Sanio’s Laws revisited. Size-dependent changes in the xylem architecture of trees.

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Supplementary Materials

Structure of the numerical model

A numerical model was employed to determine whether it was possible to predict the patterns seen in the anatomical data as a function of plant size and phylogenetic group. The model was based on a concept of maximizing net carbon gains by a plant, i.e., maximizing canopy net photosynthesis minus the carbon construction costs associated with the xylem conduit walls. The model was run by either a) assuming constant tapering within a tree and solving for the optimal tapering as a function of tree size, or b) assuming variable tapering from apex to base and solving for the optimal profile of tapering for each different tree size. Hence, given a fixed apical conduit diameter, the model simulated the trade-off between allocating a large fraction of carbon to an expensive (i.e., tapered) hydraulic system allowing for the leaf area to work at maximum rates, or vice versa allocating a smaller fraction of carbon to an untapered and inefficient hydraulic system allowing the canopy to work at lower rates.

The gross gain in carbon was calculated from the value of stomatal conductance, air carbon dioxide concentration, a response function to light availability and whole-plant leaf area. The net gains in carbon were calculated from the gross gains in carbon minus the construction costs of the xylem walls for varying tapering rates of conduit diameter. The optimal tapering was that which maximized whole-plant net gain. Xylem conduits were described as parallel tubes whose hydraulic conductivity \( k \) was calculated using Poiseuille’s law as:

\[
k = \frac{8 \pi r^4}{\eta l} m \tag{1}
\]

where \( \eta \) is viscosity, \( l \) is tube length, \( r \) is tube radius and \( m \) is the number of parallel tubes.

The water flux through the xylem may depend on both \( k \) and the driving force necessary to transport water through the conduit (because of evaporation in the leaves, this normally results in negative
values of xylem water potential (\(\Psi\), or tension, i.e., \(\Psi<0\)). Substantial evidence exists to suggest that plants operate by keeping minimum leaf water potential within fairly narrow boundaries. This has the advantage of maximising stomatal opening while preventing turgor loss and runaway cavitation (e.g., Saliendra et al. 1995, Comstock & Mencuccini 1998). Therefore, a minimum threshold xylem water potential corresponding to a maximum value of leaf transpiration rate was set. This results in a tight coordination of stomatal and hydraulic conductance (Meinzer 2002, Mencuccini 2003). The maximum sustainable transpiration rate (\(T\)) for a given minimum xylem water potential (\(\psi\)) was:

\[
T_{\text{max}} = -\frac{\Psi_{\text{min}}}{k}
\]

(2)

The transpiration rate was also expressed as a function of the stomatal conductance (\(g_s\)):

\[
T_{\text{max}} = a g_s \Delta w S
\]

(3)

where \(S\) was the leaf area, \(a\) the ratio between the diffusivity of water vapour and carbon dioxide, and \(\Delta w\) the water vapour deficit. The corresponding stomatal conductance (\(g_s\)) for the minimum xylem water potential was:

\[
g_s(\psi_{\text{min}}) = \frac{-\Psi_{\text{min}}}{a S \Delta w}
\]

(4)

The photosynthesis rate (\(P\)) may depend on several environmental factors in addition to stomatal opening. We primarily modelled the effect of atmospheric carbon dioxide concentration and irradiance, both of which increase \(P\). Since photosynthesis responses to light follow a saturating response, the following formulation was chosen (Mäkelä et al. 1996):

\[
P = \frac{g_s C_a f}{g_s + f}
\]

(5)

where \(C_a\) was the atmospheric carbon dioxide concentration, and \(f\) the following function of irradiance:

\[
f = \frac{\alpha I}{I + \gamma}
\]

(6)
where \( I \) is the photosynthetic photon flux density. The photosynthesis rate was now a function of the hydraulic conductance, as the stomatal conductance was proportional to the hydraulic conductance when xylem water potential at the top of the tree was kept constant:

\[
P = \frac{-\psi_{\text{min}} k}{a S \Delta w} C_a f + \frac{-\psi_{\text{min}} k}{a S \Delta w}
\]

