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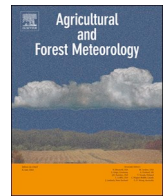
Béland, Martin
Baldocchi, Dennis

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Is foliage clumping an outcome of resource limitations within forests?

Martin Béland[a,*], Dennis Baldocchi[b]

[a] *Department of Geomatics Sciences, Laval University, Quebec City, Quebec G1V 0A6, Canada*
[b] *Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA 94720, United States*

ABSTRACT

Foliage clumping is a forest canopy structural feature influencing light interception, the inversion of light interception for estimating leaf area index, and photosynthesis rates. In this study we estimated clumping factor values at the branch level from different heights in broadleaf tree species at four sites in two climatic zones (two sites in dry climate and two sites in humid climate) using laser light. We found that branch level foliage distribution tends to be random at dry sites where water is the main limiting resource, and that foliage aggregation at the top of emergent canopy tops increases with branch height at humid site where competition for light is high. Our results suggest that high competition for light leads to the production of large amounts of leaves grouped together in high irradiance areas of the canopy, even though this significantly reduces the light interception efficiency on a per leaf area basis. A comparison of these results with foliage clumping factor values derived at larger spatial scales for two sites (one dry and one humid) revealed a crossover in the scales at which clumping arises: leaves are essentially clumped at the branch level but much less so at the plot level for the humid site, and leaves are clumped at the plot level but not at the branch level for the dry site. This suggests that the occurrence of foliage clumping may be related to the intensity of resource limitation (light or water in this case) and its availability in 3D space. Additional research is required to confirm the role of environmental conditions in determining foliage clumping across various forest biomes. Further confirmation and understanding of causal relations between abiotic stresses and canopy foliage clumping may lead to significant refinement in forest canopy radiative transfer modelling schemes.

1. Introduction

Forest canopy structure is known to be a factor of significant influence on forest productivity (Baldocchi and Harley, 1995; Parker, 1995). Metrics associated with canopy structure are useful for modelling light interception, the canopy microclimate, and the gaseous exchanges with the atmosphere (Kobayashi et al., 2012); they are also useful in interpreting the fraction of photons emitted from chlorophyll fluorescence escaping the canopy, which is increasingly being used to assess global photosynthesis from remote sensing (Yang et al., 2018; Zeng et al., 2019). The modeling of photosynthesis and evapotranspiration rates at any given time largely relies on leaf physiology, the amount, inclination and distribution of leaves, the amount of diffuse and direct light, the sun position, and the leaves' conductance (de Wit, 1965).

Historically, scientists have treated the transfer of photons through a plant canopy as an exercise of passing through gaps between leaves randomly distributed in space with a preferred leaf angle distribution (Monsi and Saeki, 1953; Ross, 1981). However, it was shown that foliage distribution within a canopy influences light availability throughout the canopy and helps the ecosystem as a whole to capture more carbon than one with the same leaf area index (LAI) and a random foliage distribution (Baldocchi and Harley, 1995). Partly because of the non-linear nature of several canopy functions, assuming foliage random distribution introduces significant biases in forest productivity models (Baldocchi and Hutchison, 1986; Chen et al., 2012; Chen et al., 2008).

Tree leaves are generally aggregated around branches, and branches aggregated around trunks. These levels of aggregation often result in a non-random distribution of leaves in space, which influences the amount of intercepted light for a given amount of leaves within a space volume (Ross, 1981; Warren Wilson, 1965). This influence has been termed the clumping effect and was first identified in forests in the early 1970s (Acock et al., 1970; Nilson, 1971). Foliage clumping is generally used by the remote sensing and forest productivity modeling communities (Baldocchi and Harley, 1995; Chen et al., 2012; Nilson, 1971). Another metric used to describe leaf aggregation is self-shading, more often used by the forest ecology community (Falster and Westoby, 2003; Pearcy and Yang, 1996). An important difference

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between the two concepts is that the clumping factor is computed within a volume and is estimated relative to a random distribution (a leaf distribution enabling the direct use of a Poisson distribution to estimate light interception for a given illumination direction), whereas self shading is a measure of the relative contribution of leaf overlap and leaf orientation in a given displayed leaf area for a given observation or illumination direction. One might say that foliage clumping has generally been considered a community level structural trait, while self-shading as a species level architectural trait, however both concepts aim to describe the interception efficiency of light by leaves (light intercepted per unit leaf area), and can in theory be applied at any scale.

The non-random dispersion of leaves in forest canopies has been observed (Baldocchi et al., 1985; Kira et al., 1969), measured (Fournier et al., 1996; Wang et al., 1990; Whitehead et al., 1990) and represented in modelling schemes through simplifications (Acock et al., 1970; Ni-Meister et al., 2010; Nilson, 1971; Nilson, 1999). The generalizations introduced to account for structure in computing canopy photosynthesis since the work of Monsi and Saeki (1953); (2005), Duncan et al. (1967) and de Wit (1965) have relied on very scarce and incomplete structural data because of the challenges involved in measuring foliage distribution, and our understanding of the drivers of non-random foliage distributions in forests remains fragmentary (Valladares and Niinemets, 2007). Direct observation of foliage clumping is challenging partly because one needs to isolate the effect of leaf overlap from leaf orientation in interpreting light transmission through foliage (de Castro and Fetcher, 1999). Over the last half century new technological tools have helped increase capacities in describing the 3D geometry of plant parts; from physical needles inserted in crop canopies in the late 50s (Warren Wilson, 1959; Warren Wilson, 1960), to photoelectric detectors in the 80s (Chason et al., 1991; Lang and Xiang, 1986), to 3D digitizing using the Polhemus magnetic digitizer (Sinoquet et al., 1998) and ray tracing modeling in the 90s (Pearcy and Yang, 1996), terrestrial lidar now offers new prospects for probing entire trees and tree parts more rapidly (Beland et al., 2019; Béland et al., 2011).

It is known that clumping may vary with scale, illumination or observation direction (Ryu et al., 2010a), and height above ground (Pisek and Oliphant, 2013). Foliage clumping at the shoot scale has mostly been mostly studied in needle-leaved species, but clumping also occurs at similar scales in broad-leaved species (Niinemets, 2007). Studies have observed that foliage at the shoot, branch or tuft scale is more aggregated in high irradiance (Delagrange et al., 2006; Farque et al., 2001; Niinemets et al., 2005; Planchais and Sinoquet, 1998), and that the aggregation increases with plant (Duursma et al., 2012), and leaf size (Falster and Westoby, 2003). Most of these studies used relatively small trees, i.e. below 3-4 m high. In one study using a broadleaf evergreen species about 15-18 m tall in New Zealand, Niinemets et al. (2005) found that clumping factor decreased (i.e. the clumping of leaves, or aggregation, increased) with increasing irradiance in foliage from two sampled trees. These results suggest that the intensity of the competition for light within a canopy may be a major factor driving leaf aggregation.

Since increased leaf aggregation reduces light interception efficiency, an increase in leaf aggregation should largely result from the availability of a limiting resource which influences the balance between the production and maintenance costs of wood structures and the advantages derived from forming leaf area, as suggested by Niinemets et al. (2004). Our main study objective is to verify this proposition by observing foliage clumping factor values at the branch scale in broadleaf forests from two climatic zones. Forests within the first climatic zone are humid and competition for light is high, and forests in the second climatic zone are dry and water is the main limiting resource. We hypothesize that clumping at the branch level increases with the intensity of the competition for light, and in environments with ample light there is no clumping at that same scale. We use a laser range finder and a terrestrial lidar to characterise leaf aggregation for

tree branches collected at different heights above ground. We also aim to determine if the observed correlations reported in the literature between foliage aggregation, solar irradiance, plant size and leaf size hold across contrasting climatic zones and vertically in forest canopies.

2. Materials and methods

2.1. Study sites

We used four sites from two climatic zones that contrast with regards to resources as a limiting factor to growth (two sites per climatic zone). In the first zone light is ample (light transmission at ground level in the 30-60% range) and water is the main resource trees are competing for, and in the second zone water is ample and competition for light is high (light transmission at ground level in the 3-10% range). The intensity of competition for light is considered here a site level dynamic which does not vary within the canopy, while the availability of light in a competitive environment does vary —mostly vertically— within the canopy. Branches from a total of eight tree species were selected to study leaf arrangement from the four different sites (the water-limited zone includes the Tonzi ranch and Russell Research Station sites, and the light-limited zone includes the Quebec and Morgan Monroe State Forest sites described below). Since the intensity of competition for light is known to largely determine maximum tree height (King, 1990; Westoby et al., 2002), we selected sites having different maximum canopy height, and to assess the effect of light availability on foliage clumping we collected branches from different positions vertically within the crowns at one of the sites. Table 1 provides a list of the species used and leaf characteristics.

