Ecological Indicators 176 (2025) 113580

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Ultrasonic acoustic emissions as indicators of tree drought stress in outdoor forest settings: Testing the concept using cut saplings

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ARTICLE INFO

Keywords:
Forest dieback
Air seeding
Sound emissions
Acoustic indices
Bioacoustics

ABSTRACT

Drought-induced air embolism (air blockage of xylem sap) is an important mechanism behind observed forest declines and serves as a physiological link between climate and reduced tree growth. It has been known since the 1980 s that vapour bubbles generated inside drying plant tissue emit ultrasonic acoustic emissions (UAEs), but it remains uncertain whether acoustic studies can be applied inside complex soundscapes of forests to monitor xylem embolism in real-time. In this study, we show that microphones mounted on, or adjacent to, stems of young birch (*Betula pendula*) and Scots pine *(Pinus sylvestris),* can indeed be used in outdoor environments to detect embolism in the xylem sap. Vapour formation via cavitation in the xylem was artificially generated inside cut saplings by a surfactant that reduced the cohesive forces of water and forced the water column inside the xylem to break. Birch trees with induced xylem embolism experienced reduction (−60 ± 11 %; mean ± sterr) in water uptake in similar to pine (−49 % ±5). Both control trees and trees with induced embolism generated UAEs, but trees with hydraulic failure due to xylem embolism emitted UAEs more frequently than control trees. The vertical distribution of UAEs from the stems differed between species where birch only emitted more UAEs than the control from basal part of the tree trunk (+58 % ±28), while these pulses where emitted more often from both basal sections (+35 % ±2) and upper sections (+53 % ±4) of the pine trunk from our treatment. We conclude that both substrate-borne and airborne UAEs can be used to indicate hydraulic failures inside forests and that bioacoustics monitoring reveal a previously unknown species-specific difference in how embolism appear inside the trunk of birch and pine.

1. Introduction

Drought is a disturbance known for causing tree mortality in all forested continents of the world (Bennett et al. 2015). For example, water limitation is an important driver of regional-scale tree mortality and forest decline in Europe (Senf et al. 2020, Laudon et al. 2024), America (Clark et al. 2016) and Asia (Du et al. 2024). Blockage and hydraulic failure due to formation of vapour bubbles (embolism) developing in the xylem sap constitute one of the main physiological mechanisms behind drought-induced tree mortality and reduced tree productivity (Brodribb and Cochard 2009, Anderegg et al. 2012, Choat et al. 2012). The realization that embolism can occur during periods of droughts and that xylem sap transport does not easily recover from this physiological condition, has served as a rationale for research linking species-specific embolism vulnerability to environmental stressors (Lopez et al. 2005). While embolism and refilling cycles could be common in some plants, it is believed that these cycles can cause fatigue and lower the xylems resistance to drought (Hacke et al. 2001). Yet, our understanding about xylem emboli formation as function of plant species and hydraulic thresholds are still limited (Choat et al. 2018). In other words, development of a non-invasive method that could monitor xylem embolism inside forested environments would be an important advancement that could lead to improved mechanistic understanding regarding how trees respond to drought in forests.

When studying embolism, one methodological shortcoming is that techniques detecting air formation along xylem conduits are typically dependent on destructive sampling of plant compartments (needles, branches or trunk discs) and artificial laboratory settings (Mayr and Rosner 2011, Cochard et al. 2013). Here, destructive sampling approaches makes it impossible to monitor temporal responses for the very same plant compartments, while artificial laboratory settings introduce uncertainties when extrapolating findings to *in situ* conditions. Noteworthy, methods considered to be non-invasive, such as magnetic resonance imaging (Holbrook et al. 2001) or *x*-ray microtomography

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https://doi.org/10.1016/j.ecolind.2025.113580
Received 16 December 2024; Received in revised form 12 March 2025; Accepted 5 May 2025
Available online 26 May 2025