(7)

The carbon gain \((G)\) for a hydraulic structure with conductivity \( k \) was calculated as the photosynthesis rate multiplied by time \((t)\):

\[
G = P t
\]

(8)

The carbon costs of the hydraulic system were estimated as the construction costs of the conduit walls. The thickness of the conduit walls \( t \) was directly proportional to the conduit radius and a function of the water potential causing 50% loss in hydraulic conductance (Hacke et al., 2001):

\[
t = r \sqrt{(-A_1 \psi_{50} + A_2)}
\]

(9)

where \( A_1 \) and \( A_2 \) are two constants relating wall thickness to the xylem water potential. Thicker walls are needed to resist the larger stresses induced by lower water potentials and to protect the conduits from implosion. The carbon cost \((C)\) for building the conduit walls was:

\[
C = \pi l ((r + t)^2 - r^2) A_3
\]

(10)

where \( A_3 \) is the carbon cost per unit volume of conduit wall. Hence, the cost of building a conduit wall was proportional to the conduit radius raised to the second power. The tapering constant \( \alpha \) was the ratio between two tube radii of adjacent ranks with ramification number \( n \) (with \( n=2 \)):

\[
n^{\alpha/2} = \frac{r_{k+1}}{r_k}
\]

(11)
All the other costs associated with the construction and maintenance of the tree structure but not dependent on conduit radius (e.g., fibres, parenchyma, roots, leaves, etc.) were not considered here, because they do not affect the optimal conduit tapering. A list of all parameter values employed in the model is given in Table S1.

For consistency with previous models (i.e., MST), mechanical constraints were always followed in our simulations, i.e., the vertical scaling of segment lengths with rank number was included as in MST.

One of the advantages of this numerical model compared to an analytical solution was that additional scenarios could be considered. For instance, scenarios based on the inclusion of pit resistance or alternatively, including variable costs associated with furcation of conduits were also considered, although they are not reported here.

**Major results**

When the model assumed uniform tapering throughout the tree (i.e., constant $a$ within a tree) the optimal conduit tapering was found to vary inversely with total number of ranks $N$ (or distance from the apex, Fig. S1). When tapering was allowed to be non-uniform among ranks within a tree (i.e., variable $a$ within a tree), the optimal tapering could be found for each rank. Because of limits to the computational time, for each tree size, the optimal tapering was found for only the new rank added at the bottom of the tree, with the tapering of the previous ranks left unaltered. The gross and net carbon gains and the costs for varying tapering of the xylem conduits were then calculated.

**General patterns for gains and costs**

Two examples of the calculations of gross gains, total costs and net gains (for the case of non-uniform tapering) are given for an angiosperm and a gymnosperm tree in Fig. S2. Each panel also
contains the curves obtained by assuming uniform tapering following MST, i.e., $\bar{a}=1/6$. Gains and
costs are always given per unit of tube, not per plant.

The gross gains function behaved similarly between the angiosperm and the gymnosperm tree, with
the size-related decline caused by the reduced assimilation rates and the increased hydraulic
resistances with height. Although hydraulic resistance built up at identical rates, the decline in gross
gains was more accentuated in the gymnosperm case as a result of the smaller conduits and the
consequent larger limitations to stomatal conductance and assimilation rate. For both scenarios,
constant tapering according to $\bar{a}=1/6$ resulted in lower gross and net gains (Fig. S2).

Additional results

The complexity of the patterns of conduit tapering within an individual was demonstrated by
incorporating a root system at the bottom of a tapered stem (Fig. S3). The construction costs of the
root system were lowered by 88%, based on the relationships in (Hacke et al., 2001), to reflect both
lower mechanical requirements as well as lower vulnerability to cavitation in roots (e.g.,
Mencuccini & Comstock 1997). Tapering occurred rapidly at the top of the tree, but it quickly
slowed down as a result of high construction costs. However, roots retained high tapering rates as a
result of their lower carbon costs (i.e., radius to thickness ratio).

