

Effect of thinning on LAI variance in heterogeneous forests

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ABSTRACT

Leaf Area Index (LAI) is a main variable controlling carbon and water fluxes. This paper estimated the effect of thinning on the spatial distribution of leaf area in French forests. While many studies have focused on average LAI, we estimated clumping and measured both average LAI and the variation around it. LAI was derived from digital hemispherical photos at three sites: an unmanaged *Fagus sylvatica* forest in temperate area (control site), a mixed Mediterranean forest of *Quercus ilex* and *Pinus halepensis*, and regeneration of *F. sylvatica* under a mature stand of *Pinus nigra* in mountainous area. LAI measurements were also made with LAI 2000 devices over 5 years (from 1994 to 1998) within forest stands dominated by either beech (*F. sylvatica* L.), by oaks (*Quercus petraea* (Matus) Liebl., *Quercus robur* (Matus) Liebl.), or by Scots Pine (*Pinus sylvestris* L.). Thinning led to a variable decrease in LAI. The coefficient of variation of LAI (CV_{LAI}) provided a useful ecological index of the level and type of thinning. For undisturbed stands, CV_{LAI} varied from 10% to 20%, corresponding to the higher average LAI values. Disturbances created by thinning increase LAI spatial variability, resulting in larger CV_{LAI} values for all stands considered. Possible explanations of these results and use in remote sensing were discussed.

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1. Introduction

Leaf Area Index (LAI) is defined as the projected area of green leaves or needles per unit horizontal ground surface area (Watson, 1947; Stenberg, 2006). It corresponds to the main surface exchange of carbon and water fluxes between the forest canopy and the atmosphere. It is also a key variable driving ecosystem functioning as many processes in a forest depend on LAI, including light and rain interception (Gash, 1979), gross productivity (Davi et al., 2006b), transpiration (Granier et al., 2000) and soil respiration (Davidson et al., 2002). Therefore, LAI variability usually explains a significant part of the variability in water fluxes from stand to regional scales (Behrenfeld et al., 2001; Sellers et al., 1997; Davi et al., 2006b).

LAI is an efficient index of ecosystem functioning at various scales since it can be derived by remote sensing (Turner et al., 1999; Chen et al., 2002; Davi et al., 2006a). Average LAI is one essential biome characteristics (Asner et al., 2003). Temporal variability of spatially averaged LAI values approximated by remotely sensed vegetation indices allows characterizing ecosystem functional types (Paruelo et al., 2001).

Spatial variability of LAI was found to be correlated to evapotranspiration and soil moisture (Grier and Running, 1977; Long and Smith, 1990; Burton et al., 1991; Jose and Gillespie, 1997). Some correlations were also found with foliage nutrient content (Vose and Allen, 1988; Hebert and Jack, 1998; Davi et al., 2006b). However, LAI interannual variation between years depends essentially on disturbances induced by thinning (Le Dantec et al., 2000), wind, fire, or severe drought. Two kinds of LAI are important for modelling: (i) the LAI which governs the fraction of light absorbed and therefore the light available in the canopy and at the ground level and (ii) the LAI which controls leaf respiration and litterfall. Clumping index (CI) corresponds to the ratio between these two quantities and depends mainly on local variation of leaf area density (leaf area per unit canopy volume area). The first corresponds to that derived from gap fraction measurements, assuming that leaves are randomly distributed within the canopy volume.

Several studies investigated the effect of thinning on spatially averaged LAI and its consequences on light transmittance (Cutini, 1996), soil and tree water status (Bréda et al., 1995), throughfall (Aboal et al., 2000; Dietz et al., 2006), and nitrogen uptake and growth (Carlyle, 1998). However, the same spatially averaged LAI value may thus correspond to very different spatial distributions depending on species, climate conditions and management history. Until now, very little attention has been paid to the effect of thinning on LAI spatial distribution. LAI can be defined over a

