

Why trees sleep? - explanations to diurnal branch movement

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Research Article

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Abstract

Physiological processes cause movements of tree stems and branches that follow a circadian rhythm, but there is a lack of quantitative understanding of the cause-and-effect relationships. We investigated the diurnal movement of tree branches using time-series of terrestrial laser scanning measurements coupled with measurements of environmental drivers and tree water status. Our results showed that diurnal movement of branches was largely explained by leaf water status. This conclusion was supported by the significantly lower overnight branch movement in leaf-off than leaf-on conditions. Our findings conclude that alteration in leaf water status causes systematic branch movements following a diurnal rhythm. Due to lower atmospheric water demand during the nighttime, tree branches settle down analogously to sleep as the amount of water in leaves is increasing. The results indicate that quantified movement of tree branches could help us to further monitor and understand the water relations of tree communities.

Introduction

Trees have seemed like relatively static objects from the human perspective, but some trees have shown diurnal movements, like the so-called “Praying Palm of Faridpore”, that was regarded as a “miracle” in Bengal in the early 20th century (Minorsky 2021). This date palm tree (*Phoenix sylvestris* Roxb.) leaned at a large vertical angle and the angle varied diurnally causing a movement of over a meter at the plant’s tip due to thermonasty according to plant biologist Dr. Bose (Minorsky 2021). However, after a century of research recent findings have shown, with the aid of terrestrial laser scanning (TLS) technologies, that trees move their branches in a diurnal pattern, in which tree branches settle down analogously to “sleep” during the night time (Puttonen et al. 2016; Zlinszky, Molnár, and Barfod 2017; Zlinszky and Barfod 2018). Species and tree individuals have shown different “sleeping” patterns in their overnight movements, but there have only been untested theories of the cause of branch movement that suggest that pulse-like fluctuations in turgor pressure would be behind the varying nocturnal behaviour of trees (Zlinszky and Barfod 2018).

Here, we theorize that the diurnal variation in leaf water content could explain the diurnal branch movement that has been recently observed. Trees and forests transfer vast amounts of water from the soil through their canopies. The driving force for water movement through the soil-plant-atmosphere continuum is the evaporation of water at leaves. The evaporation rate of water is proportional to air vapor pressure deficit (VPD) for a given stomatal conductance. Both the water potential and water content decrease at the same rate as leaf transpiration increases, although with a time lag due to hydraulic resistance and capacitance of the leaf and xylem tissues. We therefore hypothesize that:

1. Changes in leaf water content are causing systematic branch movement. Lower water content is related to an upward position.
2. Trees without leaves show less branch movement than trees with leaves.
3. Overnight movement of tree branches can be linked to changes in VPD.

We tested our theory by utilizing a time-series of TLS measurements to acquire accurate 3D snapshots of the environment that can capture the movement of tree branches between the measurements. To separate external drivers (such as VPD) of branch movement from the internal drivers (water content), experiments were done both in 1) controlled laboratory conditions where VPD and light were kept constant while soil and tree water content gradually decreased over 39 days and 2) outside where light and VPD varied naturally overnight, but trees did not experience drought stress. The long-term branch movement measurements in a laboratory were coupled with measurements of leaf water potential (LWP) and relative water content (RWC).

This study contributes to the understanding of the diurnal rhythm and different “sleeping” patterns of trees. Improved understanding of branch movements could help us to explore further various ecophysiological processes including tree water relations and wood formation, and to untap new methods to monitor these processes within and between tree communities.

Results

Variation in leaf water content causes branch movement in controlled environments

We tested how changes in leaf water content affect branch movement with Scots pine (*Pinus sylvestris* L.) seedlings in a controlled laboratory environment with minimum variation in environmental variables other than soil water availability, and found a strong relationship ($R^2 = 0.75-0.86$) between LWP and branch position during the monitoring period of 38 days (Table 1). Distinct upward branch movement occurred as the LWP decreased. A similar relationship ($R^2 = 0.64-0.83$) was found between RWC and branch movement. The strength of the relationships was dependent on the measured branch, i.e. different branches showed variation in their movement during the monitoring period.