Sensitivity analyses

The qualitative behaviour of predicted optimal tapering was insensitive to changes in the initial
parameter values, although the actual degree of optimal tapering varied considerably when the
parameter values were varied. The general trend was always such that conduits tapered at a fast rate
towards a maximum diameter during growth (Fig. S4), then they remained more or less constant
until they finally started to decline due to the growing carbon costs. High values of wall thickness
per conduit radius, cost of unit volume of conduit wall, initial conduit diameter (except at very
small values) and initial conduit number per leaf induced less tapering and caused more rapid reverse tapering. Conversely, high values of irradiance, ambient CO$_2$ concentration, photosynthetic time in one year and conduit longevity induced more tapering and reverse tapering occurred later. For the minimum xylem water potential and VPD, maximum tapering occurred at intermediate values.

Additional empirical results

A summary of all the datasets employed in this meta-analysis is given in Table S2, with information on the reference, the species name and symbol, the phylogenetic and the size group, the number of sample trees, the total number of anatomical points measured as well as the differences in Akaike Information Criterion (corrected for small sample sizes) between each model and the best performing model ($\Delta$AICc). Values of $\Delta$AICc equal to or greater than four were taken to indicate that considerably less evidence was present for a given model compared to the best alternative. If values of $\Delta$AICc for the power model were found to be greater than zero but less than four, this was taken as evidence against the alternative models, i.e., implicitly in favour of a power model. When sample size was less than nine points, no statistical analysis was carried out.

In the main paper, to standardise for the variability from species to species in absolute conduit dimension, indices of conduit tapering $T$ were calculated at two reference distances, i.e., at a distance of 10 m from the apex ($T_{10}$) and of 0.05 m from the apex ($T_{0.05}$). $T_{0.05}$ was calculated by inverting Eqn. 5 from Weitz et al. (2006)

$$r(h) = r_N n^{-\pi/2} \left[ 1 + \frac{h(n^\gamma - 1)}{l_N} \right]^{\pi/2\gamma}$$

(12)

where $r(h)$, $h$, $r_N$, $n$, $l_N$ and $\gamma$ are conduit radius at distance $h$ from the apex, conduit radius at the petiole, branch bifurcation ratio ($n$=2), petiole length ($l_N$=0.05 m) and the scaling exponent related to the taper of branch lengths ($\gamma$=1/3), respectively. The equation predicts conduit radius along a
tree axis from $h$ and $r_N$. It reduces to a simpler $\frac{1}{4}$-power function ($\alpha=\tilde{a}/2\gamma=0.25$) assuming that $l_N$ is much smaller than $h$. However, for points close to the apex this simplification is unwarranted and Eqn. 12 must be used. The slopes of two equations converge for values of $h$ much larger than $l_N$.

Hence, $r_N$ for a certain tree was estimated by

$$r_N(h^*) = \frac{r(h^*)}{\sqrt[\frac{\pi}{2}]{\frac{1 + h^*(\gamma^{-1} - 1)}{l_N}}} \tag{13}$$

where $r(h^*)$ is the conduit radius measured at the point closest to the apex at distance $h^*$ and $\tilde{a}=1/6$.

$T_{0.05}$ was then calculated as

$$T_{0.05}(h) = \frac{r(h)}{r(h=0.05)} = \frac{r(h)}{r_N(h^*)} \tag{14}$$

$T_{10}$ was calculated instead as

$$T_{10}(h) = \frac{r(h)}{r(h=10)} \tag{15}$$

Where $r(h=10)$ was estimated by fitting an empirical power function to the data below $h=10$ m.

$T_{10}$ was useful to highlight the similarity in the plateauing response of many series, which roughly tended to occur for trees taller than 10 m. However, $T_{10}$ could not be used for the analysis on the actual slope of the log-log function fitting the data, for which $T_{0.05}$ was used instead, so that all curves start from $T_{0.05}=1$ at the same distance of 0.05 m. Fig. S5 reports the same data shown in Fig.1 of the main paper but using $T_{0.05}$ instead of $T_{10}$. Fig. S5 shows more clearly that the initial slope of many of the series for all phylogenetic and ontogenetic groups is greater than predicted by the MST.

