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ARTICLE ADDENDUM

Short interval overnight laser scanning suggests sub-circadian periodicity of tree turgor

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ABSTRACT
A recent study by Zlinszky et al.,[1] uses high-resolution terrestrial laser scanning to investigate the variability of overnight movement of leaves and branches in vascular plants. This study finds among others that the investigated plants show periodic movements of around one centimetre in amplitude and 2–6 hour periodicity. Sub-circadian process dynamics of plants were so far not in focus of research, but here we compare the findings with other published cases of short-term periodicity in leaf turgor, sap flow and especially trunk diameter. Several authors have noted overnight variations in these parameters within periods of several hours and in absence of environmental changes with similar dynamics. We revisit the unknown questions of short-term plant movement and make a suggestion for future research.

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Reversible plant movements in response to external stimuli are commonly referred to as nastic, whereas the term tropism is reserved for growth responses that enable plants to curve their organs relative to a directional stimulus. Darwin studied both phenomena in detail assisted by his son Francis and published the results in the book, *The Power of Movement in Plants*, one of his last publications.[2] Since then the subject has fascinated plant morphologists and plant physiologists alike. Most often plant movement is studied at the organ level but Puttonen et al.,[3] used repeated terrestrial laser scanning to quantify changes in the overall crown shape of two independently sampled Birch (*Betula pendula*) trees. This technique uses travel time of a laser signals to calculate distances between the laser source and the target object.[4] It yields up to sub-centimeter precision, three-dimensional models (termed point clouds) of the target object with resolutions of at least one point for every few square centimeters. Recently, Zlinszky et al.,[1] scanned 22 small-sized trees simultaneously in an overnight experiment aimed to reveal the variation of circadian leaf movements across the vascular plants. To account for local movements the point cloud was divided into height intervals comprising equal counts of points (percentiles). As surrogate for canopy movement the average vertical movement of all points within each percentile was quantified. The resulting dataset showed great variety in vertical movement patterns, which we ascribe to combinations of three separate phenomena: 1) true circadian movement (sleep), occurring in diurnal cycles, 2) non-cyclic unidirectional movement (drift), comprising continuous movement in either upward or downward direction, and 3) short-term cycles of movement with periods extending from two to six hours (oscillation). We attribute the differences recorded in nocturnal crown movement in this study to variation in the respective contributions from the three vertical movement types as defined here. The results suggest that phylogenetic relationship as well anatomical features may determine shared patterns, but more data points are needed before a final conclusion can be drawn.

Judging from the plant physiological evidence neither unidirectional change in canopy shape, nor circadian canopy movement are surprising, since changes in turgor pressure are expected to produce variations in leaf position and therefore canopy shape,[5]" and both unidirectional and circadian changes in turgor pressure are known to occur. However, turgor pressure that change in cycles shorter than 24 hours has to our best knowledge not been observed before in plants. In the experiment conducted by Zlinszky et al.,[1] we rule out any role of temperature, humidity, light and wind since these were controlled for and constantly monitored. Furthermore, since the short-term oscillations recorded in individual trees were not in synchronization, we assume that the differences recorded in between species were not directly produced by environmental factors and rather an indication of an active or passive process taking place in the plants themselves. Drawing on the most recent findings we will in the following discuss the mechanisms underlying short-term nocturnal plant movement that hopefully will inspire new directions for future research.

Fluctuations of leaf or branch position are related to changes in turgor pressure cascading across the canopy[6] but also influenced by the physical properties of the trunk, branches and leaves. Zlinszky et al.,[1] observed that the amplitude of movement is lower in sclerophyllous leaves, presumably due to their high content of lignin, which makes them less flexible. Metabolic processes that lead to periodic fluctuations in the concentration of osmotically active solutes in the cytoplasma of living cells embedded in the xylem may explain changes in turgor pressure in absence of light and associated

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movement. A new understanding is emerging from the complex relationship between the biotic and abiotic transport systems in trees.[7] Clearly rays play an important role in radial solute transport in trees and may cause gradual changes in water potential in response to environmental factors[8] as well as internal regulation.

