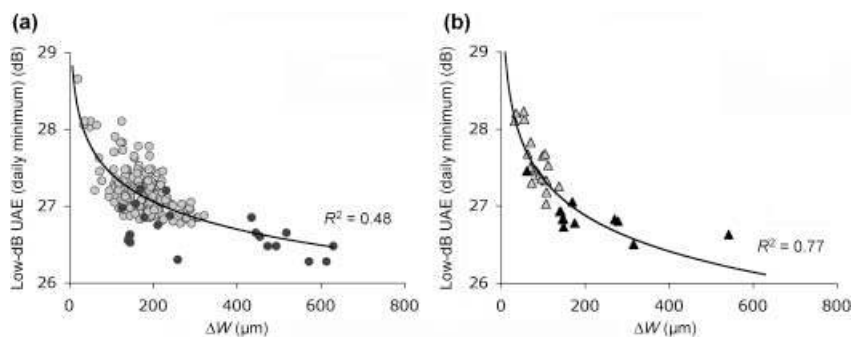


Fig. 7 Daily minimum values of ultrasonic acoustic emission (UAE) of (a) pubescent oak (*Quercus pubescens*) and (b) Scots pine (*Pinus sylvestris*) in relation to daily averages of tree water deficit (ΔW) over the two seasons 2003 (black symbols) and 2004 (grey symbols).

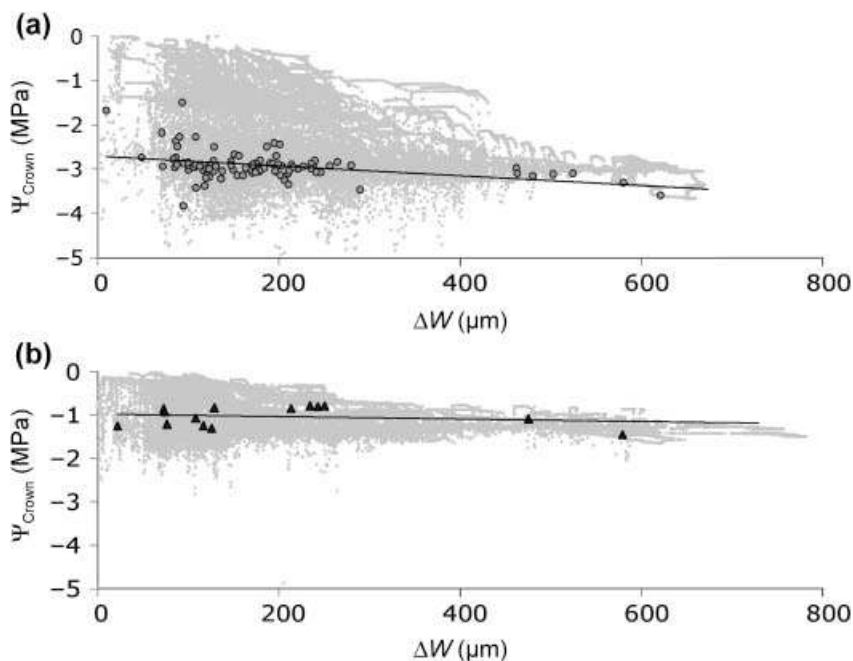


Fig. 8 Modelled leaf water potentials (Ψ_{Crown}) are related to measured tree water deficits (ΔW) of (a) pubescent oak (*Quercus pubescens*) and (b) Scots pine (*Pinus sylvestris*). Bold symbols indicate the conditions at the initial increase from the low-dB range to the high-dB range in a day. The light grey symbols represent the entire set of data. Values of Ψ_{Crown} below the regression line are assumed to induce cavitation.

Dependence on water relations

Tree water relations seem to trigger not only cavitations but also the low-dB UAE. On a typical day, the low-dB UAE course follows the inverse course of ΔW . The more the stem expands as a result of refilling of bark tissue with water (Steppe *et al.*, 2006), the louder the UAE becomes in the low-dB range (Figs 4, 6). The inverse pattern can be observed during the day. With increasing daylight and the onset of transpiration, the stem shrinks and the low-dB UAE starts to decrease. The decrease is gradual and continuous until cavitation occurs, at which point UAE abruptly jumps to the high-dB range.