(Brodersen et al. 2010, Torres-Ruiz et al. 2017) are still dependent on destructive sub-sampling of tree compartments when studying embolism. However, since the discovery that drying leaves and needles generate both audible sound (Milburn and Johnson 1966) as well as ultrasonic sound (Tyree et al. 1984), acoustic monitoring has served as a non-invasive laboratory-based tool to study xylem embolism inside plants (Cochard et al. 2013). Acoustic approaches target ultrasonic (>20 kHz) acoustic emissions (UAEs) that are generated as the water column inside the xylem experience vaporization of liquid water (cavitation) as the negative hydrostatic pressures during drought exceed the cohesive forces of water. Number of UAEs originating from cavitation bursts is believed to be a function of number of tracheids experiencing embolism (Tyree et al. 1984), where the energy of the burst is reflecting the volume of the affected xylem cell (Johnson et al. 2009, Mayr and Rosner 2011, Ponomarenko et al. 2014). It has also been demonstrated that non-conducting (dead) cells may emit UAEs when they dehydrate (Kikuta 2003).To date, acoustic methods have mainly relied on laboratory apparatuses handling only segments of plants (Tyree and Sperry 1989, Rosner et al. 2006, Ponomarenko et al. 2014) or measurements done on drying plants inside acoustic chambers (Nardini et al. 2024) or greenhouses (Khait et al. 2023). However, Zweifel and Zeugin (2008) demonstrated that UAEs from cavitation could be detected from trees growing *in situ* if the bark was removed. The rationale for removal of bark was that UAEs show great attenuation in plant tissues and previous studies attempting to acoustically detect cavitation from intact plants with intact bark has to date failed (Khait et al. 2023).

However, before acoustic monitoring of embolism can become a practical tool for foresters interested in *in situ* monitoring xylem embolism, there are lingering research questions that need to be answered. Can UAEs from xylem embolism be detected inside complex soundscapes of forest without removing the bark of the trees? Is there interference from UAEs derived from other process than cavitation? The latter question is motivated by studies suggesting that UAEs may be generated by respiration or cambial processes (Zweifel and Zeugin 2008), micro-bubble formation inside the xylem (Laschimke et al. 2006) or pressure waves making the xylem function like organ-pipes (Dutta et al. 2022). What adds further uncertainty to the use of acoustic detection of embolism *in situ* is the notion that true cavitations are not occurring inside the xylem but rather that emboli are formed as air enters the xylem via inter-vessel pit membranes ('air seeding') (Nardini et al. 2024). Clearly, uncertainties regarding involved processes, sound interference and attenuation of high frequency sounds constitute a challenge for detecting embolism acoustically inside complex soundscapes of forests. However, we notice that advancements, both in acoustic hardware technologies and in post-processing filtering of background noise (Rosner et al. 2006, Mayr and Rosner 2011, Wolkerstorfer et al. 2012, Oletic et al. 2020, Bonisoli et al. 2024), have improved precision of bioacoustics approaches since the pioneer work on xylem sap cavitation in the 1980 s (Tyree et al. 1984). Therefore, we hypothesized that field-based and non-invasive microphone systems can register increased frequency of UAEs originating from tree-trunk xylem embolism inside a forested environment. We test our hypothesis on whole trees (*Betula pendula* and *Pinus sylvestris*) in a forested setting where we artificially enhanced xylem embolism formation within our treatments and compared their acoustic profiles with that of control trees.

2. Methods

Our outdoor experiments were conducted near the Svartberget Research Station (64°14′32.2″N 19°45′36.4″E) in northern Sweden. The area (located 230 m.a.s.l) is part of the boreal climate zone and has a mean annual temperature of 1.8 °C and mean annual precipitation of 614 mm (Laudon et al. 2013). Here, we selected a forested site that represented a complex soundscape due to its outdoor setting. Background sound sources included forest sounds (wind, rain, birds, insects, etc.) as well as potential background disturbances from easily audible sources coming from cars passing at a nearby (50 m) road as well as human voices coming from visitors to the research station (50 m).