To compare the observed slopes for the first 3 m below the apex against MST predictions for $T_{0.05}$ (Fig.2 and Table 1 of the main text), distances were first linearly rescaled such that $D=0.05$ m became $D^*=1.00$ m, then log-log relationships without intercept were forced through the point $(D^*=1.00, T_{0.05}=1)$ for both empirical fits and theoretical lines. Since Eqn. 12 from Weitz et al.
(2006) does not yield a perfect power law, the best power-law approximation for the first 3.0 m was used to obtain the theoretical slope equivalent to MST for $\ddot{a}=1/6$. This procedure yielded 0.5544 as a reference slope (equivalent to 0.1861 for a regression based on Eqn.12 not forced through the origin and using $D$ as opposed to $D^*$ coordinates). RMA slopes given in Table 1 refer to the back-transformed values for regressions not forced through the origin using $D$ coordinates, i.e., they should be compared against the expected value of 0.1861.
Reference List


Figure Legends

Fig. S1. Optimal tapering coefficient $\bar{a}$ as a function of distance from the apex (or total number of ranks $N$) assuming constant tapering within a tree (i.e., $\bar{a}$ is independent of rank number and positive) for four different values of conduit radius. Note that $\bar{a}$ is used in this graph, not $T$.

Fig. S2. An example of how the model calculated gross photosynthetic gains, total carbon construction costs and net gains (the difference between the first two) for trees of variable number of ranks (hence distance from the apex). The first panel shows an example for a gymnosperm tree, the second panel for an angiosperm tree. Apart from the differences in initial number of conduits per leaf, initial conduit size and wall thickness parameters, all other parameters were identical between the two simulations. Each panel also shows identical calculations carried out assuming constant tapering within each tree and during growth following MST, i.e., with $\bar{a}=1/6$.

Fig. S3. In this simulated coniferous tree, conduits tapered for a few metres below the tree apex at a constant rate corresponding to $\bar{a}=0.20$. Tapering eventually slowed down towards the base as a result of large construction costs. Tapering returned to positive values at a distance of about 20 m from the apex where the root system (which has much lower construction costs than the stem) was hypothesised to begin.

Fig. S4. An example of the impact of allowing variable maximum tapering rates just below the apex of angiosperm and gymnosperm trees. The higher the maximum tapering rate allowed, the quicker the plant reaches the stage (distance from the apex or number of ranks) at which carbon costs become limiting. At identical maximum tapering rates, gymnosperms always reach the carbon-limiting stage sooner than angiosperms, as a result of thicker conduit walls (per unit conduit diameter) and more numerous conduits per leaf. In gymnosperms, reverse tapering is also seen at the base of the trees as a result of these high construction costs.
Fig. S5. Tapering profiles for two phylogenetic groups (angiosperms and gymnosperms) and two ontogenetic classes (large and small plants). The Y axis represents a tapering coefficient (i.e., $T_{0.05,i} = r_i / r_{0.05}$, where $r_i$ is conduit radius at distance $x$ from the apex, and $r_{0.05}$ is conduit radius estimated at a distance of 0.05 m from the apex, hence all curves go through the point $T=1$ at distance=0.05 m) so that across-species variability in absolute conduit size is eliminated. Notice that most series taper faster than predicted by the MST power curve in the first few meters (except in the large angiosperms). The black curve gives the theoretical MST scaling, while the thick red curves in the two panels at the bottom give an output from the numerical model. Species abbreviations can be found in Table S2. Letters and numbers next to a species code refer to different treatments, age classes or sampling sites within a study.
Fig. 1

Distance from the apex, m

Tapering constant, a

- Apical radius = 2 µm
- Apical radius = 4 µm
- Apical radius = 8 µm
- Apical radius = 16 µm
Fig. 2