Table 1

Summary of statistics for linear regression models for individual branches between relative water content (RWC), leaf water potential (LWP) and branch movement. Mean, minimum (Min), maximum (Max) and standard deviation (Std) for coefficient of determination (R^2) and root mean square error (RMSE) calculated from six and nine branches from seedlings 1 and 2, respectively.

	Movement vs. RWC (seedling 1)	Movement vs. LWP (seedling 1)	Movement vs. RWC (seedling 2)	Movement vs. LWP (seedling 2)
Mean R^2	0.83	0.86	0.64	0.75
Min R^2	0.71	0.50	0.38	0.57
Max R^2	0.95	0.94	0.84	0.97
Std R^2	0.11	0.18	0.16	0.13
Mean RMSE (cm)	4.98	4.02	8.86	4.66
Min RMSE (cm)	2.72	2.82	5.94	1.70
Max RMSE (cm)	6.96	8.34	11.82	6.39
Std RMSE (cm)	1.81	2.12	2.04	1.50

Overnight branch movement is greater in leaf-on conditions

Overnight branch movement was measured during windless nights during leaf-on and leaf-off conditions. The observed branches showed considerable overnight movement in our experiment (Table 2). The general trend was that the branches moved downwards during the night and then “bounced” back up after sunrise. The overnight movement of branches in all the observed trees was significantly smaller ($p < 0.05$) in leaf-off conditions. The median overnight movement of tree branches measured from the branch tips was between 5.3 cm and 8.3 cm in leaf-on conditions in August and between 1.8 cm and 3.5 cm respectively in leaf-off conditions in October. The largest branch movements were observed in the larger trees.

Table 2

Median, minimum (Min) and maximum (Max) of overnight branch movement in leaf-on and leaf-off conditions for trees characterized by species diameter at breast height (DBH) and height.

Tree characteristics		Leaf-on			Leaf-off			
Species	DBH (cm)	Height (m)	Median (cm)	Min (cm)	Max (cm)	Median (cm)	Min (cm)	Max (cm)
Silver Birch (<i>Betula pendula</i> Roth.)	42.1	22.1	8.3	4.5	13.1	3.5	1.8	14.5
Norway maple (<i>Acer Platanoides</i> L.)	6.2	5.9	5.3	1.9	8.6	1.8	0.4	4.1
Norway maple	19.5	9.1	7.5	2.6	15.6	2.2	3.5	5.6

Overnight branch movement is controlled by atmospheric water demand

Similar overnight branch movement patterns were observed with all three test trees. As VPD decreased during the night, the branches moved downwards. VPD reached its minimum value at the time of sunrise at 06:00 am and the lowest branch positions took place 40 min (small Norway maple) (Fig. 1), 60 min (Silver birch) (Fig. 2) and 80 min (large Norway maple) (Fig. 3) after the VPD minimum, and started moving upwards towards the initial position at sunset. We found that overnight branch position and VPD were strongly correlated and that there was a time lag between the change in VPD and branch movement (Table 3). The larger trees showed a larger time lag than the small one.

The Norway maples showed slightly higher correlations with VPD than the Silver birch, but all of the trees showed strong ($R^2 > 0.57$) correlations with VPD. The time lag between VPD and overnight branch movement seemed to vary to some extent also within trees, as can be observed from the variation in the R^2 in Table 3.

Table 3

Median, minimum (Min) and maximum (Max) of coefficient of determination (R^2) of linear regression models between vapour-pressure deficit (VPD) and the overnight branch movements measured in August in leaf-on conditions. Number of observed branches were 14, 13 and 17 for Silver birch, small Norway maple and large Norway maple, respectively. Characteristics of the trees are presented in Table 2.