In the adjacent forest, we selected 32 trees with eight trees in each treatment-specific group with the following properties: i) *Betula* control, height = 223 ± 5 cm (average ± stderr), Ø =2.0 ± 0.1 cm; ii) *Betula* treatment, height = 224 ± 6 cm, Ø =1.9 ± 0.1 cm; iii) *Pinus* control trees, height = 181 ± 6 cm, Ø =3.5 ± 0.2 cm; and iv) *Pinus* treatment, height = 183 ± 6 cm, Ø =3.2 ± 0.2 cm. We covered all trees with a non-transparent tarp to cease photosynthesis prior cutting and transportation to the study site within 30 min. Here, trees were cut under water when submerged in a water tank to avoid air seedings in the xylem sap and were held in fixed volume bottles with water to allow re-activation of photosynthesis after tarp removal. The tree was allowed to adopt to the new conditions for 1 h after cutting. At this pre-treatment stage, we measured stomatal water conductance of annual shoots using a portable Li-Cor 6400xt (Lincoln, N.E., USA). Stomatal conductance was converted to leaf/needle transpiration by normalizing measured fluxes to the leaf/needle surface area (mmol water cm^{-2}), where the latter was inferred from scanned images analysed using ImageJ software. Calculated leaf/needle transpiration rate is henceforth in the text referred to as 'transpiration' for simplicity. During the experimental phase involving birch trees (20 June to 2 July), average air pressures were 12 ± 0.6 hPa, daily max temperature 21 ± 2 °C and precipitation 2 ± 1 mm (climate data from the Svartberget Research Station). For the pine trials (3 July to 12 July), average air pressures were 13 ± 0.5 hPa, daily max temperature 20 ± 1 °C and precipitation 4 ± 2 mm.

We used a paired study design, where we analysed the acoustics of a control and a treatment tree using two contact microphones per tree and day (see description of microphone system below), where one was mounted about 0.3 m from the base (lower microphone) and one about 1.3 m from the base. The control tree received tap water while the other tree (treatment) was exposed to a solution of Tween-80 (0.5 % v/v). This mixture has been shown, through measures conducted using calibrated surface tensiometers, to have a surface tension of 36 N m^{-1}, corresponding to about half the surface tension of water (Chu and So 2001). The weaker cohesive forces for the Tween-80 (0.5 % v/v) has also been shown to cause xylem embolism in transpiring *Pinus sylvestris* seedlings (Hölttä et al. 2012). We monitored the acoustic signals in these two-growth media for 3 h. After 3 h, we repeated the plant transpiration measurements. Water loss from the containers, measured volumetrically with a graded measuring flask (precision 0.1 ml) at the end of the experiment, was used as a measure of total water uptake.

*Microphone systems*To monitor sounds from the trees, we employed two distinct acoustic recording setups: (i) four 32-bit, 2-channel recorders (Zoom F3) each equipped with a pair of active inline preamplifiers (sE Electronics DM2 TNT) one per channel, accompanying adapters (6.3″ female to male XLR connectors), and rubber-sealed, shielded contact microphones (LeafAudio, Leipzig), one per channel; and (ii) a 32-bit, 2-channel recorder (Zoom F3) with a single active inline preamplifier (sE Electronics DM2 TNT) and a condenser ultrasound microphone (Avisoft Bioacoustics CM16/CMPA-P48). We henceforth in the text refer to the first systems as the 'contact microphone system' and the second as the 'distant microphone system' as it had no physical contact with the trees. Both systems operated at a 192 kHz sampling rate. The contact microphone systems were mounted directly on each tree trunk without removal of the bark: one microphone was positioned approximately 0.2 m from the base and the other at a height of about 1 m. The distant microphone system was set up on a tripod with its microphone directed toward the lower 0.2 m of the trunk at a distance of <3 cm. Both microphone systems were covered with sound-attenuating polyurethane (PU) foam to the sides of the microphone to enhance the signal-to-noise ratio of the focal acoustic source.