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range of spatial support domains such as the region (10 km × 10 km), the site (≈1000 m × 1000 m), the stand (≈100 m × 100 m), the plot (≈20 m × 20 m), or at even smaller scales (e.g., trees, shoots). LAI spatial distribution can be approached using either the coefficient of variation of LAI (CV_{LAI}) or clumping index (CI) which are obviously closely related. However, their relationship will mainly depend on the scales considered. Variation of leaf area density approached by CV_{LAI} and CI may occur from the stand level to the tree, branch and shoot levels. By selectively eliminating trees, thinning practices are expected to impact leaf area density distribution at the stand to the tree levels, while branch and shoot levels will be marginally affected, except when thinning focuses on species selection. The typical footprint of individual LAI measurements when using indirect methods (Jonckheere et al., 2004) is the plot scale corresponding to a small number of trees. At the plot scale, CI will therefore detect leaf clumping between adjacent crowns and inside the crown. Conversely, CV_{LAI} computed over a series of individual LAI measurements at the stand or regional level will mainly detect variability in tree distribution over larger length scales.

Accounting for LAI spatial variability is important because of the non-linear dependency of ecological processes to LAI (Davi et al., 2006b), as well as their direct dependency on LAI spatial distribution. Indeed, in previous works, Dufrêne et al. (2005) using uncertainty analysis highlighted the necessity to account for parameters variability in process-based models: neglecting the spatial parameter variability of LAI (or other parameters) led to a Net Ecosystem carbon Exchange (NEE) overestimation of 29%. In another study, Davi et al. (2006b) have shown that NEE and Transpiration increased non-linearly with LAI, showing strong saturation for high LAI values. On the other hand, the importance of the CI in carbon models, in which the foliage is separated into sunlit and shaded leaves, has been demonstrated by Chen et al. (2003). Clumping was shown to be the first source of NEE spatial variability in a young beech stand (Davi et al., 2006b). Quantifying the dynamics of CI and CV_{LAI} after thinning is thus important to advance understanding and modelling of forest ecology.

The objective of this paper is to describe effects of thinning on average LAI and its spatial distribution characterized by CI and CV_{LAI} . For this purpose an experiment was conducted in broad-leaved, coniferous and mixed forests subjected to several thinning practices. The study considers both the stand and the regional scales.

2. Material and methods

2.1. Sites description

2.1.1. Stand scale: three sites

Three sites were used for the stand scale analysis. They correspond to particular ecosystems showing various level of complexity in terms of forest structure and species composition.

2.1.2. Lamanon

The site, located north of Marseille near Lamanon (43°42'N; 5°03'E; elevation 120 m, slope < 10°) is made of an overstorey of Aleppo Pine (*Pinus halepensis* Mill.) above an understorey of Holm Oak (*Quercus ilex* L.). The understorey is dominated by boxwood (*Buxus sempervirens*). Climate is Mediterranean with a mean annual temperature of 13.9 °C and a mean annual rainfall of 663 mm. Three plots were further studied north of Alpilles with a colluvial soil including: the “control” plot (30 m × 40 m), where no thinning was conducted, the Lamanon Oak plot (30 m × 30 m), where all Aleppo Pines were removed, and the Lamanon Pine plot (30 m × 30 m), where all oaks were removed. Lamanon Oak and

Lamanon Pine plots were thinned in February 2006 leading to a 40% and 30% basal area decrease, respectively, for the Lamanon Oak plot (from 28 to 17 m² ha⁻¹) and for the Lamanon Pine plot (from 30 to 21 m² ha⁻¹). Pine dominated at 13.09 m in mean height, varying between 6.3 and 16.3 m high; Holm Oak had a mean height of 5.41 m. Hemispherical photographs were taken over a regular grid every 5 m before and after thinning leading to a total of 49 photos for Lamanon Oak and Lamanon Pine plots and 64 photos for the control plot.