The first site is located near Ione, California, USA, on the Tonzi ranch (38.43°N, 120.96°W, elevation: 177 m). The site is a savanna dominated by blue oak trees (*Quercus douglasii*), it is generally flat and receives on average about 560 mm of rain annually, with most precipitation concentrated during the winter months. The Tonzi site is in the dry sub tropical hot summer climatic zone. The tree density is about 144 trees per hectare and mean tree height is about 9.5 m (Ma et al., 2007), the average gap fraction is about 60% at 57° view zenith angle (Ryu et al., 2010b). The average leaf size for the blue oaks at this site is about 3.5 cm (S.D. = 0.9 cm) along the midrib and 2 cm (S.D. = 0.7 cm) across (Béland et al., 2014a).

The second site is located within the Russell Research Station near Lafayette, in Contra Costa County, California, USA. The site is a wildland and forestry research station managed by the University of California, Berkeley. The 115 hectares facility includes coastal woodland, scrublands, oak woodlands, grasslands, riparian areas and conifer plantations. As a result of hilly terrain (elevation from 215 m to 388 m) and land management, this site holds various tree species and microclimatic conditions. Annual precipitation averages 690 mm. Trees from the woodlands on the hill tops were selected for this study. The area selected is part of the dry sub tropical hot summer climatic zone, and the mean tree height is about 8 m. No value for tree density is available but it is estimated slightly higher than at the Tonzi ranch site. The species used are Interior Live Oak (*Quercus wislizeni*), Valley Oak (*Quercus lobata*), Black Oak (Quercus kelloggii), Bay Laurel (*Umbellularia californica*).

The third site is located about 20 km north of Quebec city, Canada, on a privately owned forested land (46.92°N, 71.40°W, elevation: 150 m). This site is in the temperate humid warm summer climatic zone. The annual average precipitation is 1200 mm. The site is a mixed forest dominated by sugar maples (*Acer saccharum*) and American beech (*Fagus grandifolia*). The maximum tree height is about 25 m.

The fourth site is located within the Morgan Monroe State Forest in south-central Indiana, USA (39.32°N, 86.41°W). The site is with the temperate humid hot summer climatic zone and receives on average 1032 mm of precipitation. The selected trees are located about 200 m from the site's eddy covariance flux tower, the average gap fraction at

Table 1
Synthesis of branch sampling and field measurements for each specie used in this study.

Specie	Field site/annual precipitation	Number of branch samples	Height of branch samples	Method(s) used	Laser probe size	Approximate leaf size (across and along midrib)	Voxel size	Poisson law correction factor	Method used for measuring leaf orientation
Blue Oak	Tonzi / 560 mm	10	5 m	Clumping device	5 mm	2 cm – 3.5 cm	30 cm	1.05	Measured using digital photographs for entire canopy, erectophile distribution used (0.54 in horizontal direction)
Interior Live Oak	Russell / 690 mm	10 + 2	2-5 m	Clumping device and TLS	5 and 8 mm	2 cm – 4 cm	30 cm	1.06	Measured using TLS for 2 samples. 0.5 value used for clumping device samples (10)
Valley Oak	Russell / 690 mm	10 + 2	2-5 m	Clumping device and TLS	5 and 8 mm	4 cm – 7 cm	30 cm	1.12	Measured using TLS for 2 samples. 0.5 value used for clumping device samples (10)
Black Oak	Russell / 690 mm	10 + 2	2-5 m	Clumping device and TLS	5 and 8 mm	8 cm – 12 cm	30 cm	1.2	Measured using TLS for 2 samples. 0.5 value used for clumping device samples (10)
Bay Laurel	Russell / 690 mm	10	2-3 m	Clumping device	5 mm	2 cm – 8 cm	30 cm	1.08	Not measured, 0.5 value used
Sugar Maple	Quebec / 1200 mm	8	4-25 m	TLS	8 mm	Emergent : 6 – 6 cm Non-emergent : 10 – 10 cm	40 cm	1.1	Measured using TLS for all samples
Red oak	Morgan Monroe / 1032 mm	1	40 m	TLS	8 mm	8 cm – 12 cm	40 cm	1.1	Measured using TLS for all samples
White oak	Morgan Monroe / 1032 mm	3	40 m	TLS	8 mm	11 cm - 16 cm (strong indentation)	40 cm	1.1	Measured using TLS for all samples

that location is about 3% at 57° view zenith angle (Benson, 2018). The trees are within a deciduous broadleaf forest comprised predominantly of sugar maple (*Acer saccharum*), white oak (*Quercus alba*), red oak (*Quercus rubra*) and tulip poplar (*Liriodendron tulipifera*). The maximum tree height is about 40 m.

2.2. Branch sampling and measurement methods

The estimation of foliage clumping at the tree branch scale requires fixing a volume space, here we chose a cube of side dimension selected according to leaf size so that leaves are sufficiently small within the volume space to enable the use of a Poisson law (Béland et al., 2014a). For all samples, the branch was placed inside a cubic frame. Tripods were used to hold the branches for measurements in the same orientation as it was when fixed to the tree. Leaves that protruded from the box were not removed, the interception of laser light by leaves and wood outside the box was accounted for in the method used. We used a light transmission approach computed using laser probes to determine the area of leaves displayed in a given probing direction.

Clumping can be quantified in different ways using light transmission and Beer's law: negative binomial model (Baldocchi et al., 1985; de Wit, 1965; Whitehead et al., 1990), and the Markov model (Nilson, 1971). The Markov clumping factor has been widely adopted, perhaps because it can represent both the clumped and regular dispersion of foliage (the positive binomial model is needed to describe the case of regular dispersion). By observing light transmission through the box volume, measuring leaf area within the box volume, and estimating the leaf projection factor for the leaves inside the box volume, we enabled the estimation of the clumping factor through the inversion of the Markov model (Nilson, 1971), as:

$$\Omega = \frac{-ln(T)}{LAD \cdot \delta \cdot G} \tag{1}$$

Where G is the value for the leaf projection factor in the observation/illumination direction (also called the direction cosine, defined as the mean cosine of the zenithal angle between vectors normal to the leaves and the solar illumination direction), δ is the length of the path traveled by the laser pulses, T is the fraction of light transmission which considers only laser pulses hitting leaves and pulses going through the volume without making contact (laser pulses hitting wood are recorded but considered as noise for the purpose of estimating clumping here). A value of one for the clumping factor (Ω) refers to a random distribution, values below one refers to clumped or aggregated distributions, and above one to regular distributions (leaves intercepting more light than a random distribution). All leaves inside the box volume were collected, placed in hermetic plastic bags and the leaf area was measured using a LI-3100 leaf area meter (Tonzi and Russell sites), or a flatbed scanner and the WinFolia software (Régent Instruments Inc., Québec, QC, Canada) (Quebec and Morgan-Monroe sites) within 24 hours of collecting the leaves. For each sampled branch, the orientation of leaves is measured using various approaches listed in Table 1.