Lag (h)	Silver birch			Norway maple			Norway maple		
	Median R^2	Min R^2	Max R^2	Median R^2	Min R^2	Max R^2	Median R^2	Min R^2	Max R^2
0	0.26	0.08	0.57	0.42	0.07	0.60	0.20	0.03	0.51
0.5	0.35	0.03	0.52	0.51	0.05	0.73	0.30	0.07	0.62
1.0	0.45	0.06	0.57	0.62	0.07	0.77	0.40	0.14	0.73
1.5	0.53	0.01	0.69	0.66	0.27	0.77	0.52	0.21	0.75
2	0.57	0.01	0.70	0.66	0.31	0.79	0.63	0.31	0.73
2.5	0.55	0.00	0.72	0.60	0.27	0.80	0.70	0.44	0.77
3	0.54	0.00	0.78	0.48	0.22	0.77	0.74	0.39	0.83

Discussion

We had three hypotheses aiming to explain the observed branch movement and their spatiotemporal patterns. The first one was that in a controlled environment leaf water content would be related to the changes in branch position. This was tested in a drought experiment where leaf water content decreased gradually. The water stress was characterized by measures of RWC and LWP, which both explained the upward movement of branches towards a more severe drought during the monitoring period. LWP explained a slightly larger portion of the branch movement, which may be due to smaller variability of values between individual needles.

Branch movement is more difficult to capture in field conditions due to the effect of wind. Thus, we focused on measuring overnight branch movement during windless nights during the summer and fall. We hypothesized that there would be a distinct difference in overnight branch movement between leaf-on and leaf-off conditions, which was verified with our measurements. Overnight branch movement was significantly lower in leaf-off than leaf-on conditions, which supports our first hypothesis that leaf water content would have a direct link with branch movement since branches with leaves have a larger diurnal variation in transpiration rate which causes a larger diurnal variation in water content and thus larger diurnal branch movements.

Often, changes in leaf water content are driven by atmospheric water demand (or VPD) as water vapour diffuses through stomata while plants take CO_2 in for photosynthesis, especially in conditions where soil

water availability is not a limiting factor (Elfving, Kaufmann, and Hall 1972). Therefore, we hypothesized that a decrease in VPD would cause a downward branch movement, because a decreasing VPD increases leaf water content. Our findings supported this hypothesis. VPD explained 57%-70% of overnight branch movement of single trees. It should be noted that there were differences in the time lag between VPD and overnight movement between branches. Based on visual observations of the movement of branches in Figs. 2 and 3 it seems that the larger the overnight branch movement is, the longer is the time lag between VPD and branch movement. Branches with a larger amount of leaves and leaf area are likely to show greater overnight movement due to the larger mass of water within the leaves, and therefore the amount of water exchanged with the atmosphere is also greater.

Other factors that could influence the movement of branches include local illumination and atmospheric conditions. Branches that receive a greater photon influx and are warmed more by the sun should transpire more and therefore have a greater amplitude of diurnal branch movement based on our theory. If our theory is correct and branch movement is driven by variation in leaf water content, we could expect that tree stress, which often causes changes in stomatal behaviour and transpiration (Zhou et al. 2014), could be detected as altered patterns of diurnal branch movement. We could also expect that the local growing environment with variables such as fertility and length of day, would influence the diurnal branch movement patterns.

Mechanical factors that affect the magnitude of branch movement are the angle of the branch relative to the stem, branch thickness and wood properties. Branches that point more straight up are less affected by gravitational differences that variation in mass can induce. Branches that have a greater leaf area in relation to branch thickness and have lower wood density are likely to show larger overnight movement. Increase in the water content and mass of the branches and needles during the nighttime will cause the branch to move downwards. Changes in the turgor pressure of living cells affect the elasticity of the cells, which could further influence branch movement, but separating the effect of turgor pressure and water status is complicated by the strong correlation of the two variables (Tyree and Hammel 1972). The amount of movement of the branches due to a given weight load can be described mathematically if the flexural rigidity of the branch, branch length and the distribution of the weight on the branch are known (Niklas 1999).

Monitoring the movement of branches could have applications in determining the water status of plants, especially in controlled environments. The benefit of the technique lies in its ability to measure several entire trees simultaneously rather than just a part of trees like dendrometers do (Puttonen et al. 2019). Variation in water dynamics within trees could be detected using the presented technique, which could help us to monitor and understand within tree water dynamics in detail. The cost of laser scanning instruments is decreasing enabling novel practical solutions to water status monitoring that do not involve spectral measurements or tedious manual measurements of leaf water content or water potential using the pressure chamber or more expensive measurements of water potential using psychrometers which also require close monitoring and maintenance (Zhu et al. 2019; Boren and Boschetti 2020; Zhang et al. 2015). The benefit of laser scanning in a greenhouse environment would be that it is not so

sensitive to viewing angle or illumination conditions compared to spectral information and can give accurate distance measurements from a 50 m distance and beyond. Plant growth can also be measured using the same instrument.