2.1.3. Ventoux

This flat site (44°6'N, 5°49'E elevation 1120 m, slope < 10°) located on the southern face of Ventoux mountain is dominated by black pine (*Pinus nigra* ssp. *nigra*). Climate is typical of low altitude mountains with 9.25 °C mean annual temperature and 1068 mm mean annual rainfall. An area of 6 ha was selected over calcareous soil on a limestone regolith parent rock with a southern aspect moderate slope (Nouals and Jappiot, 1996). Adult pines were planted in 1920 and the last thinning before that of 2006 was conducted in 1981. The average tree height of pines was 19.5 m. Below the overstorey, a natural regeneration layer of young black pine and beech was growing. The beech regeneration had a large range of age and height. The average height of the three tallest beeches per cell of 400 m² is about 3 m. The thinning conducted in January 2006, led to a decrease from 39 down to 15 m² ha⁻¹ for the basal area (G) and from 469 to 177 stems ha⁻¹ in stem density for mature trees. The cutting was conducted using three modalities (3 × 2 ha): (i) one plot was thinned following a “seeding cut” (S) leading to a decrease of basal area of 68% (from 44 to 14 m² ha⁻¹); (ii) another plot following “a gap cut” (G) decreases the basal area by 53% (from 37 m² ha⁻¹ to 18 m²); (iii) and the last plot following a “seeding cut plus a gap cut” (S + G) leading to a decrease of basal area of 64% (from 39 to 14 m² ha⁻¹). Hemispherical photographs were taken at five dates: November 2005 (before the forest thinning), April 2006 (winter), August 2006 (summer), February 2007 (winter) and August 2007 (summer), every 20 m leading to a total of 148 photos for each date. At this site, we analyzed the effect of thinning not only just after the thinning in 2006, but also 1 year after in 2007.

2.1.4. La Tillaie

“La Tillaie” is a 36 ha natural forest located in Fontainebleau (48°43'N, 2°68'E, elevation 120 m) dominated by beech (*Fagus sylvatica* L.). Climate is temperate with 10.6 °C mean annual temperature and 750 mm mean annual rainfall. Soil types are luvisols and podzols with a calcareous substratum at approximately 1 m deep and humus types ranging from mull to moder. This old forest has been protected for royal hunting since the 17th century and has not been subjected to forestry practices since that time and was considered as the control site for this study. A 80 m × 100 m plot was selected. It is characterized by a gradient in canopy openness, from a clearing in the western side to a dense pole stand in the eastern side. The average density was 659 stems ha⁻¹ with a 32 m² ha⁻¹ basal area and an average tree height of 13.5 m. Hemispherical photographs were taken in 2001 and 2002 every 10 m. A description of the site was given in Davi et al. (2006b).

2.2. Regional scale: Fontainebleau forest

Fontainebleau forest is located in a 17,000 ha mixed deciduous forest at an average elevation of 120 m (48°25'N, 2°40'E). A total of 40 plots approximately 6.5 ha were used to represent the Fontainebleau region: 12 were dominated by beech (*F. sylvatica* L.), 17 by oaks (*Quercus petraea* (Matus) Liebl., *Quercus robur* (Matus) Liebl.), 11 by Scots Pine (*Pinus sylvestris* L.). These stands

were selected in the plateau of the southern part of Fontainebleau forest to represent the main Fontainebleau stand types, based on stand age, tree density and biomass (Le Dantec et al., 2000). Deciduous plots were mainly located on flat terrain on windborne sands, while coniferous stands were found on the hilly part of the forest on the sandy or the sandstone, with shallow soils. All stands are managed by the French forest service “Office National des Forêts”. Regular thinning and other forestry practices are carried out and appear to be the main factors of spatial and temporal variations in LAI and other canopy structure characteristics (Le Dantec et al., 2000). LAI measurements were made with LAI 2000 (LI-COR Inc., NE, USA) devices from the end of June to the middle of July over the 1994–1998 periods. However, all stands were not sampled every year, leading to a total of 162 available plot characteristics over the 200 potential ones. For each plot and according to its size, 40–150 measurements (71 in average) were taken on several transects at 5–10 m intervals. More details were given in Davi et al. (2006a).

2.2.1. LAI measurements

Two distinct sets of LAI measurements were used here: hemispherical photographs were used for the stand scale analysis, while PCA-LAI 2000 measurements were used for the Fontainebleau regional scale study.