We used two different methods to determine light transmission which are adapted to the various leaf sizes of the species sampled: the first method uses a "clumping device", and the second a terrestrial lidar instrument (TLS). The two methods made use of laser probes with different diameters (5, and 8 mm) so that the probe diameter is small relative to the size of the leaves to minimize the underestimation of light transmission resulting from finite size probes (Warren Wilson, 1963). The use of TLS has the advantage of providing information on both the leaf projection factor (combining the zenithal and azimuthal directions) and light transmission, thus allowing to isolate the effect of leaf projection from foliage dispersion in the observed intercepted light. While for the clumping device, a projection factor derived from generic leaf angle distribution functions can be used, but the projection factor is then not specific to the measured branch and does not account for preferential azimuthal orientation.
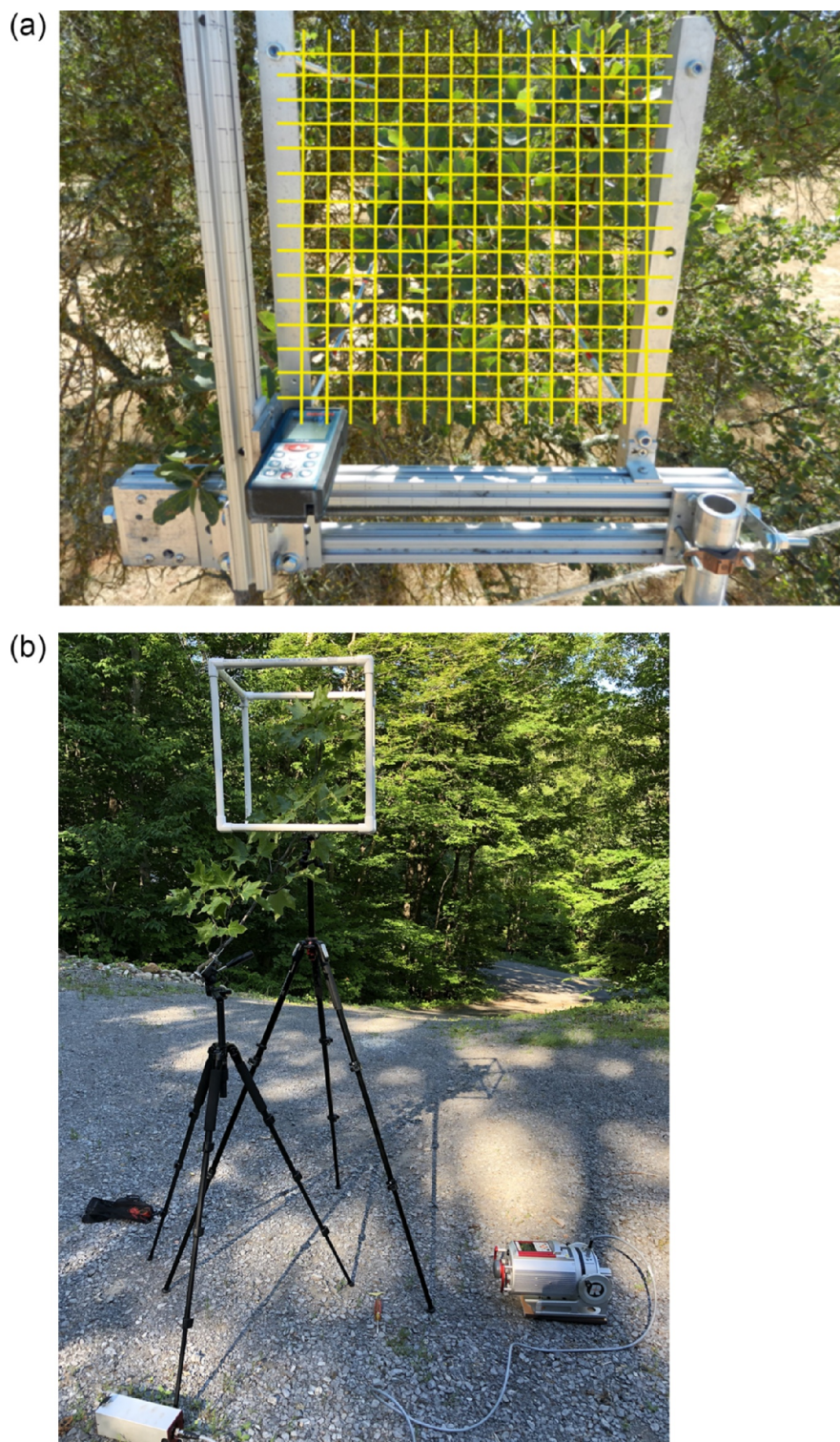
Fig. 1. (a) Front view of the clumping device with laser pointer and gridded measurement pattern overlaid on the picture. (b) Image of the terrestrial lidar instrument on the ground and an illumination zenith angle of 24 degrees.

We designed and built the clumping device to compute light transmission through the cubic volume. The device has a fixed frontal dimension of 30 × 30 cm, and allows measuring transmission at variable depth of 20, 30 and 50 cm. A laser range finder (Bosch brand, model GLM80) was fixed to the front of the cubic volume to sample, and can be moved along the two 30 cm axis of the volume front side. The size of the laser light was measured to be about 5 mm in diameter 40 cm away from the device. Transmission measurements were made at 2 cm intervals along both axis of the cubic volume front, yielding a total of 196 measurements per sample (see Fig. 1a). For each measurement position, the operator noted whether the laser light (1) came in contact with a leaf, (2) came in contact with wood, or (3) traversed the volume without making contact with plant material. For cases one and two the distance between the laser range finder and the plant part was also recorded. For all sampled branches the clumping device was positioned horizontally and oriented with regards to the branch position in the

crown so that its direction is towards the crown center.

The TLS method uses a Riegl VZ-400 instrument with a laser wavelength at 1550 nm and a pulse diameter of about 8 mm at a distance of 5 m (see Fig. 1b). The TLS measurements were made from multiple positions and the point clouds were aligned to a common coordinate reference system using targets, with a registration accuracy within 1 cm. To isolate the effect of leaf position from leaf orientation in light transmission, a leaf projection factor (the proportion of leaf area projected on a plane perpendicular to an observation direction) was estimated for each lidar scan direction. To achieve this, between 25 and 50 leaves within the box from each sample were isolated within the lidar point cloud and a plane fitted to each leaf to compute its azimuthal and zenithal orientation with regards to the lidar scan direction. The leaf projection factor was computed for each scanning direction as: cos (zenith angle between leaf normal and probing direction) * cos(azimuthal angle between leaf normal and probing direction). The intensity of the reflected laser energy was used to distinguish returns from leaves and branches or twigs. An appropriate apparent reflectance threshold to separate leaf from wood returns was identified by fitting a Gaussian function to the binned apparent reflectance data from the TLS using the approach described in Béland et al. (2014a). A return having less than half the mean leaf reflectance was considered to be centered outside the leaf edges and tagged as noise and ignored in the light transmission computations.

At the Tonzi site, ten branches were sampled at a height of about 4 m from the ground, without cutting them from the tree; the branches were accessed using a scaffolding. All selected branches were located on the south side of the crown, well exposed to solar irradiation. Visual observations suggested that leaf arrangement was not significantly different at the top of crown compared to the areas selected for sampling on sun exposed sides of crowns. For the blue oak leaves, no preferential azimuthal direction was observed visually. Leaf angle distributions were derived for different heights from the eddy covariance tower at the site using the digital photography approach presented in Ryu et al. (2010b). Light transmission was measured using the clumping device method.

At the Russell Station site, branch samples were cut from the tree and brought to the ground for measurements. A 4m ladder was used to collect the samples from branches exposed to different light conditions. A first ten branches were sampled and measured using the clumping device using the clumping device method (the 30 cm probing depth only was recorded). This initial branch samplings revealed two elements: (1) azimuthal leaf orientation did not appear random for the species at this site, and (2) clumping appeared to be different when observing a branch in a direction tangential to the tree crown envelope vs in a direction towards the crown's center. To isolate the effect of leaf position from leaf orientation on light transmission, and to investigate the effect of viewing direction, we used the TLS method on a second set of six additional branch samples with the instrument set at two positions about 5 m from the branch with perpendicular viewing directions (positions 1 and 3 in Fig. 2a).

At the Quebec site, eight branches from sugar maple trees were collected at different heights, including the top most part of the canopy. Four samples were collected from the lower canopy level, one sample was collected from a non-emergent tree top (at a height of about 15 m), and three samples were collected from emergent tree tops (at heights of about 25 m above ground). The branch from a non emergent tree top was shaded by taller trees on the south side, but had an open access to diffuse light coming from the north side. The trees were climbed using arborist style techniques, and a pruner attached to an 8 feet pole was used to cut branches from the upper most part of the canopy. The branches were then brought on the ground for measurement. Light transmission and leaf orientations measurements were done using the TLS method. To assess the effect of view zenith angle on the clumping factor value, two protocols were used to position the TLS: a first protocol used scans from five directions from a distance of about 4 m with

the instrument at the same height as the branch (see Fig. 2a), simulating solar illumination from the horizontal direction. For the second protocol, the lidar instrument was positioned on the ground and the branch was positioned about 1.9 m above ground, the distance between the projected position of the branch on the ground and the instrument was about 0.9 m, resulting in an illumination incidence angle of about 24 degrees (see Fig. 2b).

At the Morgan Monroe site, tree climbing techniques were also used to collect branches at the top of the tallest trees (about 40 m above ground). Three branches from white oak, and one branch from red oak were collected for measurements. The light transmission and leaf orientations measurements were done using the TLS method and the second instrument positioning protocol.

For each tree species, the bias introduced by the use of the Poisson law was computed following the approach described in Béland et al. (2014a), and the correction values applied to the clumping factor are provided in Table 1 (9th column). When computing the clumping factor from measurements made with the clumping device, all probes going through the cubic volume have the same length, hence δ has a constant value for all individual probes. The light transmission is computed as:

$$T = 1 - \frac{\text{\# of leaf hits}}{\text{\# of leaf hits} + \text{\# of gaps}} \qquad (2)$$

When using measurements from the terrestrial lidar, laser pulses can have significantly different path lengths as they travel through the cubic volume, and following Jensen's inequality a bias in clumping factor values would be introduced by using an average value for δ. To avoid this bias, we used the VoxLAD model (Béland et al., 2014b) which accounts for the effect of Jensen's inequality when estimating foliage clumping. This model uses a modified form of Eq (1), more details on the lidar data processing methods are provided in Supplementary Material Methods S1.