In summary, the findings of our experiments support the hypothesis that branch movement is driven by variation in leaf water content. However, further studies should be conducted to verify this inference with a wider range of different tree and plant species. The measurements of branch movements could open new avenues in understanding whole plant water relations and provide implications also for forest health and resilience monitoring. Although it can be challenging to explicitly quantify the changes in leaf water content in a branch based on its dimensions, the branch movement can give rapid information on the direction and speed of change in leaf water content. When the movement of a branch has stopped, there is no change in leaf water content, and an upward or downward movement indicates that a change in leaf water content is occurring in either direction. It could be observed that there were differences between branches in the timing and the slope of overnight branch movement, which could be caused by differences e.g. in stomatal behaviour or branch mechanical or structural characteristics. When individual branches can be observed, we can simultaneously observe the changes in leaf water content in a vertical gradient in a tree or a plant. However, the main limitation in the field is obviously the requirement of windless conditions, which hampers the measurements and applications.

Material And Methods

Laboratory experiment

A drought experiment was carried out by controlled reduction of water availability with two seven year old 1.5 meters tall potted Scots pine (*Pinus sylvestris* L.) saplings were carried out at a laboratory in $\sim 21\text{ }^{\circ}\text{C}$ at the Viikki campus of University of Helsinki between December 2019 and January 2020. The saplings were growing outside of greenhouses until they were taken indoors for the experiments. After this the saplings were kept well-watered for 7 days, after which watering was stopped and the experiment started. A light source (High Pressure Sodium) was fixed on top of each sapling and lights were configured to 12h/12h light/darkness illumination cycle. Light intensity was tested with a PAR sensor (Li-190 Quantum sensor, LI-COR Inc., Lincoln NE, USA) and it was $\sim 1200\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ at the top and $\sim 300\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ at the bottom of canopies of the seedlings.

The saplings were monitored with TLS measurements at 16-time intervals during the monitoring period between 4th December and 13th January. A single TLS measurement was done from a 1.5 m distance from the saplings using a Trimble TX5 scanner (Trimble Inc., Sunnyvale, CA, USA), which utilizes a 905 nm wavelength and phase-shifting measurement technique to measure distance to the target. Five pieces of white 99 mm diameter spheres were used as reference targets for registering all of the 16 multitemporal point clouds spatially together.

Measurements of water status were carried out 16 times, right after the respective TLS measurements by taking needle samples. The needle samples were used to measure LWP and RWC. A set of five needles was taken from the sapling at each time point for both measurements. The needles were selected randomly from the current year needles, from the upper half of the canopy. LWP was measured from the five needles using the Scholander pressure chamber (PMS-1000; PMS Instruments, Albany, OR, USA) with the help of binoculars. A mean value was calculated from the five LWP measurements. The five needles which were used for measurement of RWC were cut in half and weighed for fresh mass (FM). Then the pieces were tied together with tin string and were completely embedded into milliQ water. After 24 hours in 5 °C water turgid mass (TM) was measured, after which samples were placed into the oven to 60 °C and their dry mass (DM) was measured 24 hours after. RWC was then calculated using Eq. 1:

$$\text{RWC (\%)} = [(FM - DM) / (TM - DM)] * 100 \quad (1)$$

Field experiment

To test how tree branch movement can be explained by VPD and whether there are differences in overnight branch movement between leaf-on and leaf-off conditions, we collected TLS time-series in Masala, Southern Finland (Kirkkonummi, N. 60° 9.674', W. 24° 32.807'). The experiment focused on quantifying overnight branch movement coupled with measurements of environmental conditions that can be linked to tree physiological processes. The experiment site was on the edge of a semi-eutrophic mixed boreal forest stand, consisting of Norway spruce (*Picea abies* H. Karst.), Silver birch, Norway maple, European oak (*Quercus robur* L.) and small-leaved lime (*Tilia cordata* Mill.). The overnight measurements were taken first on August 24th and 25th, 2016 with leaf-on conditions and later again with leaf-off conditions on October 18th and 19th, 2016. Figure 4 shows the overview of the measurement site. Both measurements focused on two Norway maples (Table 2), and a Silver birch.