2.3. Hemispherical photographs for the stand scale

Photographs were taken below the canopy on a grid, at 1.5 m above the ground using a digital camera (CoolPix 950 and 880, Nikon Corporation, Tokyo, Japan) equipped with a fisheye lens. Measurements were made on cloudy days or early in the morning to get more contrast between leaves and gaps (sky/clouds) and avoid direct sunlight. Photographs were taken using automatic exposure, since under or over exposition did not improve the analysis. The gap fraction (P) was derived using the CAN_EYE free software (http://www.avignon.inra.fr/can_eye). CAN_EYE allows classifying interactively and concurrently a set of images exploiting the three colours. Once pixels were classified either as sky or vegetation (leaves and branches), gap fraction was computed for 10° of azimuth angle (ϕ_i) and 5° of zenith angle (θ_i) sectors. The area considered was restricted to zenith angles lower than $\theta_{\max} = 60^\circ$ to prevent problems with a large fraction of mixed pixels.

In these conditions, the footprint of individual photos corresponds to a disk with radius equals to $1.73 \times$ height of canopy. Further details on LAI derivation from gap fraction using hemispherical photographs can be found in Weiss et al. (2004) and Demarez et al. (2008).

The azimuthal averaging LAI (LAI_{AA}), assuming random distribution of leaves is computed for each individual photo according to Miller's formula (1967), where gap fractions are averaged over all azimuth for each zenith angle (LAI_{AA} for azimuthal averaging) (Eq. (1)). Note that because zenith angles are restricted to the $0-\theta_{\max}$ range, Eq. (1) corresponds to an approximation of the original formula, where the denominator partly compensates for the restricted range of zenith angles.

Comparison was achieved with the method proposed by Campbell & Norman (1989), where the leaf angle distribution is explicit and assumed to be ellipsoidal (Campbell, 1986). Results (Table 1) show very good consistency between both methods. Miller's formula was thus finally used for LAI estimation.

$$LAI_{AA} = -\frac{2\sum_{i=1,9}\ln P(\theta_i)\cos(\theta_i)\sin(\theta_i)}{1 - \cos(\pi/3)} \quad (1)$$

An alteration of the original Miller's formula proposed by Gardingen et al. (1999) was used (Eq. (2)) over each photo to account for leaf clumping and approximate the actual LAI values azimuth explicit (LAI_{AE}). To prevent a logarithm of zero, a minimum gap fraction of one pixel was assumed when applying Eqs. (1) and (2) to actual photos.

$$LAI_{AE} = -\frac{2\sum_{i=1,9}\sum_{j=1,36}\ln P(\theta_i, \phi_j)\cos(\theta_i, \phi_j)\sin(\theta_i, \phi_j)}{1 - \cos(\pi/3)} \quad (2)$$

$$CI = \frac{LAI_{AA}}{LAI_{AE}} \quad (3)$$

The ratio between these two LAI estimates (Eq. (3)) provided the clumping index (CI). CI is therefore low when the canopy is clumped. CI was averaged over each stand over all individual photos available.

As discussed in Section 1, clumping occurs at a range of scales. The last scales of clumping corresponding to branch and shoots were not accessible here from hemispherical photos because resolution in azimuth was too coarse (10°). Consequently, CI values measured here were mainly representative of clumping due to position of trees and branches inside the disk sampled by the photographs.

On each site and each period of measurements, mean and variance of LAI were computed using n measurements ($48 < n < 148$). More details were given in Davi et al. (2006b). Note that here the term LAI is used as a proxy for PAI (plant area index) since green leaves, trunks and branches were accounted for. A total of 1198 photos were taken on three sites and processed consistently to estimate the average LAI, CV_{LAI} and CI for each stand.

2.4. PCA-LAI 2000 for the regional scale

LAI measurements were made using a ground-based optical instrument, the Plant Canopy Analyser LAI-2000 (LI-COR Inc.) (Gower and Norman, 1991). Because PCA-LAI 2000 requires less time both for measurements and processing than photos, it was preferentially used at the regional scale. This instrument uses a fisheye optical sensor with five concentric ring detectors to measure the fraction of blue (below 490 nm) radiation transmitted at the bottom of the canopy. The three LAI-2000 upper rings ($0-13^\circ$, $16-28^\circ$, $32-43^\circ$) were used to estimate LAI (Dufrêne and Bréda, 1995).