The cavitation-inducing conditions were found to be associated with shifting thresholds for VPD and potential transpiration (Fig. 5), depending on the current tree water status. The higher the ΔW was, the more extreme the microclimatic conditions had to be to induce more cavitations. Thus, cavitation did not necessarily occur only in extremely dry weather. A reasonable explanation for the shifting threshold for cavitation is given in Tyree & Sperry (1989).

They concluded that, during a drought period, the most vulnerable xylem elements embolize first at a certain water potential and are then followed by the less vulnerable xylem elements at lower water potentials over the following days. Modelled leaf water potentials (Zweifel *et al.*, 2007) support this idea and suggest an almost constant cavitation threshold at *c.* -3 MPa for pubescent oak and *c.* -1 MPa for Scots pine (Fig. 8). Similar values for oak and pine species have been reported in other studies (Jackson *et al.*, 1995; Cochard *et al.*, 1996; Perks *et al.*, 2004; Holtta *et al.*, 2005). When there is enough water to rehydrate the stem tissues, the embolized xylem elements become refilled and the threshold for further cavitation is re-set to more moderate conditions. This explanation is also supported by early studies of Milburn (1973) and Pena & Grace (1986).

In contrast to the high-dB UAE, the low-dB UAE showed no abrupt changes and seemed to depend completely on ΔW (Fig. 7). During periods with cavitations, the measurements suggested that the low-dB sound was continuous without interruption. The low-dB UAE restarted its own course almost

exactly on the continuously measured course of the inverse ΔW after a 'cavitation break'. Even very slight changes in ΔW , for example between two cavitation periods, were detectable in the low-dB UAE, and were particularly evident in pubescent oak on 27 June 2004 (Fig. 6a). However, it was not possible to monitor the exact course of low-dB UAE during cavitation, as it was covered by the high-dB signals.

No attenuation as a result of the changing tissue water content

To find the origin of the low-dB UAE, it is essential to know whether there could be a constant sound source whose intensity is changed by attenuation, for example by the changing tissue water content. If this cannot be excluded, it can be assumed that the low-dB UAE could also be of abiotic nature. However, Tyree & Sperry (1989) concluded that the velocity of sound propagation through water-saturated wood is about the same as in dry wood, but higher than in pure water. This means that the ultrasonic waves measured on the surface of tree stems are mainly propagated through cellulose and not through water. Further, our test of the sensitivity of the measurement system indicates that sound sources detected as UAE are likely within a distance of < 30 cm (Fig. 1). We therefore exclude the possibility that attenuation continuously changes with stem water content and maintain that it is more likely to be attributable to a change in the low-dB UAE source itself.

Possible origins of the low-dB UAE

The high-dB UAE is very likely to be induced by cavitations, which can be explained by the cohesion-tension theory. There is, however, no comparable theory to explain the pattern of the low-dB UAE and the corresponding tissue water content. To find possible origins of the low-dB-UAE, we looked for physiological dynamics that produce a similar diurnal pattern to that of the low-dB UAE course. Dynamics such as those of sap flow, which could produce a water flow noise in the low-dB range, did not fit at all (Fig. 4). The highest low-dB UAE occur before dawn, which is when the least water movement occurs because the water potential gradients from the day before will have mostly levelled off within the tree by then.

Another possible origin of sound could be the mechanical noise of the stem radius expanding and shrinking. Kikuta & Richter (2003) reported a slight increase in UAE signals depending on the hydration status of living *Evonymus latifolia*. However, they counted UAE peaks and did not continuously record low-dB UAE. Their finding might support our result that high-dB signals occur sooner in well-watered plants rather than being a strong indication of a mechanical noise. Further, this theory does not explain why the low-dB UAE does not stop when the stem stops expanding towards dawn (Fig. 6). If stem expansion or contraction really produced a UAE-relevant sound, we would expect the diurnal low-dB UAE

course to resemble the first deviation of ΔW , which is obviously not the case.