2.1. Processing of acoustic data

Audio files were analyzed using a custom Python script designed to detect and quantify acoustic pulses within a defined frequency range (20–65 kHz). To isolate high-frequency sounds, we applied an 8th-order Butterworth high-pass filter (48 dB per octave roll-off) at 20 kHz. Pulse detection was performed using a prominence threshold to identify significant peaks in the power spectrum. Detected pulses were logged with relative and absolute timestamps, frequency, and power values.

2.2. Statistics

Both tree physiological and bioacoustics data were not normally distributed within the two groups (failed a Kolmogorov-Smirnov test of normality). Therefore, differences between the control and the treatment were tested using a nonparametric Wilcoxon Signed-Ranks Test, paired by the day of measurements. We used total water uptake (ml tree^{-1}), frequency of UAEs (Hz), power of the UAEs (dB) and total number of UAEs (numbers) during the 3-hour test period as dependent variables, while we used the treatment/control ratio (unitless) of the transpiration measurements when comparing conditions prior and after exposure to Tween-80. To assess to what extent substrate-borne UAEs transitioned into airborne signals, we compared UAE numbers measured using the contact microphone system (mounted at the lower part of the stem) with the distant located microphone, using a Pearson linear regression. Here, the residuals where visually inspected and judged to fulfil the assumption of normally distributed data. All statistics was conducted using IBM SPSS Statistics, Version 29.

3. Results

In the birch trees with induced embolism (Fig. 1a), the water uptake was lower in comparison to the control trees (Table 1, Z = -2.521, P = 0.012). Here, control trees used 68 ± 11 ml (average ± stderr) water while the birch with embolism used 25 ± 6 ml, corresponding to an average reduction of about 60 % in our pairwise comparison. In comparison to pre-exposure conditions, the transpiration rate decreased (Z = 2.533, P = 0.012) by about 50 % after our embolism treatment (Fig. 1b). Similar to birch, the average water uptake and transpiration rates of pine decreased (Fig. 2ab). Control pine trees used 231 ± 21 ml,

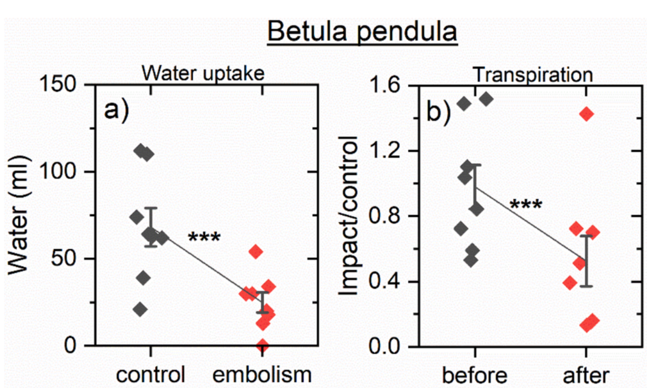

Fig. 1. A) Effect of the induced embolism on water uptake during the experiment. Measures for the control birch trees (black diamonds) and the treated birch trees (red diamonds) are plotted separately. b) Effects of induced embolism on birch transpiration. Here, treatment responses are expressed as a ratio between the pairwise measurements for trees with embolism and control (impact/control ratio). Measured values prior to the treatment (black diamonds) and after the treatments (red diamonds are plotted separately. Error bars indicate standard error around the mean values. Statistical significant ($P < 0.05$) difference between the control and treatment is indicated with *** in the panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

while pine with induced embolism utilized 118 ± 41 ml, corresponding to a reduction (−49 %) in water uptake (Z = -2.524, P = 0.028). Notably, the water uptake in the control pine trees was on average more than three times higher than for the control birch trees. However, needle transpiration did not differ between control and treatments.