Measurements were achieved at about 1.3 m height under clear sky conditions and very low solar elevation: less than 2 h after sunrise or before sunset (Le Dantec et al., 2000). Note that LAI-2000

Table 1
Effect of Leaf angle distribution by comparison of Miller and Campbell algorithm for the calculation of LAI and comparison of CV_{LAI} calculated from azimuthal averaged LAI and azimuth explicit LAI

	Vtx BT	Vtx AT	Lam Pine BT	Lam Pine AT	Lam Oak BT	Lam Oak AT
LAI_{AE} Miller	2.63	0.94	1.95	1.19	2.39	1.41
LAI_{AE} Camp.	2.61	0.91	2.02	1.14	2.49	1.38
$CV_{LAI AE}$	19.37	55.12	13.84	34.51	15.56	45.09
$CV_{LAI AA}$	20.01	60.82	18.09	40.39	17.68	48.46

does not allow computing CI and only provides estimates of LAI_{AA} values.

2.5. Effect of spatial sampling sensitivity on CV_{LAI} and CI estimates

Since metrics of spatial variability are expected to depend on sampling, this issue was first investigated before going further in the analysis of results. The effect of spatial sampling was investigated over the three sites by comparing 5–10 m (Lamanon control site in 2006), 10–20 m (La Tillaie in 2002) and 20–40 m (Ventoux in 2005) grid spacing. Results show (Fig. 1a) that CV_{LAI} was marginally impacted when spatial sampling was degraded from 5 to 10 m or from 10 to 20 m. Conversely, over Ventoux in 2005, CV_{LAI} decreased slightly but significantly from 19.3% to 16.8%, when grid spacing was doubled. It is thus concluded that the effect of grid sampling is expected to be small in the range 5–40 m sampling distance. However, in the following analysis, CV_{LAI} will always be computed using the smaller grid distance available.

Apart from the sampling distance, spatial resolution of individual measurements associated with their footprint may also impact estimates of both CV_{LAI} and CI. The footprint of photos depends directly on the angular range used and on canopy height. The effect of angular range (0–60°, 0–50°, 0–40°, 0–30°) was thus analyzed before and after thinning on two study areas showing contrasted tree height and foliage clumping: Lamanon Pine and Ventoux. Results show that reducing the angular range significantly increases CV_{LAI} (Fig. 1b).

The range of zenith angles used may also impact CI estimates, since CI is expected to vary with zenith angle (Baret et al., 1993; Kucharik et al., 1999; Walter et al., 2003). Results show (Fig. 1c) that CI increases in three cases when the range of zenith angles is reduced: as expected leaf clumping is larger (lower CI) for more vertical directions in relation to the distribution of trees.

Conversely, a slight decrease was observed in Lamanon before thinning, probably because of the limited gaps lying between tree crowns. Despite all these effects, the differences between study site and thinning effect on LAI remains valid when using zenith angles between 0° and 60°. In the following analysis, the angular range was set to its maximum (0–60°) to get closer to Miller’s assumption and provides more accurate estimates of the average LAI.

3. Results

3.1. Stand scale

3.1.1. Mean LAI

Mean LAI values showed strong variation before thinning (BT) (Fig. 2; Table 2) between sites: from 3.5 (“Lamanon”) up to 7.6 (“La Tillaie”). “Ventoux” before leaf fall of beeches had intermediate values (4.1).

In Lamanon where two species (Holm Oak and Aleppo Pine) co-dominated the canopy, selective thinning consisting in removing one species from each stand, allowed for the computation of the respective LAI of each species as the difference between LAI measured before and after (AT) thinning. Results (Table 2) show that in Lamanon, Holm Oak and Aleppo Pine are co-dominant in terms of canopy LAI (and cover), although pines were taller than oaks. Thinning decreased LAI by 44% for “Lamanon oak” plot and 31% in “Lamanon pine”.