3. Results and discussion

For the blue oak trees at the Tonzi site, leaf area density varied from 1.48 to 4.73 m²/m³. Although leaf orientations were not measured directly for the individual branch samples (leaf orientations were measured using digital photographs taken at different heights from a walk-up tower, following the approach of Ryu et al. 2010b), a careful visual assessment of the sampled branches photographs suggests a weak preferential azimuthal direction in leaf orientation. The light transmission values ranged from 0.49 to 0.80 for the 30 cm depth volume. The foliage clumping factor ranged from 0.81 to 1.33, with an average of 0.98 (95% confidence interval (CI), 0.87–1.09; see

Fig. 3). This average value for foliage clumping is very close to a random dispersion of leaves (omega = 1); values below 1 refer to clumped foliage.

The clumping factor values for the different probing depths (20, 30 and 50 cm) for the blue oaks indicate a slight increase in the clumping factor with probing depth, i.e. leaves are more aggregated when the volume probed is shallow than when it is deep. This suggests an interaction between the probing depth and the space between the twigs along the blue oak branches, and may express a positioning of twigs that minimize mutual shadowing and maximize the potential for light interception as light penetrates deeper into the crown. Further results relating to probing depth are provided in Figs. S1 and S2.

Results from the group of ten samples from four species measured at the Russell station site with the clumping device are shown in

Fig. 4. Inspection of the field photographs of the sampled branches suggest that the observed high variability in clumping factors is mainly due to the orientation of leaves with regards to the probing direction. The average values obtained for all branch samples suggest a close to random distribution for the species at the Russell station site, and the average clumping factor across all species at this site was 0.98 (CI,
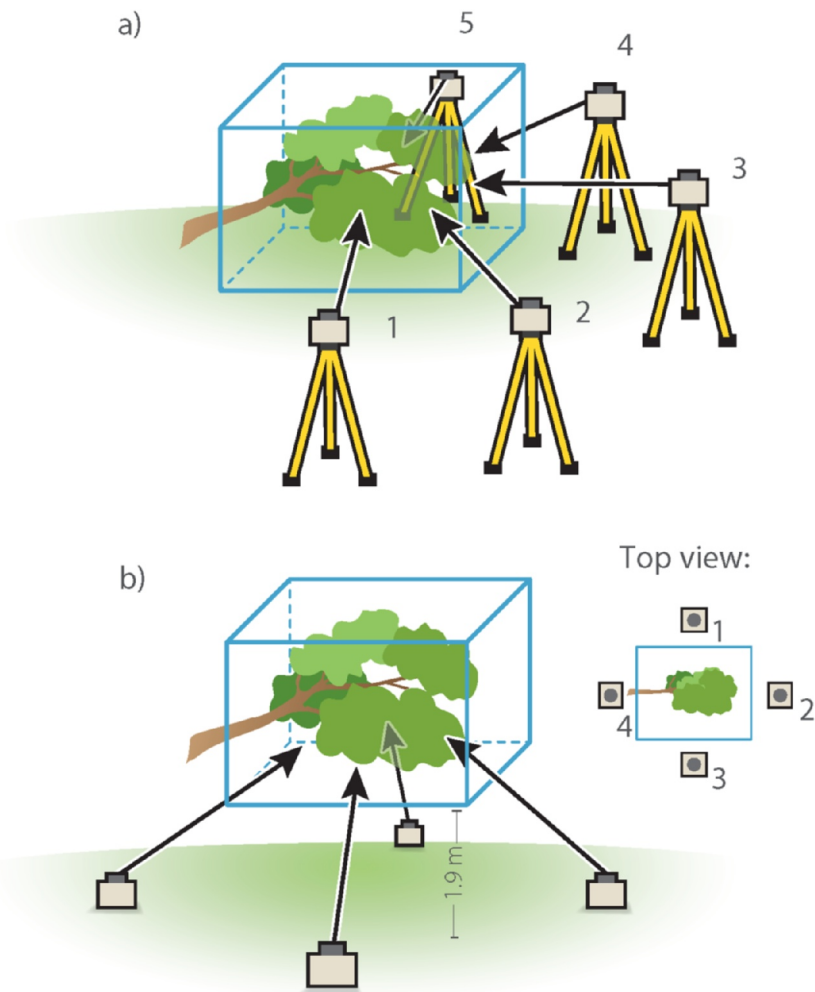
Fig. 2. Illustration of the terrestrial lidar measurement protocols used at the Russell Station (a), Quebec (a and b), and Morgan Monroe (b) sites. For the top protocol the TLS instrument is positioned at the same height as the branch (view zenith angle is 90°). For the bottom protocol, the TLS instrument is positioned on the ground, about 1.9 m below the branch, resulting in a view zenith angle of 24°. For both protocols, numbers refer to the scan positions used in figures showing results for the three sites mentioned above.

0.90–1.06).

Results from the estimation of clumping factor for the second group of branches measured with a terrestrial lidar are presented in

Fig. 5. These results suggest that all three species studied have lower clumping factor values when illuminated from the side (light coming in the direction of the tangent to the tree crown envelope) than when the light is traveling towards the crown's center. Note that this effect does not result from leaf orientation (azimuthal asymmetry), as a leaf projection factor is computed for each individual viewing -or probing- direction and for each branch. Average values for clumping factors were between 0.79 and 1.1 (average of all measurements: 0.90, CI: 0.68–1.12). Black oaks appeared particularly efficient at displaying leaves in a regular pattern towards the dominant incoming light direction.

Results from the sugar maples at the Quebec site using protocol 1 (horizontal illumination angle) are presented in

Fig. 6. The results show a significantly lower clumping factor value for the branch sampled from the emergent part of the canopy (average of 0.44, CI: 0.35–0.53) vs branches in the lower canopy part (average 1.07, CI: 0.92–1.23). Visually, the branches in high light condition appeared to grow much more leaves with shorter twigs closer together. The sugar maple branches from emergent tree tops measured at the Quebec site using protocol 2 (with a 24 degrees zenithal illumination angle) had similar clumping factors to the emergent branch illuminated

from the horizontal direction (see

Fig. 7). The lower level branches had slightly higher clumping factors (averaging about 1.2) than from the horizontal illumination direction. This suggests that illumination —or observation— zenith angle has a limited effect on the branch level clumping factor. Lower level sugar maple branches had leaf area densities between 0.99 and 2.34 m^2/m^3, and the emergent branches between 4.82 and 6.29 m^2/m^3.

The clumping factors for the oak branches at the Morgan Monroe site are shown in

Fig. 8. The factors are remarkably constant across illumination directions and between branches, even though the leaf area density within the cubic volume ranged from 3.53 to 7.39 m^2/m^3. The average clumping factor over all branches was 0.32 (CI, 0.27–0.37). The half width of the 95% confidence intervals for clumping factor estimates at all sites were within about 20% of the mean values derived, indicating that the number of branches sampled was appropriate to support the findings considering that the differences between upper/lower canopy branches and wet/dry sites were much higher than 20%.

Across all sites used here, no clear relationship was found between leaf size and foliage clumping factor

Fig. 9). A more consistent relation ($R^2 = 0.92$) was found between leaf area density and clumping within the Quebec site, because leaf area increased with height and clumping factor decreased with height

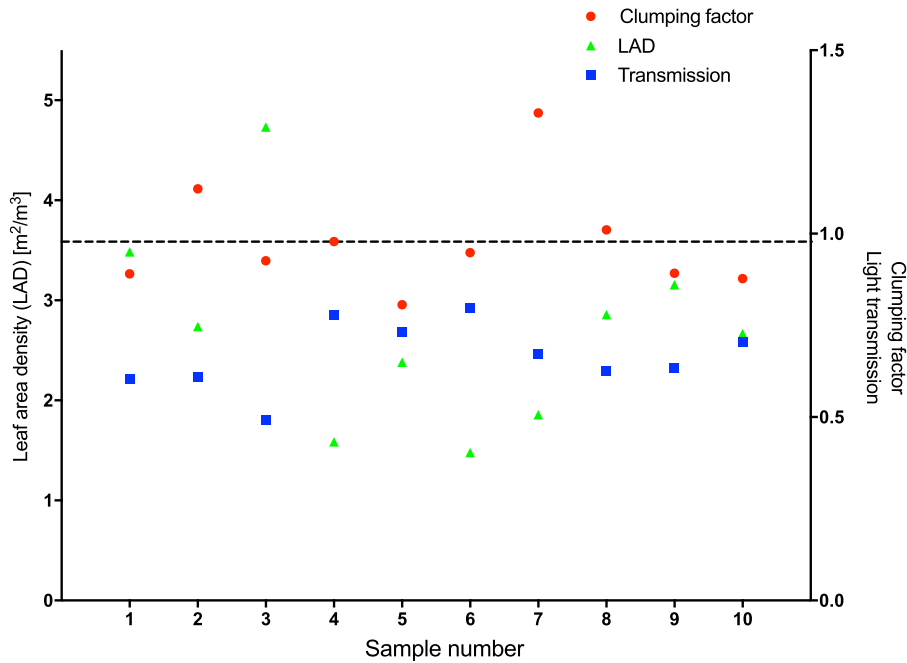Fig. 10). The relation was weaker when considering all four sites

Fig. 3. Leaf area density, light transmission and foliage clumping for the ten samples at the Tonzi field site. Results for the 30 cm depth volume are shown.