The measurements in August were done in leaf-on conditions that covered twilight and night. The measurements were done with three terrestrial laser scanners mounted on tripods. FARO Focus 3D X 330 (FARO Inc., Lake Mary, FL, USA) was located on an open road approximately 20 meters from the trees. The two other scanners were located on the roof of a nearby building (FARO Focus 3D S 120 – southern, Trimble TX5 – northern) approximately 35 and 20 meters from the trees, respectively. The height difference between the scanner on the road and those on the roofs was approximately 10 m. The trees were monitored for 9 hours in total, in which 130 separate scans were collected. Altogether 123 of 130 scans representing 41 data acquisition times were selected based on subjective estimation of wind speed (not detectable or very small airflows).

October data were collected in leaf-off conditions using two laser scanners, namely FARO X330 and Leica Scanstation P40 (Leica Geosystems AG, Switzerland). Both scanners were placed on the building roof. In total, 57 simultaneous scans were taken with both scanners during the monitoring period. Five spheres of 0.099 m radius were used as reference targets in all of the measurements facilitating the co-registration of the TLS scans.

TLS data processing

The point clouds from each measurement location were co-registered to a common arbitrary coordination system using the external sphere targets as reference points. The registration was performed in FARO Scene point cloud processing software. The spheres were mainly located automatically from the point cloud and a sphere of 9.9 cm radius was fitted on them. After all spheres were located, their coordinates were registered with the sphere coordinates scanned from the first scan file. Point cloud data collected with the Leica scanner was pre-processed with Leica Cyclone (v. 7.3) but followed the same procedure for georeferencing. Due to the different scanner number and positioning, the reference target positions were different between the leaf-on and leaf-off measurements and the complete time series were not georegistered with each other. Each tree was then manually delineated from the point clouds for further processing.

To monitor the crown dynamics, each delineated tree point cloud was segmented using a similar approach as in Puttonen et al. (2019). The segmentation approach begins by doing first an Euclidean clustering for the initial point cloud with predefined minimum cluster size and point number. After the initial segmentation, the consequently measured point clouds are labeled based on the previous segmentation. Individual segment movement over time is monitored by following the movement of their centroid. The segmentation framework works under the assumption that segment movement between the consequent scans is smaller than the monitored cluster size.

All the experiments were conducted according to international guidelines and had permissions. The identification of the plant material was conducted by the main author. No voucher specimen of the plant material has been deposited in a publicly available herbarium.

Quantifying branch movement

The timing of the movement maximums was determined from consensus of cluster centers located on the tips of branches. Stable branch clusters were determined with following thresholds: i) They had to be present throughout the experiment window, ii) the relative standard deviation of their point number had to be less than 30% compared to their initial size, and iii) their maximum movement within the timeframe had to be more than 3.0 cm. The last threshold filtered out clusters located on the tree stems and large branches.

For the laboratory experiment, six and nine branches were selected for further investigation from the two pine seedlings. The movement of branches was quantified as Euclidean distance from the first measurement in all the experiments.

For all trees, one to two clusters located on the stem were selected as fixed references to confirm the point cloud clustering stability. In all cases, the stem cluster centers showed less than one-centimeter displacement from their initial position thus confirming the clustering stability.

Statistical analysis

Linear regression modelling was used to determine the relationship between leaf water status and branch movement for the laboratory experiment as well as for overnight branch movement and VPD. Regression

models were built between the movement of each branch, which was our response variable, and RWC, LWP and VPD, which were our predicting variables. Coefficient of determination (R^2) and root-mean-square-error (RMSE) were used to examine the goodness of fit of the developed regression models. Student's *t*-tests were used to test the significance of differences between the overnight movement of branches in leaf-on and leaf-off conditions.