Two processes recently reported in the literature suggest themselves as possible origins of low-dB UAE: the respiration and the metabolic growth activity of cambium or ray parenchyma cells. These processes, however, were not measured in this study. The two processes are coupled to each other (Maunoury *et al.*, 2007; Teskey *et al.*, 2008) and, according to Saveyn *et al.* (2007a,b), produce diurnal courses of CO₂ efflux from the stem similar to the courses of the bark water content under dry conditions. What seems to be crucial is the actual degree of drought stress. As long as the water content, and thus the turgor pressure, are sufficient for growth, the diurnal course of respiration follows temperature (Maunoury *et al.*, 2007; Saveyn *et al.*, 2007b, 2008; Teskey & McGuire, 2007). However, as soon as drought stress becomes more severe, respiration no longer follows temperature but is more closely related to stem water content (Saveyn *et al.*, 2007a,b). The missing water in the cambium and phloem cells is assumed to inhibit the biochemical activity of growth and respiration, independent of the current temperature. This finding has been recently corroborated at a higher level of organization by a report of distinct increases in total ecosystem respiration during wet periods after a drought (Granier *et al.*, 2007).

The measurements obtained from Scots pine and pubescent oak at our site indicate that the trees were at a drought stress level at which respiration corresponded to tree water deficit and not temperature. Under such conditions, the low-dB UAE and the stem water content match stem respiration, which, in turn, is coupled to metabolic activity. At night and during periods when the turgor pressure in the cambium increases, radial growth occurs (Steppe *et al.*, 2006) and leads to an increase in the maintenance metabolism. As a consequence, respiration increases, which probably causes the increase in UAE within the low-dB range. The low-dB signal we measured could, it seems, be produced either by the expansion of newly built cells (not water-related tissue expansion) or by an increased concentration of CO₂ (Saveyn *et al.*, 2008; Teskey *et al.*, 2008).

A potential mechanism to explain low-dB emissions

One recently published theory by Laschimke *et al.* (2006), which partially contradicts the cohesion-tension theory, suggests that a bubble system causes the ultrasonic emissions. They demonstrated how air-saturated water forms clusters of gas bubbles in the pits and holes of the wall in the water-conducting systems of both a 4-yr-old *Ulmus glabra* and a perforated glass capillary. These micro-bubbles are initially spherical (*c.* 1–50 µm in diameter, depending on pore size), and with increasing size coalesce to form flat bubble aggregates. The abrupt regrouping of the wall-adherent spherical bubbles may well be the reason for the UAE peaks (> 26 dB) they detected. Further, the authors concluded, from studying the

temporally highly resolved waveforms of UAE, that coalescing bubbles lead to a 'violent vibration' which might be another source of UAE in the low-dB range. Their theory could probably help to explain our high- and low-dB UAE in a mechanistic way.

In combination with our observations of the timing of increased low-dB UAE, the increased production of CO₂ during the night, as a result of the turgor-dependent physiological activity of the cambium (growth and maintenance metabolism), could explain why more gas is infiltrated into the water-conducting system. The additional CO₂ leads to more bubbles or increases the size of bubbles, which in turn increases the number of coalescences and thus the intensity of the low-dB UAE. Our speculation that the low-dB UAE is not affected by the high-dB UAE, but is just acoustically drowned, is consistent with the fact that a water-conducting cell undergoing cavitation is well insulated from its neighbouring cells and, thus, the low-dB-producing bubble system is not disturbed.

Conclusion

We found convincing evidence that, in addition to the well-documented cavitation-induced UAE, there is another biotic source of UAE that leads to low-dB signals which closely follow the stem radius changes de-trended for growth. The origin of the low-dB UAE is uncertain. However, there is some evidence that these signals are produced by stem tissue processes that depend on water saturation such as growth, respiration and maintenance metabolism. If this assumption is correct, we would expect a change from the water dependence of the low-dB UAE to a temperature dependence, with consequently a different temporal pattern under less drought-stressed conditions. To test this and to obtain a more complete mechanistic explanation, further investigation of low-dB UAE in trees is needed.

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