We registered UAEs using both the contact microphone system (Supporting Information Fig. S1) and the distant microphone system (Supporting Information Fig. S2). A summary of the acoustic properties (frequency and power) of the UAEs and their relation to weather conditions, water uptake, their total numbers and calculated relative (%) effects in our pairwise comparisons are also shown in the supporting Information (Table S1). In short, there were no differences in frequency and average powers between the control and treatment or between the birch and pine ($P > 0.6$). Here, the UAEs were characterized by an average frequency of about 30 kHz and their power average power varied typically between −66 dB and −72 dB.

There were on average + 58 % ±28 more UAEs detected in the Tween-80 treatment than in the control birch when measured using the lower sensors at the base of stem (Fig. 3), i.e. an effect corresponding to an extra 0.2 events min^{-1} (Z = 2.530, P = 0.011). For birch, there was no difference between control and treatment when measured using the upper contact microphones ($P > 0.3$) and the UAEs were much less frequent (−92 %) in this section of the tree trunk. The total number of UAEs was also higher in the pine trunk with embolism in comparison to the control. However, in contrast to the birch, UAEs were elevated both in the lower (Z = 2.530, P = 0.011) and upper parts (Z = -2.588, P = 0.010) of the pine trunk. For the lower part of the trunk UAEs increased with an average + 35 % ±5, while this increase was + 52 % ±10 in the upper part of the stem. We noted, however, that UAEs in general were more frequent in our birch trees than in the pines.

There was a positive correlation between substrate-borne UAEs measured using the contact microphone system and the airborne UAEs measured using the distant microphone system (Fig. 4, R2 = 0.77, $P < 0.0001$). However, the average slope of the regression indicated that the distant microphone captured only about 82 % of the emitted substrate-borne vibrations.

4. Discussion

In line with our hypothesis, inducing embolism by treatment with the detergent Tween-80 enhanced the rate of UAEs occurring in the stems of birch and pine trees. Indeed, this shows that the sound of collapsing water columns can be detected inside tree stems in a forest setting, despite its complex soundscape and risk for attenuation of the high-frequency sounds emitted inside the trees. The latter is worth noting, given that a previous study has observed that it is difficult to detect UAEs coming from trunk cavitation from plants with bark in indoor greenhouse environments (Khait et al. 2023). Nevertheless, both the passive contact microphones and the condenser ultrasound (distant) microphone managed to capture substrate-borne and airborne UAEs coming from intact tree trunks without any removal of bark. Moreover, our bioacoustics approach was able to identify an intriguing difference in responses between birch and pine. That is, UAEs induced by our treatment were emitted both from basal and upper sections of the trunk for pine, but only from the basal part of the birch, suggesting contrasting modes of hydrological failures inside the two species linked to their different xylem anatomies where birch has a mixture of vessels and tracheids while pine only has tracheids.

Our surfactant treatment caused a rupture in the water column in the sapwood, similar to findings by Hölttä et al (2012), and as indicated by the reduced water uptake observed in both birch and pine. In our treatments, the frequency of UAEs increased with the same magnitude as the reduction in water uptake: in birch, UAEs increased at the base of the trunk with about 58 % at the same time as the water uptake was reduced with about −60 %, while the UAEs increased with on average 33–45 % for pine that experienced a reduction in water uptake with about −35 %

Table 1
Summary statistics of a pairwise Wilcoxon Signed-Ranks Test assessing differences between control trees and our treatments. Water uptake and ultrasonic emissions (UAEs) were measured volumetrically (ml) and numerically (total numbers), while effects on leaf/needle transpiration was evaluated by comparing the measured impact/control ratios prior and after our treatment. Effects on UAEs were measured on negative ranks as indicated by negative Z-scores. Significant effects ($p < 0.05$) are shown in bold.