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Figures

Selected branch locations in the object point cloud

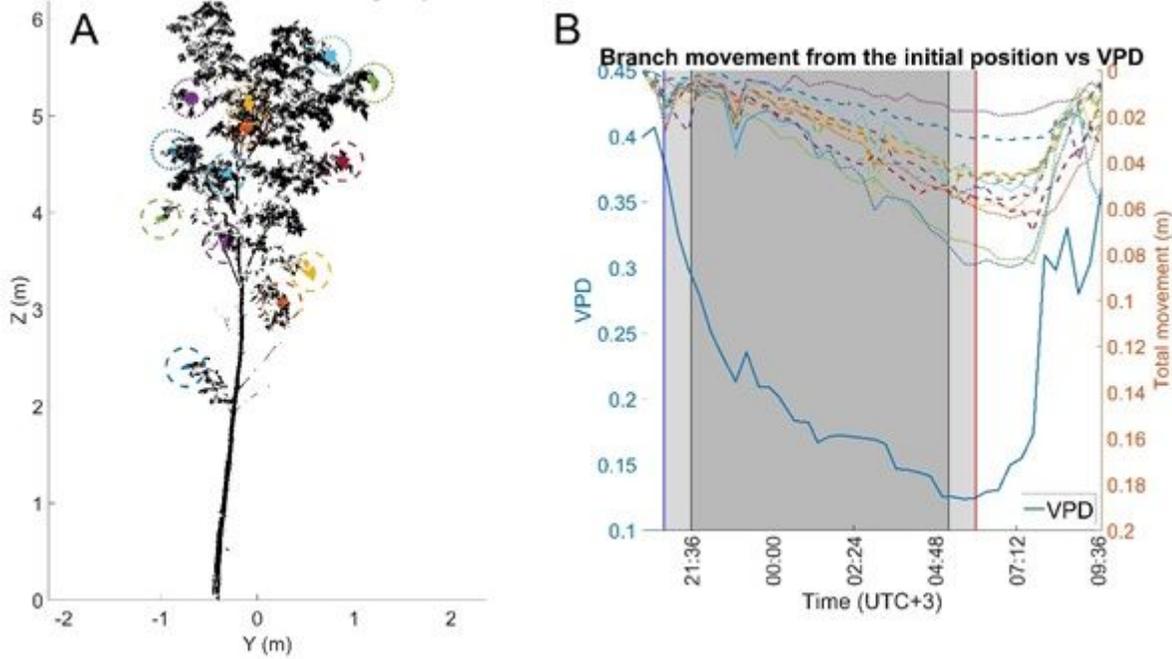


Figure 1

A) Point cloud of the small Norway maple (Norway maple L.) in August 2016 in leaf-on conditions. Movements were analyzed by detecting the same cluster of points from each time point. Horizontal axis shows the distance of the tree width with respect to the point cloud mean and the vertical axis shows the tree height. Point sizes in the colored clusters are emphasized for visual clarity. B) Overnight branch movement during monitoring period. Branch movements are marked with the dashed and dotted lines (right y-axis) and the vapour-pressure deficit (VPD) with the solid blue line (left y-axis). The times of sunset and sunrise are marked with the blue and red vertical lines, at 8:40 pm and 6:00 am respectively (y-axis). Civil twilight time is marked with the light gray area, and time of nautical and astronomical twilight with the dark gray area.