($R^2 = 0.52$). Across all sites, a relationship with an exponential form was observed between branch sampling height and clumping factor Fig. 11). Our results indicate there is a relation between leaf clumping at the branch scale and leaf area density, at least within the Quebec site where leaves were sampled at different heights. The observed negative relationship indicates that in portions of the canopy having higher number of leaves in a given space, leaf clumping factors were low (indicating that leaves were aggregated or clumped). These results agree with results from Falster and Westoby (2003). However, we did not observe a relation between clumping and leaf size across the sites from different climatic zones. This is partly explained by leaf size and clumping being variable vertically at temperate sites, making this relation not directly observable across climatic zones. Our results also agree with Planchais and Sinoquet (1998) and Niinemets et al. (2005) regarding an increased light interception efficiency in lower light for the humid sites, but not at the dry sites, where average clumping factor remained close to 1 (random distribution) for all species and we did not find a direct relation with their exposure to sunlight.

The foliage clumping factor at branch scale was found to correlate with sampling height, which agrees with such a relation suggested by
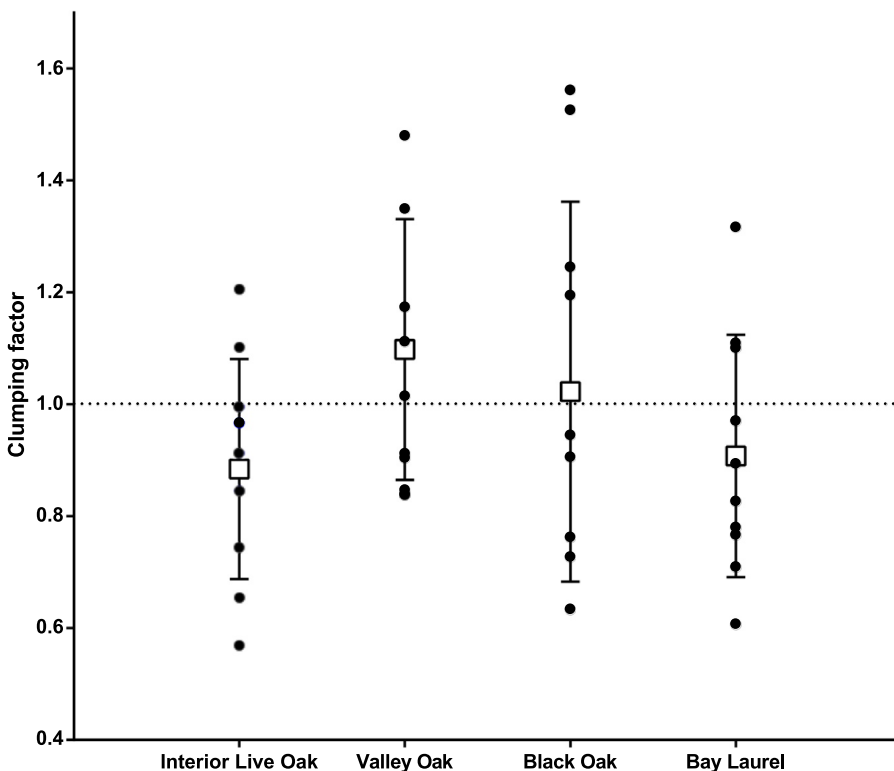

Fig. 4. Foliage clumping estimation for the Russell Station species. Results shown here are from the first group of branches sampled (measured with the clumping device). Note that leaf projection factor has a significant impact on individual values for some of these species displaying a strong azimuthal prevalence in leaf orientation (see text for details). Vertical bars refer to the standard deviation for all samples from each species.
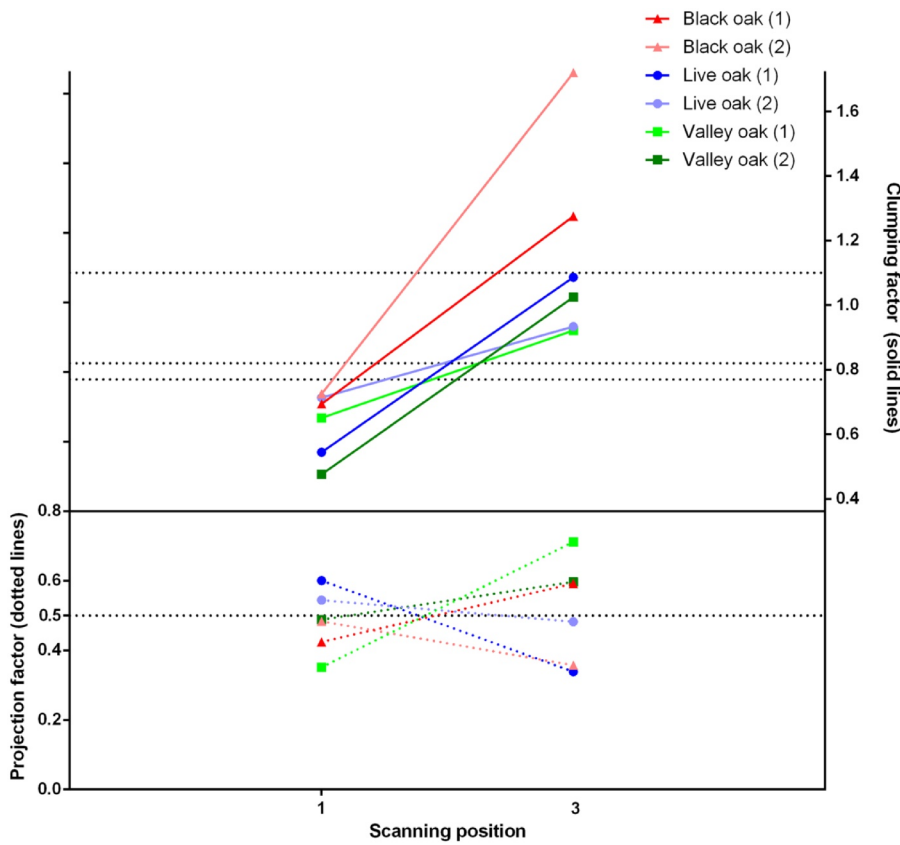
Fig. 5. Results from leaf projection factors and foliage clumping estimation for the second group of branches sampled at the Russell Station site. Scan positions 1 and 3 correspond to position locations for protocol 1 shown in Fig. 2a. Position 3 is facing the direction that the branch is protruding from the tree (facing the support holding the branch). The doted horizontal lines refer to the average clumping values for—from the top—the black oaks, live oaks, and valley oaks.
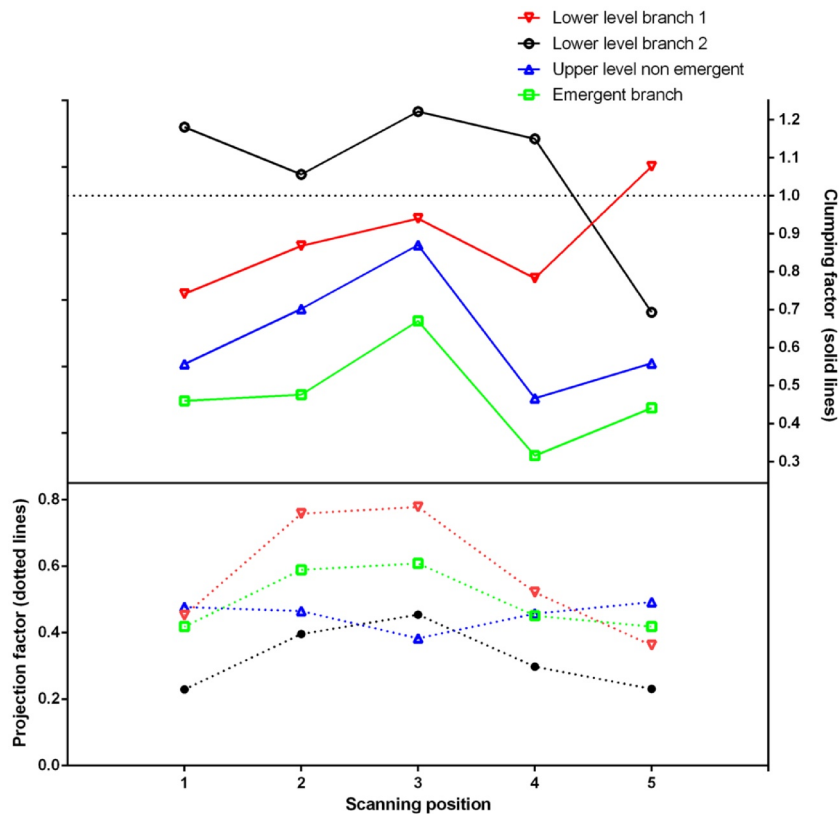