Gymnosperms

Angiosperms
<table>
<thead>
<tr>
<th>conduit tapering, T</th>
<th>0.5</th>
<th>1.0</th>
<th>1.5</th>
<th>2.0</th>
<th>2.5</th>
<th>3.0</th>
<th>3.5</th>
<th>4.0</th>
<th>4.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance from apex, m</td>
<td>0</td>
<td>5</td>
<td>10</td>
<td>15</td>
<td>20</td>
<td>25</td>
<td>30</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3

Stem

Root
Distance from the apex, m

Conduit tapering, T

Fig. 4

- angiosperms, max=0.5
- angiosperms, max=0.4
- angiosperms, max=0.3
- angiosperms, max=0.2
- gymnosperms, max=0.5
- gymnosperms, max=0.4
- gymnosperms, max=0.3
- gymnosperms, max=0.2
SMALL ANGIOSPERMS

LARGE ANGIOSPERMS

SMALL GYMNOSPERMS

LARGE GYMNOSPERMS

Fig. 5
Table S1. List of parameter values employed in the numerical model. List A gives all parameters common to both angiosperms and gymnosperms. List B gives the parameters specific to each phylogenetic group.

List A. Common parameters.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Angiosperms and gymnosperms</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irradiance</td>
<td>1000 μmol m$^{-2}$ s$^{-1}$</td>
<td>Estimated</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>400 μmol m$^{-2}$ s$^{-1}$</td>
<td>(Makela et al. 1996)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>0.04 mol m$^{-2}$ s$^{-1}$</td>
<td>Estimated</td>
</tr>
<tr>
<td>$C_a$</td>
<td>350 μmol mol$^{-1}$</td>
<td>Estimated</td>
</tr>
<tr>
<td>VPD</td>
<td>0.015 mol mol$^{-1}$</td>
<td>Estimated</td>
</tr>
<tr>
<td>Photosynthetic time in one year</td>
<td>180 days, 6 hours per day</td>
<td>Estimated</td>
</tr>
<tr>
<td>Element length at petiole</td>
<td>0.05 m</td>
<td>(Weitz et al. 2006)</td>
</tr>
<tr>
<td>Leaf area per petiole</td>
<td>5.4*10$^{-4}$ m$^2$</td>
<td>(Mencuccini et al. 1997)</td>
</tr>
<tr>
<td>Minimum leaf water potential</td>
<td>-2.0 MPa</td>
<td>(Mencuccini et al. 2005)</td>
</tr>
<tr>
<td>Stem base water potential</td>
<td>-0.5 MPa</td>
<td>(Irvine &amp; Grace 1997)</td>
</tr>
<tr>
<td>$\psi_{50}$, xylem water potential causing 50% loss of hydraulic conductance</td>
<td>-2.0 MPa</td>
<td>Mencuccini &amp; Cochard (unpubl. data)</td>
</tr>
<tr>
<td>$A_3$, carbon cost per unit volume of conduit wall</td>
<td>46875 mol C m$^{-3}$</td>
<td>(Siau 1971), assuming C is 50% of dry matter</td>
</tr>
</tbody>
</table>