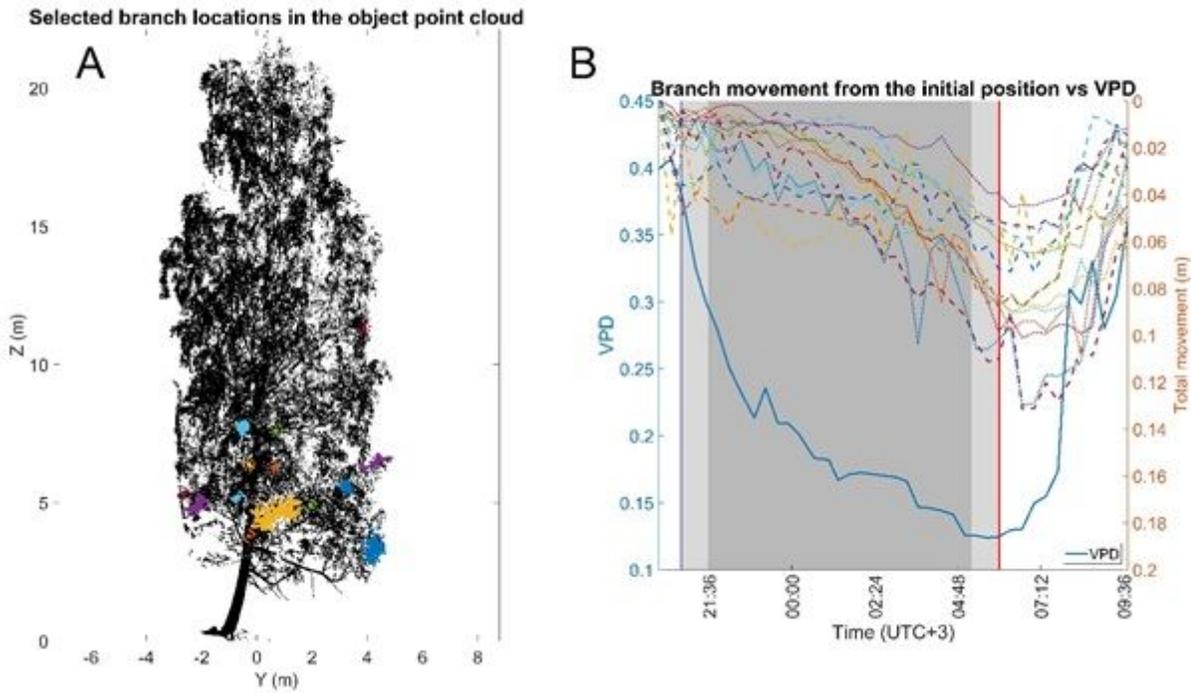


Figure 2

A) Point cloud of the Silver birch (*Betula pendula* Roth.) in August 2016 in leaf-on conditions. B) Overnight branch movement during monitoring period. Branch movements are marked with the dashed lines and the vapour-pressure deficit (VPD) with the solid blue line. The times of sunset and sunrise are marked with the blue and red vertical lines, at 8:40 pm and 6:00 am respectively. Civil twilight time is marked with the light gray area, and time of nautical and astronomical twilight with the dark gray area.