Fig. 6. Leaf projection factors and foliage clumping estimated for branch samples at the Quebec site using measurement protocol 1 (horizontal illumination direction (view zenith angle of 90°), as illustrated in Fig. 2). Scanning positions correspond to position locations shown in Fig. 2a.
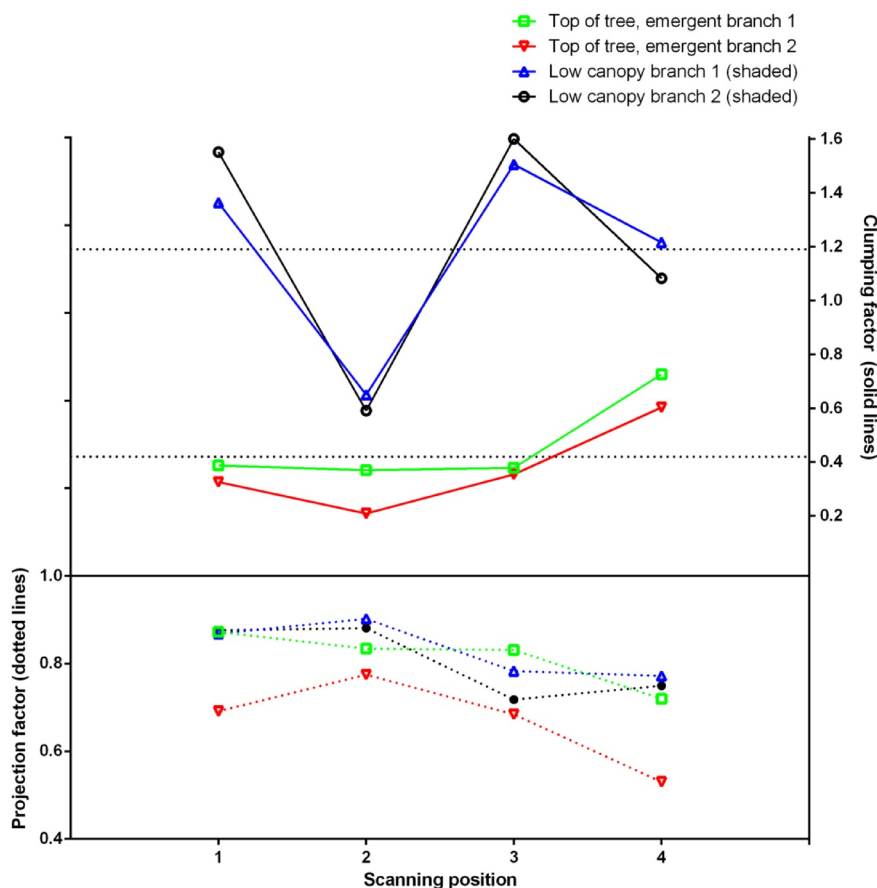
Fig. 7. Leaf projection factors and foliage clumping estimated for branch samples at the Quebec site using measurement protocol 2 (24 degrees zenithal illumination direction, as illustrated in Fig. 2). Scanning positions correspond to position locations shown in Fig. 2b.

Duursma et al. (2012), and supports the hypothesis that high irradiance availability at the branch level is associated with higher foliage aggregation (lower clumping factor) in ecosystems where competition for light is intensive. Samples collected at multiple heights above ground were only used for one site in our study, and we do not suggest that the correlation between branch height and clumping is universal. The sampling height is used here as a proxy for both the intensity of the competition for light at the site level, and for the variation in available light which scales vertically with cumulative LAI and gap fraction. The competitive pressure for light exerted by neighboring tree crown on a given tree branch is likely an important driver of clumping. Whether a tree has reached its maximum height may be another driver of branch level clumping, since a tree investing primarily in height growth may invest less in leaf production, at least not at the cost of significant reduction in light interception efficiency. This is supported by an observed relation between stand age and site level clumping (Brown and Parker, 1994), and the relation between foliage efficiency (bole volume increment per unit of foliage biomass) and competitive status (crown length/height) (Le Goff and Ottorini, 1996).

Additional factors not present at the sites used are expected to influence the relationship between branch height and foliage clumping. For example, in very tall trees where gravity and path length resistance greatly limit water transport, or in trees where top of canopy leaves can reach high temperatures leading to stomatal closure, the trade-off between the amount of leaves produced at canopy tops and the cost of biomass production and maintenance is expected to reflect these water transport limitations. How these two factors influence branch level foliage clumping in very tall canopies and in tropical rainforests remains unknown.

With the exception of branches in lower canopy levels, only the top

most branches of tree crowns were selected for sampling at the two humid sites in our study. Our visual observations of the branching patterns within the canopy suggest there is a rapid transition between highly aggregated leaves at the canopy top and much less aggregated leaves within the canopy (likely a response to a rapid vertical decrease in available light). This transition was thus not fully described here, and requires further sampling to characterise it in different ecosystems. In the temperate zone the transition between highly aggregated and regular dispersion patterns appears to happen in the first 3-5 meters of the canopy tops. We suspect this transition distance may be longer in humid tropical areas where sun elevation angles are higher and allow greater vertical light penetration in the canopy top-most section.

Our results may have additional implications for research on the relation between light gradients and leaf morphology. Leaf mass per area (LMA) is known to be determined by hydrostatic constraints and light availability (Ellsworth and Reich, 1993), but it remains unclear what factors drive the relative importance of water potential and light availability in forests (Coble and Cavaleri, 2014). Could the branch scale high leaf density and low light interception efficiency observed here at the top of the sugar maple and red/white oak trees have an influence on leaf morphology towards maximizing CO_2 assimilation? Could it be related to observed differences in the main determinant of LMA (light or water) between broadleaf deciduous and evergreen trees (Coble and Cavaleri, 2014).

3.1. Potential ecological advantages of increasing leaf aggregation in high irradiance

Foliage clumping relates to some theoretical form of efficiency for leaves to capture light as a function of the resources invested in
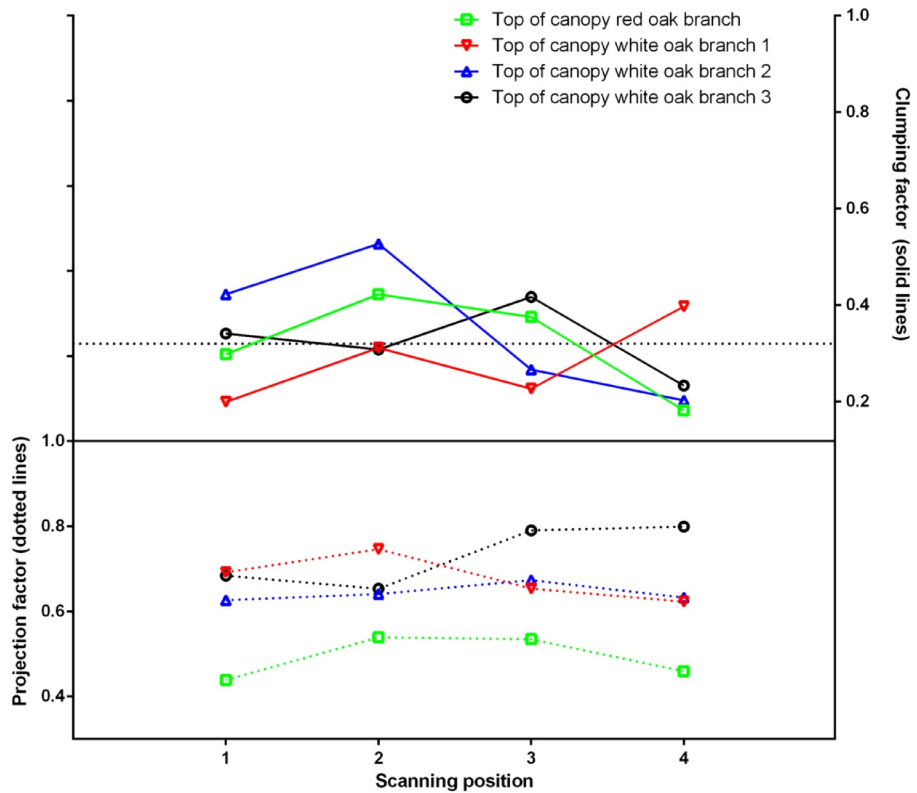
Fig. 8. Leaf projection factors and foliage clumping estimated for samples collected at the Morgan Monroe site using measurement protocol 2 (24 degrees zenithal illumination direction). Scanning positions correspond to position locations shown in Fig. 2b.