List B. Parameters specific to each phylogenetic group.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Angiosperms</th>
<th>Gymnosperms</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conduit diameter at petiole</td>
<td>12 μm</td>
<td>5 μm</td>
<td>Mencuccini, unpublished data</td>
</tr>
<tr>
<td>Number of conduits at petiole</td>
<td>5</td>
<td>80</td>
<td>Mencuccini, unpublished data</td>
</tr>
<tr>
<td>Longevity of conduits</td>
<td>5 years</td>
<td>10 years</td>
<td>Estimated</td>
</tr>
<tr>
<td>$A_1$</td>
<td>6.0*10$^{-9}$ Pa$^{-1}$</td>
<td>1.8*10$^{-8}$ Pa$^{-1}$</td>
<td>fitted from data in Hacke et al. (2001)</td>
</tr>
<tr>
<td>$A_2$</td>
<td>0.005 μm</td>
<td>0.03 μm</td>
<td>fitted from data in Hacke et al. (2001)</td>
</tr>
<tr>
<td>Author</td>
<td>Species</td>
<td>Symbols used in figures</td>
<td>Phylogenetic group</td>
</tr>
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<td>--------</td>
<td>---------</td>
<td>------------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>(1)</td>
<td>Scots pine – large islands</td>
<td>Sc.pi. L</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(1)</td>
<td>Scots pine – small islands</td>
<td>Sc.pi. S</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(1)</td>
<td>Picea abies – large islands</td>
<td>Pi.ab. L</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(1)</td>
<td>Picea abies – small islands</td>
<td>Pi.ab. S</td>
<td>gymnosperm</td>
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<tr>
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<td>Sc.pi.</td>
<td>gymnosperm</td>
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<td>Pi.ab.</td>
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<td>Pi.ru.</td>
<td>gymnosperm</td>
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<td>La.la</td>
<td>gymnosperm</td>
</tr>
<tr>
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<td>Pseudotsuga menziesii</td>
<td>Ps.me.</td>
<td>gymnosperm</td>
</tr>
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<td>Larix decidua</td>
<td>La.de.</td>
<td>gymnosperm</td>
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<tr>
<td>(7)</td>
<td>Picea abies</td>
<td>Pi.ab.</td>
<td>gymnosperm</td>
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<tr>
<td>(8)</td>
<td>Pinus cembra – treeline</td>
<td>Pi.ce. T</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(8)</td>
<td>Pinus cembra – medium elevation</td>
<td>Pi.ce. H</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(8)</td>
<td>Larix decidua – treeline</td>
<td>La.de. T</td>
<td>gymnosperm</td>
</tr>
<tr>
<td>(8)</td>
<td>Larix decidua – medium elevation</td>
<td>La.de.H</td>
<td>gymnosperm</td>
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<td>Pi.sy.</td>
<td>gymnosperm</td>
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<td>Ts.ca.</td>
<td>gymnosperm</td>
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<td>(11)</td>
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<td>gymnosperm</td>
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<td>Pita.</td>
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<td>Ps.me.</td>
<td>gymnosperm</td>
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<td>Ps.me.</td>
<td>gymnosperm</td>
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<td>gymnosperm</td>
</tr>
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<td>Abies concolor</td>
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<td>(18)</td>
<td>Pinus contorta – open second growth</td>
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<td>gymnosperm</td>
</tr>
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<td>(18)</td>
<td>Pinus contorta – sphagnum bog</td>
<td>Pi.co. SB</td>
<td>gymnosperm</td>
</tr>
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<td>(19)</td>
<td>Acer pseudoplatanus (grafted 1)</td>
<td>Ac.ps. g1</td>
<td>angiosperm</td>
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<td></td>
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<td>19</td>
<td>Acer pseudoplatanus (grafted 4)</td>
<td>Coomes et al. 2007; (2), Atmer &amp; Thörnqvist 1982; (3), Jackson 1959; (4), Bailey &amp; Shephard 1915; (5), Yang et al. 1986; (6) Becker et al. 2003; (7), Anfodillo et al. 2006; (8), Petit et al. 2007a; (9) Sanio 1872; (10), Ewers &amp; Zimmermann 1984; (11), Trendelenburg &amp; Mayer-Wegelin 1955; (12), Resch &amp; Arganbright 1968; (13), Dinwoodie 1963; (14), Lee &amp; Smith 1916; (15), Bethel 1941; (16), Bailey &amp; Tupper 1918; (17), Anderson 1951; (18), Kienholz 1931; (19), Petit et al. 2007b; (20), Zimmermann 1978; (21), Weitz et al. 2006; (22), Leitch 2001; (23), James et al. 2003.</td>
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<td>Acer pseudoplatanus (field 4)</td>
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<td>Fraxinus excelsior</td>
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<td>Nothofagus solandri var. cliftonioides– low elevation</td>
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<td>Schefflera morotoni</td>
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<td>Anacardium excelsum</td>
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<td>Ficus insipida</td>
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