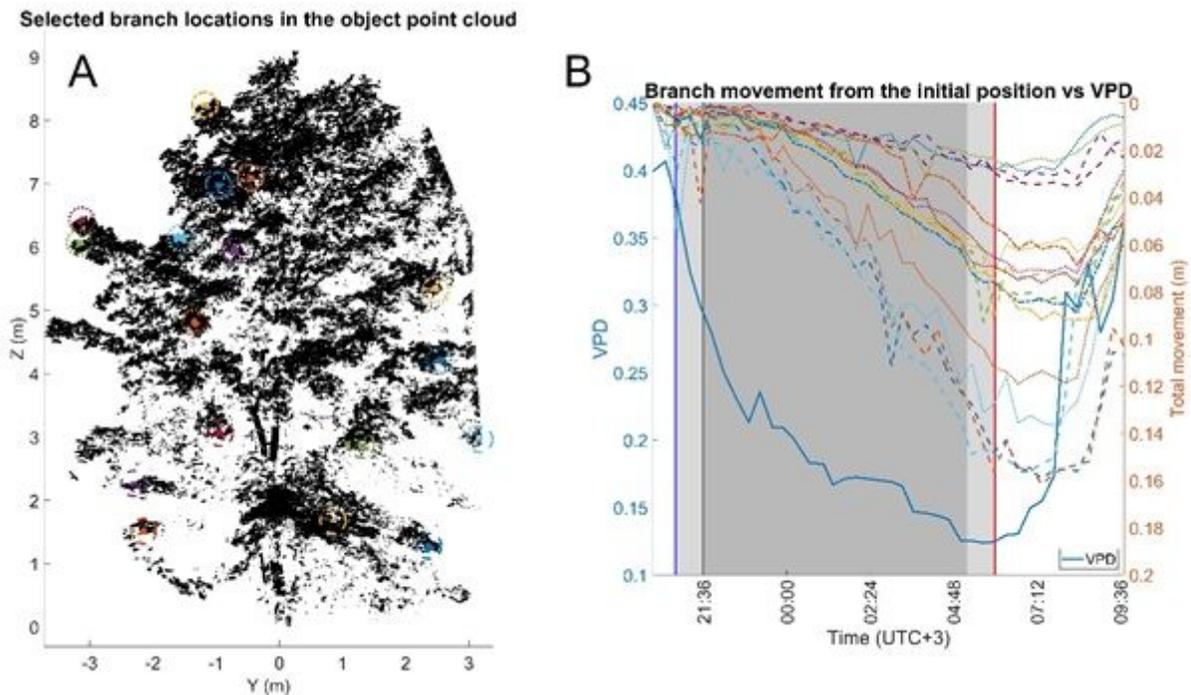


Figure 3

A) Point cloud of the large Norway maple (*Acer platanoides* L.) in August 2016 in leaf-on conditions. B) Overnight branch movement during monitoring period. Branch movements are marked with the dashed lines and the vapour-pressure deficit (VPD) with the solid blue line. The times of sunset and sunrise are marked with the blue and red vertical lines, at 8:40 pm and 6:00 am respectively. Civil twilight time is marked with the light gray area, and time of nautical and astronomical twilight with the dark gray area.

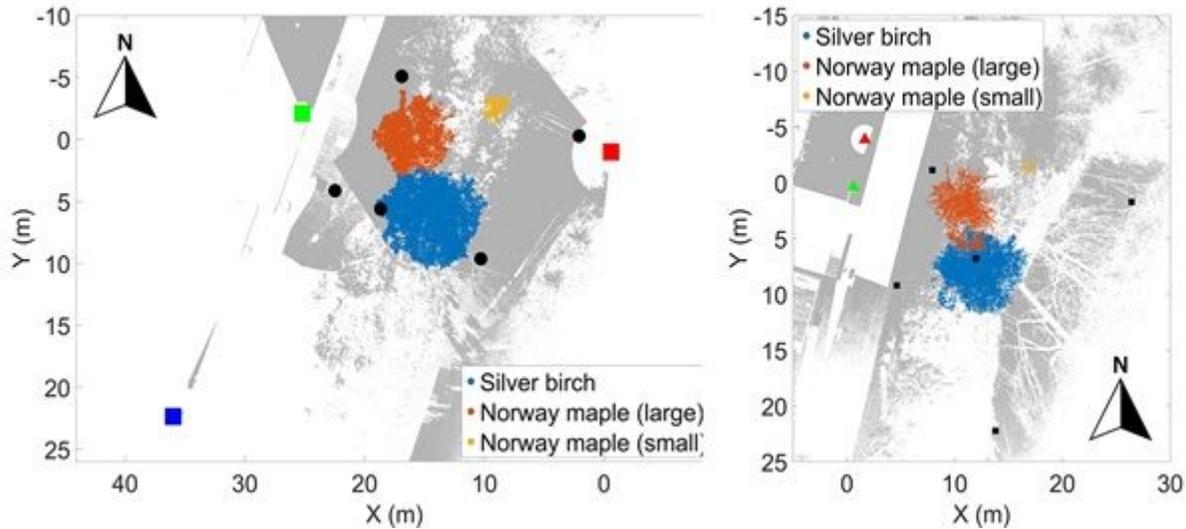


Figure 4

Left) Measurement configuration in leaf-on (24-25 August 2016). Scanner locations are marked with colored boxes: being the FARO Focus X330 (red); FARO Focus 3D 120 S 1 (dark blue); and TRIMBLE T5X (green). The gray points denote the combined point cloud of all three scanners. The trees monitored are marked with different colors in the figure; in addition, the small Norway maple is highlighted with a red rectangle. The five reference sphere locations are marked with black circles on the point cloud. Right) Measurement configuration in leaf-off (18-19 October 2016) conditions. Scanner locations are marked with colored triangles: being the FARO Focus X330 (red); Leica Scanstation P40 (green). Both configurations are North-oriented, but their coordinates are not in the same reference coordinate system due to the differing placement of the laser scanners and the reference targets.