producing a given amount of leaves. It was shown in our study and elsewhere (Farque et al., 2001; Niinemets et al., 2005; Planchais and Sinoquet, 1998) that branches in areas of a canopy benefiting from high irradiance have leaf distributions at the branch level which are well

below this theoretical efficiency; why could this be? Duursma et al. (2012) suggested that a clumped or aggregated distribution has advantages of being less costly in supporting structure for a given leaf area. Niinemets et al. (2004) mentioned that the investment
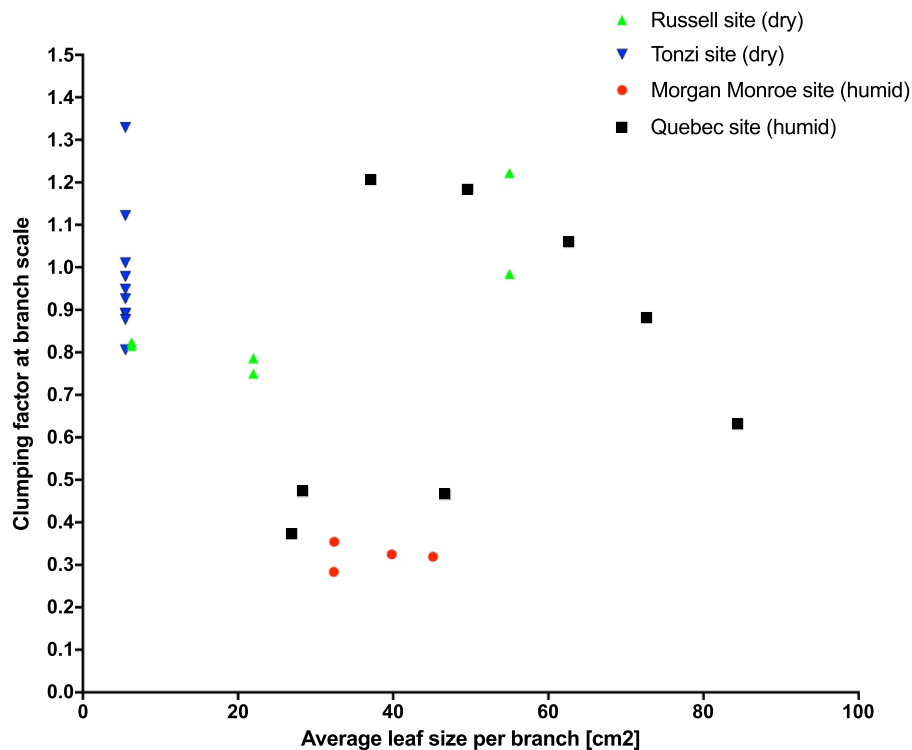
Fig. 9. Relation between average leaf size and the observed foliage clumping factor (averaged over all illumination directions) at the branch level for all sites.
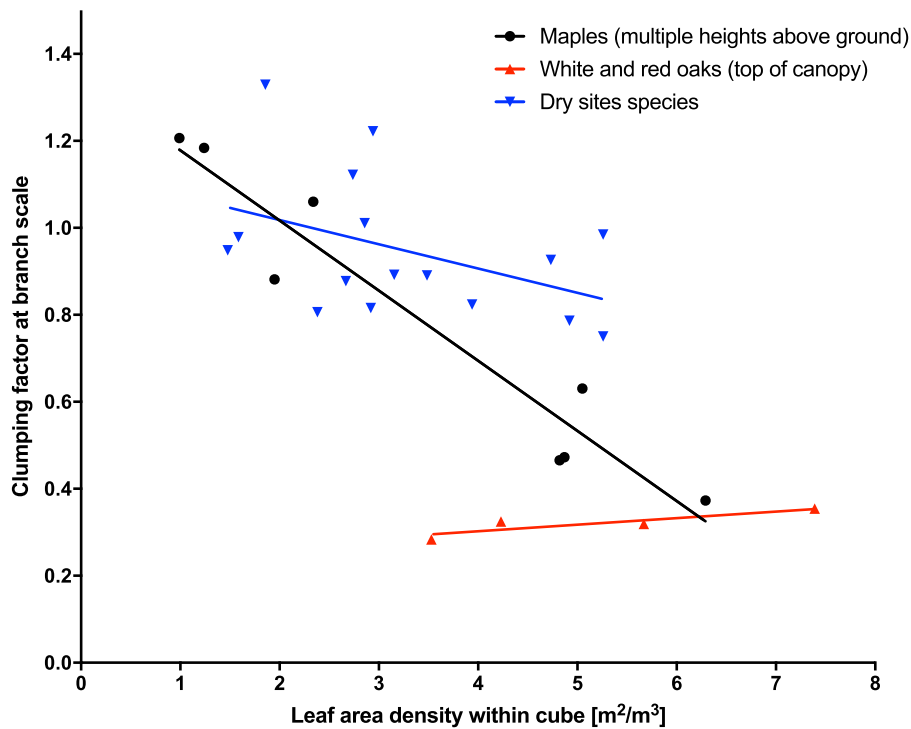
Fig. 10. Relation between leaf area density (LAD) within cubic volumes and the foliage clumping factor (averaged over all illumination directions).

in support structure per leaf mass and area is larger at high than low irradiance. Pearcy et al. (2004) stated that minimizing self shading is costly "since it requires investment in stems and petioles to minimize leaf overlap.", and that "displacement of the leaf area away from the point of attachment of the petiole increase the movement of force, requiring additional investment in support". At the canopy level, Baldocchi and Harley (1995) and Baldocchi and Wilson (2001) showed

that where leaves in the upper canopy layer were sun saturated, clumping allowed more light deeper into the canopy where leaves were shaded and unsaturated, which helped increased canopy photosynthesis as a whole.

Further consideration of this relation between the costs and benefits of lowering light interception efficiency should encompass constraints and opportunities imposed and offered by the environment when trees
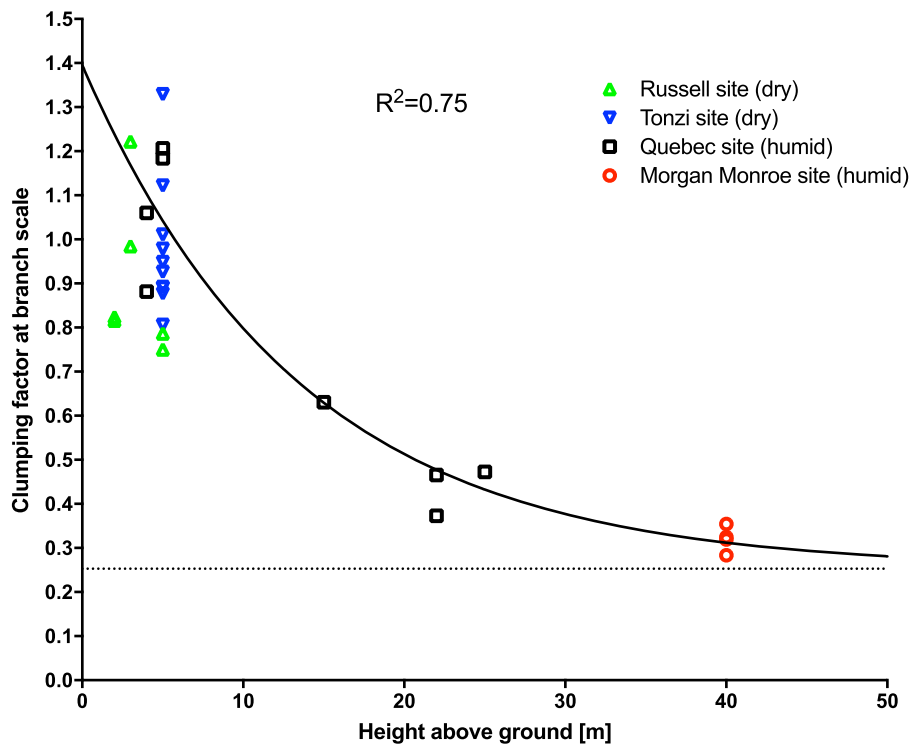