Tree	Group	Measurement	N	Unit	Ranks (+/-)	Z-value	P-value
Birch	Control vs treatment	Water uptake	8	ml	8/0	−2.521	**0.012**
	Control vs treatment	Transpiration	8	untiless	8/0	−2.521	**0.012**
	Control vs treatment	UAEs (lower)	8	number	8/0	−2.524	**0.012**
	Control vs treatment	UAEs (upper)	8	number	5/2	−1.035	0.301
Pine	Control vs treatment	Water uptake	7	ml	6/1	−2.197	**0.028**
	Control vs treatment	Transpiration	8	untiless	4/4	−1.122	0.262
	Control vs treatment	UAEs (lower)	8	number	8/0	−2.530	**0.011**
	Control vs treatment	UAEs (upper)	8	number	8/0	−2.588	**0.010**

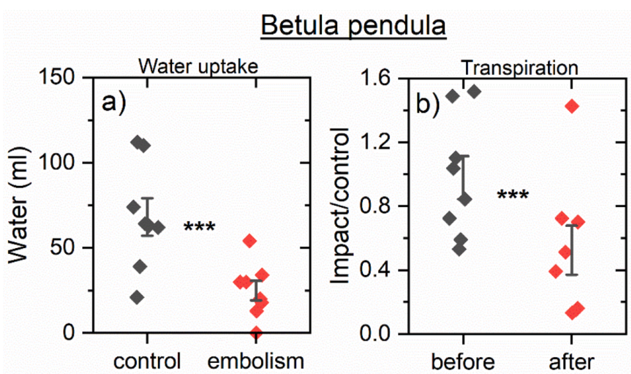

Fig. 2. a) Effect of the induced embolism on water uptake during the experiment. Measures for the control pine trees (black diamonds) and the treated pine trees (red diamonds) are plotted separately. b) Effects of induced embolism on pine transpiration. Here, treatment responses are expressed as a ratio between the pairwise measurements for trees with embolism and control (impact/control ratio). Measured values prior to the treatment (black diamonds) and after the treatments (red diamonds are plotted separately. Error bars indicate standard error around the mean values. Statistical significant ($P < 0.05$) difference between the control and treatment is indicated with *** in the panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table S1). Indeed, a proportional response between UAEs and hydrological responses inside the trunk is a prerequisite for extracting quantitative information regarding drought responses inside trees. Differences between control and treatment relating to water uptake, transpiration and UAEs were notably larger for birch than pine, a finding in line with the general notion that gymnosperm xylems are less sensitive to cavitation than that of angiosperms (Maherali et al. 2004, Dulamsuren et al. 2019, Franklin et al. 2023). While the exact mechanism behind drought induced embolism at a species-specific level remains largely unresolved, our results support previous studies showing that *Betula pendula* is more vulnerable to embolism than *Pinus sylvestris* (Cochard et al. 2005). Between species differences in sensitivity for embolism has typically been attributed to differences in the xylem conduit sizes, where increased diameter of the conduits increase risk of cavitation (Sperry et al. 1994, Köcher et al. 2012). However, the different structures and function of cavities (bordered pits) in the cell walls of the xylem conduits has been argued to be a more direct driver of cavitation resistance (Li et al. 2016). In these cavities are pit membranes situated that both regulates water transfer between xylem conduits, as well as limits the spread of emboli and pit membrane properties have been highlighted of central importance for xylem embolism. For example, pit membrane thickness is believed to affect sensitivity for embolism in angiosperms (Li et al. 2016) and size differences between the non-porous (torus) and the porous area (the margo) has been listed as strong predictors of cavitation in conifers (Bouche et al. 2014). While we cannot determine to what extent the width of xylem sap conduits or the pit membrane properties contributed to the more frequent cavitation in birch, we note that more frequent UAEs at the basal part of the trees support the notion that size of conduits are main drivers of cavitation.