In classical plant physiology, most metabolic and transport processes are explained as relatively constant flows with negligible fluctuation in time, especially at the level of the entire plant.[9,10] Even current tree water transport models that take diurnal changes into account do not consider fluctuations shorter than 24 hours.[11] The findings of Zlinszky et al.,[1] are interpreted as revealing short-term periodicity in turgor at the level of the whole tree overnight, when the plant is redistributing photosynthates and optimizing its capability to perform photosynthesis the following day. Periodic changes in the turgor pressure of single cells may possibly be a result of changes in solute concentrations, which, at the cell level, are a consequence of internal processes such as carbon storage, transport across membranes or cytoplasmic flow through plasmodesmata[12] or at the scale of multiple cells influenced by the transport of metabolites. At the tissue level adjacent gradients in turgor pressure are formed by concerted osmoregulation.[13] This may involve both active transport against a concentration gradient and conversion of carbohydrates into osmotically inert forms such as starch. To our best knowledge short-term regulation of turgor pressure has never been identified for which reason we can only speculate on the ecophysiological implications and significance for the fitness of the plant. A few observations have been published of fluctuations in turgor pressure of leaf patches, which are somehow reminiscent of our findings for entire trees.[14,15]

We find it likely that regulation of hydraulic pressure gradients in the secondary xylem, most probably in concerted action with the adjacent live tissues may be responsible for the short-term canopy movements observed in our study. Minute fluctuations overnight in tree stem diameter, water transport speed, or water potential have been widely reported on in the scientific literature.[16–19] Typically these phenomena are considered of minor role only and not the subject of an elaborated discussion. Based on our results we suggest that canopy movements reflect cycles of a hitherto unknown pumping mechanism, which causes reversible volume changes of the live cells embedded in the xylem similar to the suggestion of Török,[20] which proposes that solutes move in pulses instead of a constant steady-state flow along a network of tubular xylem vessels. We suppose that the aquaporins situated in the membranes of the paratracheal parenchyma cells surrounding the vessel may play an important role in generating these pulses. They are known to perform various transport and signalling functions and are probably crucial for plants' ability to respond to environmental stimuli.[13] They are for example known to play a key role in the hydraulic regulation in roots where water uptake and delivery to shoots requires transport through living tissues, and have been demonstrated to be capable of rapid changes influencing radial transport.[21] More studies are needed to establish a relationship between the minute changes occurring in stem diameter on one hand, and shape changes of the living cells in the xylem on the other hand. If indeed water transport takes place in pulses between sections of the trunk, it would only have to counteract the hydrostatic pressure corresponding to the height of a given section and not the hydrostatic pressure of the entire height of the tree, an issue that has been the subject of much discussion.[10]

Zlinszky et al.[1] as well as Puttonen et al[3] recorded several examples of oscillation being synchronized across the whole plant, but also cases where the upper and lower branches of a tree or shrub move in opposite directions, which could be ascribed to pulses in turgor pressure travelling through the tree. Unfortunately, neither trunk diameter nor sap flow were measured in the two mentioned experiments.

Diurnal variations in stem diameter are typically explained by changes in the water potential within the stem.[22,23] Such variations are typically attributed to the phloem, but it has been shown that the xylem is also capable of reversible changes in diameter in relation to water pressure, especially if not strongly lignified.[24,25] Interestingly Cocozza et al.,[26] report overnight periodic fluctuations of 2–3 hours of both sap flux density and stem radius on olive trees (*Olea europaea*) and similarly Pesonenet al.,[18] showed overnight fluctuation of stem girth in Norway spruce (*Picea abies*). Raschi et al.,[19] demonstrated cyclic variations in sap flow overnight in some species of Oak, and De Schepper and Steppe[9] measured overnight sap flow fluctuations that were unaccounted for by their model. Chan et al.[27] also observed a "shorter variation last(ing) for only a few hours around pre-dawn" in stem diameter growth, which they attributed to water potential fluctuations in the trunk. The study of Zlinszky et al.,[1] opens up for new research into sub-diurnal temporal dynamics of plants and how this phenomenon relates to transport of solutes and signalling within the tree. A question outstanding is whether the identified pulses affect the entire tree at one point in time or whether they travel up the stem in waves. We suggest a simple experiment performed with several dendrometers placed at various heights along the same woody stem, similar to Zweifel et al.,.[25] As study organism we suggest species of *Magnolia* in which we recorded the most distinct sub-circadian cyclic movements of the crown.

The observation of concerted sub-circadian periodic movement of tree leaves and branches definitely suggests some form of synchronized short-term periodicity at the level of the whole tree canopy. Previous observations of similar reversible periodicity in tree diameter and sap flow provide the first clues on how to explain this, but dedicated research is necessary in order to explain the role and mechanism of this process.

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