Comparison between LAI measured in October 2005 and August 2006 show that thinning in Ventoux decreased LAI by about 60% (Fig. 3). After thinning, LAI of pine measured during winter was similar between 2006 and 2007 (1.2 and 1.1). A comparison between summer and winter measurements averaged over all points without beech trees shows that the seasonal variation of LAI for pine is very small ($\Delta L < 0.1$). Consequently, LAI from beech

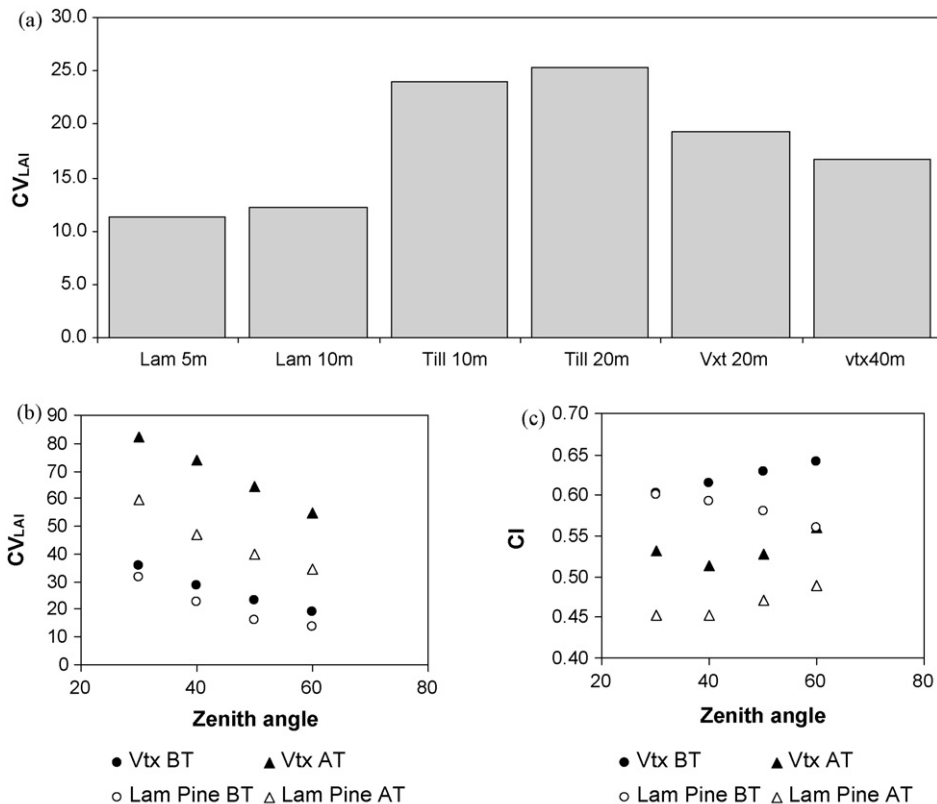


Fig. 1. Effect of sampling resolution on CV_{LAI} , and the zenith angles (0–30° to 0–60°) kept for the estimation of CI and CV_{LAI} .