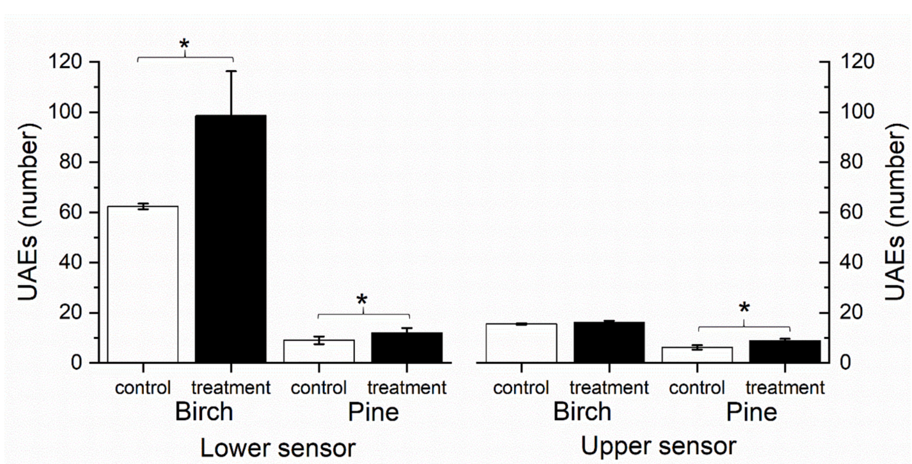

Fig. 3. Bar-plot showing the number of UAEs pulses detected using the contact microphone system mounted at the base of the stem (lower sensor) and at height of the stem (upper sensor). The number of UAEs are reported for the control (white bar) and the treatment (black bar) for the birch trees (left) and the pine (right). Significant ($p < 0.05$) differences are indicated with *.

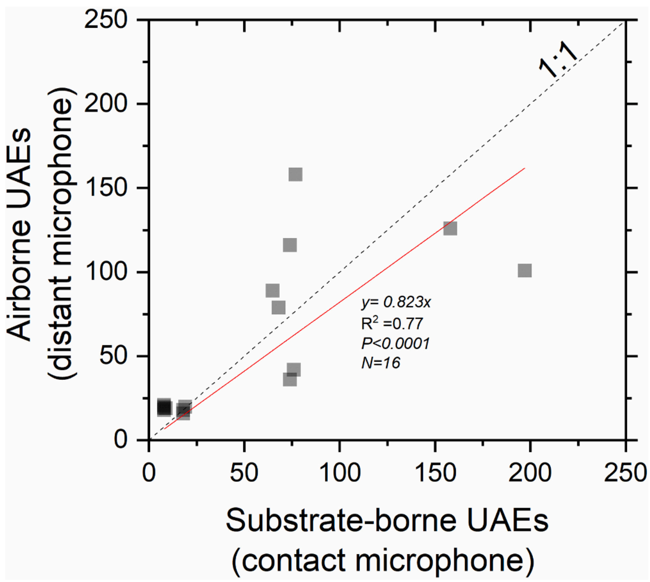

Fig. 4. Comparison of the number of UAEs detected for the birch and pine trees using the lower contact microphone system (x-axis) and the distant microphone collecting only airborne sound (y-axis). Note that overlapping points are indicated with darker colours. Dashed line represent the 1:1 line, while the red line show the regression line with the zero intercept. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

That is, xylem conduits decrease in size with increasing height in both birch and pine (Lintunen and Kalliokoski 2010), and more frequent emboli formation in larger conduits at the base serves as a plausible explanation for UAEs being more common at lower parts of the trunk.