Fig. 11. Relation between height above ground at which the sampled branch was collected and the foliage clumping factor (averaged over all illumination directions).

occupy space to forage for resources. We suggest that four additional considerations to explaining why lower interception efficiencies are observed in canopy tops in forests where competition for light is intensive:

(1) the penumbra effect (arising from the solid angle between the sun and a point in the canopy) is often not considered when estimating light interception efficiency (Denholm, 1981). The non-punctual nature of the sun irradiance slightly increases light interception efficiency at the branch level in broadleaf trees (Baldocchi and Collineau, 1994).
(2) branch movement from wind can be quite important in tall canopies, even under low wind conditions (Tong and Hipps, 1996). This constant movement of leaves results in a higher number of leaf clumps being exposed to direct light over short time laps. It is known that leaves can respond rapidly to sunflecks so they are able to rapidly take advantage of even short exposures to high levels of direct light (Pearcy, 1990; Van Gardingen and Grace, 1991; Way and Pearcy, 2012).
(3) diffuse light interception is potentially very high in temperate zones where clouds are frequent, at which time light becomes highly diffuse. This light incident from multiple directions may advantage trees with high leaf densities in the upper canopy part.
(4) In hotter environments with high light and high vapor pressure deficits, there may be an advantage in having lower leaf aggregation through leaf clustering potentially increasing the leaf boundary layer thickness from increased wind turbulence near the leaves, resulting in better transpiration and evaporative cooling (Blonder and Michaletz, 2018; Helliker and Richter, 2008; Michaletz et al., 2015). Also, since leaves absorbing radiation become thermal energy emitters, leaves are better able to avoid excessive leaf temperature by keeping away from each other (Schuepp, 1993).

3.2. Integration with foliage clumping factors at larger spatial scales

For the Tonzi (dry) and Morgan Monroe (humid) sites used here, published values of clumping factor at the plot level are available from studies by Ryu et al. (2010a) and Pisek and Oliphant (2013). The plot level foliage clumping factor estimates from these studies are 0.49 for Tonzi and 0.75 for Morgan Monroe. The comparison of these values with the results obtained here at the branch level for these two sites is shown in
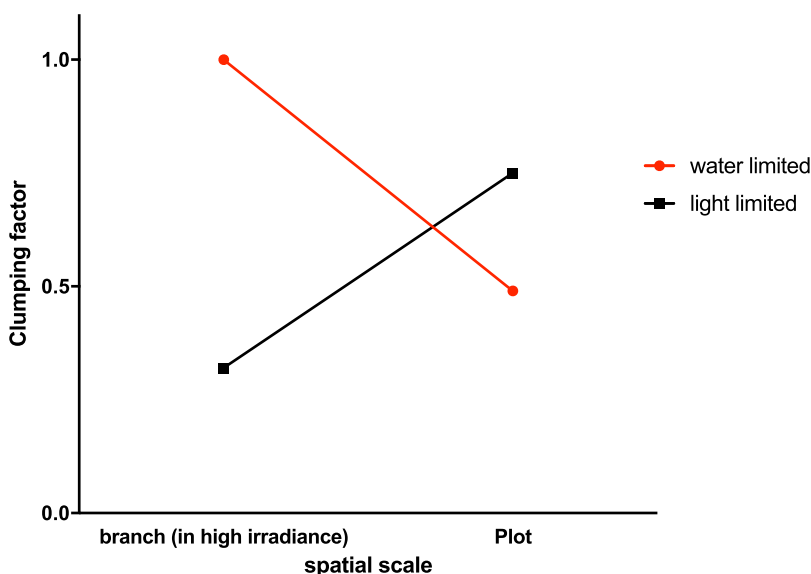
Fig. 12. This figure shows a crossover in the scales at which clumping arises in the light vs water limited sites. The comparison of these results suggests that the scale and location at which a limiting resource (light or water) acts upon the development of trees and tree parts may be an important control of foliage clumping. Very little is currently known about the controls of foliage clumping and the relative role of environmental conditions vs tree genetics. For a given species assemblage, is foliage clumping controlled by tree morphology and inherited branch development patterns, or by pressure from resource limitation? Here we provided the first evidence of a large gradient in foliage clumping at the branch level across contrasting climatic zones, and more evidence is required to determine whether environmental conditions is the dominant driver. One approach to addressing this question could be to consider red or white oak trees isolated in a field, would we find in those trees such a high level of aggregation in top most branches as we found in the oaks growing in the highly competitive canopy of the Morgan Monroe State Forest?

At the water limited sites used in this study, we showed that foliage clumping arises at larger spatial scales than the branch. This large scale clumping may partly result from tree crowns being spread across the landscape (Ryu et al., 2010a; Sankaran et al., 2004) —possibly as a result of heterogeneous accessibility to underground water, and also a way to reduce the integrated leaf area of the landscape to enable evaporation to match precipitation rather than potential evaporation (Baldocchi et al., 2010; Budyko et al., 1974) —, and also partly from possible within crown clumping resulting from tree branching architecture. At humid sites, even though crowns are joined, it is known that plot level clumping is often present (Baldocchi et al., 1985), but little is known about how leaf arrangement at different spatial scales interact to yield the plot level clumping observed in forests. More research is needed to assess the level of clumping at these intermediate spatial scales across climatic zones. Future studies investigating clumping at various spatial scales could make use of new 3D laser scanning instruments and data processing algorithms such as QSM (Raumonen et al., 2013) and VoxLAD (Béland et al., 2014b), as they provide a valuable means to characterize tree branching architecture and foliage dispersion in fine detail at the plot level.

4. Conclusion

In this paper we investigated the variation in tree leaf projection factors and leaf clumping at branch level between species, at various heights above ground and across two contrasting climatic zones and

Fig. 12. Relation between branch level foliage clumping for branches in high irradiance and foliage clumping at the plot level for two sites: one light limited (Morgan Monroe) and one water limited (Tonzi). Branch level clumping values are the average of all blue oak branches at Tonzi, and all white and red oak branches at Morgan Monroe. Branches are specified to be in high irradiance because all branches sampled at both sites have access to ample light (this relation would be different if branches in the lower canopy were included for the Morgan Monroe site). Plot level foliage clumping values are from Ryu et al. (2010a) at Tonzi, and Pisek and Oliphant (2013) at Morgan Monroe, and the plot spatial extents correspond to the coverage by digital hemispherical photographs at view zenith angle 57 degrees used to derived the estimates in the Pisek and Oliphant (2013) study, and the 300 m x 300 m area measured with a LAI-2000 instrument in the Ryu et al. (2010a) study.

ecotones. We did not observe a clear relation between foliage clumping and leaf size across the sites used. We observed higher tree foliage clumping at the branch level in higher leaf area density branches and in branches sampled near maximum tree height – which are proxies respectively for light availability at branch level and the intensity of competition for light at the site level. This latter finding supports the hypothesis of increased benefits from producing large amounts of leaves around the supporting biomass having access to higher irradiance in light limited forests. This could be explained by the high structural biomass production and maintenance cost to reach canopy tops, the high return on investment for leaves produced on those branches that have access to high irradiance levels, as well as additional benefits from penumbra, branch movement in windy conditions and diffuse illumination conditions. In water limited ecosystems, branch level leaf distribution was found to be generally random. This could allow better transpiration and evaporative cooling while taking advantage of sunlight incoming from different directions as the sun moves across the sky throughout the day.

Comparing our findings to published values of foliage clumping at the plot scale for two of the sites used (Tonzi being mainly water limited, and Morgan Monroe light limited) suggested that the scale and location at which clumping arises may be driven by the availability of the main limiting resource; light limitation increases leaf aggregation vertically towards a maximum in high irradiance locations of the canopy, and water limitation increases aggregation horizontally at a landscape scale. Further research considering intermediate spatial scales where foliage clumping occurs is needed to assess the relative role of resource limitation, as well as research in forests where water transport and leaf temperature at canopy tops are major constraints to carbon assimilation.

In light limited forests, since most of the sunlight is intercepted within a relatively thin layer of the upper canopies, understanding the structure of those canopy top layers is paramount, as it is there that most of the carbon and water vapor exchanges takes place. The findings presented here have important implications for considering scale emergent properties in modeling carbon uptake and evapotranspiration, through understanding potential interactions of these structural properties with leaf temperatures and stomatal conductance in the regulation of carbon assimilation and evapotranspiration rates.

Authors' contribution

MB and DB designed the study, MB collected the field data and performed the data processing and analysis. MB drafted the manuscript and DB edited and revised the manuscript.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108185.

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