The frequency of UAEs that we measured in excess for our birch treatment (average of + 0.2 UAEs minute^{-1}) overlaps with that reported for drying plants by Khait et al (2023) who detected on average 0.6 to 0.17 UAEs minute^{-1}. We interpret this as an indication that our surfactant treatment generated acoustic responses comparable to those caused by drought. We observed high signal to noise ratio for our UAEs measured during daytime (Fig. S1-2), suggesting minute interference from background ultrasonic sounds. This latter finding is also expected as ultrasonic biophony is generated by nocturnal animals (bats and rodents) communities (Farina and James 2016). Nevertheless, we detected UAEs also coming from the control trees, especially for birch. The existence and origin of UAEs coming from other within-plant processes than cavitation is debated. Low-dB UAEs coming from trunks of Scots pine were suggested to be caused by processes being part of respiration or cambial activities due to their diurnal trends (Zweifel and Zeugin 2008). These findings were later refuted and suggested to be an artefact of the temperature sensitivity of the sensors (Steppe et al. 2009). In our paired experimental design, where control trees and Tween-80 treated trees where acoustically monitored in pairs, we can exclude that observed differences were caused by temperature-sensitive hardware. Therefore, UAEs occurring in our control trees suggests either that; i) control trees experience cavitation; or ii) there are indeed other within-tree processes besides cavitation that generate UAEs. The first explanation seems most likely, especially as UAEs coming from the control trees follow the same vertical trends as the Tween-80 induced cavitation, i.e. UAEs were more frequent at the base of the control trees where our experiment suggest cavitation occur if the tensile forces exceeds the cohesive forces of water. What also points towards cavitation being the main source of the UAEs in the control trees is their similarity in frequency (about 30 kHz) with the UAEs generated during our treatment that indicate a common process. However, optical observations indicate that the propagation of air from conduit to conduit (air seeding), a process that occur after cavitation initiated the first nucleation of air in the xylem, also generate UAEs (Ponomarenko et al. 2014). With this observation in mind, we cannot exclude that some UAEs in the control trees were derived from air seedings initiated by *in situ* cavitation or by our experimental handling of the trees. While we cannot rule out non-cavitation sources for our UAEs, we find their existence less likely. Laschimke et al (2006) proposed that UAEs where coming from microbubbles attached to xylem vessel walls and that these bubbles, serving as a force-transmitting medium for xylem sap, release high-frequency sound when they abruptly regroup adherent to the vessel wall. We note that the water transport framework proposed by Laschimke et al (2006) suggest that xylem sap is moved without negative pressure and thus, that that UAEs are not affected by the water's cohesive forces. This latter theory is not supported by our results; in our treatment, the reduced cohesive forces of water led to an increase in the rate of UAEs as well as a reduction in water uptake. The mismatch between predictions made by the Laschimke et al (2006) model and our observations, makes us consider the microbubbles in the xylem as an unlikely source of the UAEs in the control trees.

5. Conclusions

Over the past decades, laboratory-based acoustic studies have explored the potential of using xylem sap acoustic signals to detect xylem embolism *in situ* for forest-grown. Our findings demonstrate that commercially available microphone systems can be used as non-invasive tools that detect UAEs generated by collapsing water columns within the xylem of cut trees placed inside forests. From the perspective of future *in situ* applications, it is promising that microphones can detect xylem embolism in complex soundscapes of forests and that airborne UAEs can be used to remotely detect hydraulic failures in the xylem. Yet, future studies are needed to further assess to what extent acoustic approaches can be used to study embolism inside mature trees. For example, thicker bark and attenuation of ultrasonic frequencies may constitute considerable challenges for acoustic approaches applied to larger trees than those tested in our study.

Interestingly, the vertical variation in UAEs suggests that bioacoustics approaches can reveal species-specific differences in embolism, and thus, that our approach can be applied to enhance our understanding regarding species-specific responses to drought. Yet, it is also important to recognize that acoustic monitoring of xylem embolism is, at the current stage of knowledge, more qualitative than quantitative, and likely have limited ability to inform about cavitation events occurring prior to recordings. Still, it seems that UAEs coming from trees growing offers a promising avenue for studies aiming to increase our understanding about embolism and mechanisms behind this process.

CRediT authorship contribution statement

J. Klaminder: Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This has been made possible by the Swedish Infrastructure for Ecosystem Science (SITES), in this case at the research Station at Svartberget and through funding from Knut and Alice Wallenberg foundation [no.2018.0259]. SITES current funding (2023-2028) is through the Swedish Research Council grant number 2021-0016 and we also acknowledge funding for acoustic research to JK from The Swedish Research council (Dnr 2021-05445). We also thank Lena Brolin and Mattias Åsberg Gencturk for assistance during the fieldwork.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113580.

Data availability

Data will be made available on request.

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