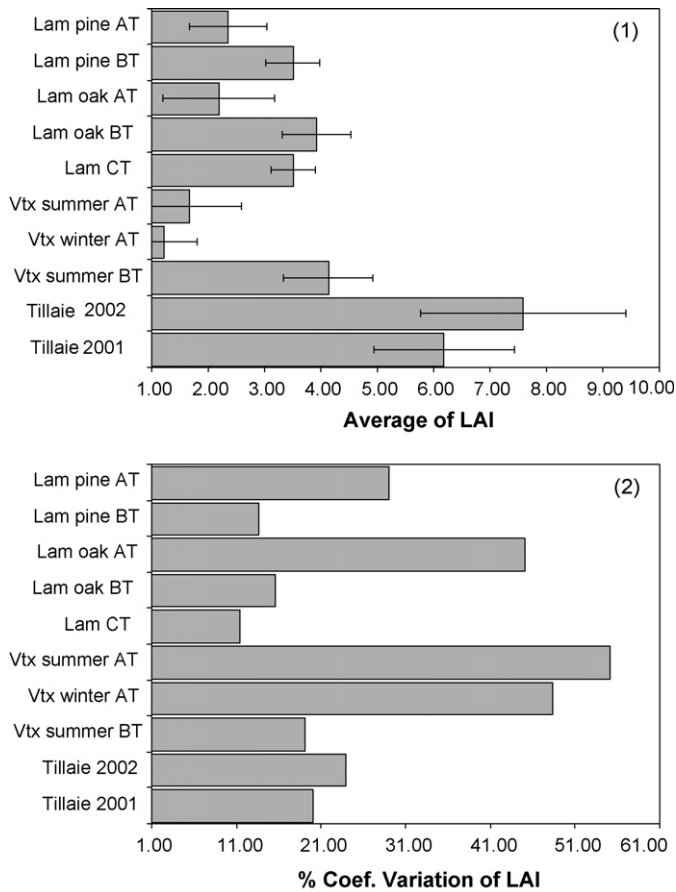


Fig. 2. Average (1) and coefficient of variation (2) LAI estimated by hemispherical photographs in 10 situations on three different ecosystems: "Tillaie", an old growth beech forest; Vtx, a beech regeneration under pine trees in mountain area; Lam, a Mediterranean oak-pine forest. In Lam and Vtx, AT means after thinning and BT means before thinning. Error bars represent the standard deviation.

trees was estimated as the difference between winter and summer measurements over all the Ventoux points. Beech trees represent between 29% (2006) and 39% (2007) of the total LAI, with significant interannual variation. LAI decrease due to thinning in Ventoux site (Fig. 3) was lower in plots where G cut was conducted. There were no significant variation of LAI between winter 2006 and winter 2007 (no positive reaction of pines). Conversely, LAI slightly increased by 0.25 (Fig. 3) in summer between 2006 and 2007, due to an increase in beech regeneration. This increase was higher in S

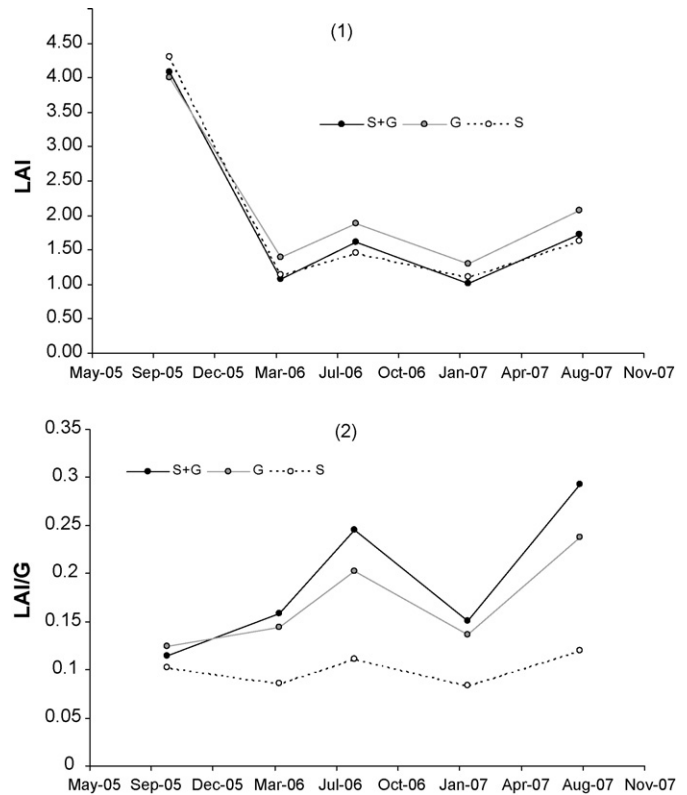


Fig. 3. In "Ventoux" site, dynamics of mean LAI_{AE} (1) and of the ratio between LAI and basal area (2) after three thinning types: seeding cut (S), gap cut (G), gap + seeding cut (S + G).

and G cut (10%) than in S + G (6%). The ratio between LAI and basal area strongly increased in plots where G and S + G cut were conducted (Fig. 3), while remaining around 0.1 in S cut. This ratio obviously increased during the summer because of beech regeneration.

3.1.2. Clumping index

CI varied greatly between ecosystems as expected (Fig. 4) with values in the range of those found in the literature (Chen et al., 2006). CI was lower (0.5 in average) in pine-dominated ecosystems (Lamanon after thinning and Ventoux in Winter), than in broad-leaves or mixed forest (0.6 on the average). In mixed forests, selective thinning shows contrasting effects: removing oaks led to a decrease of CI ("pine" plots in Lamanon and Ventoux) while

Table 2

Characteristics of the sites, thinning treatments, and LAI measurements achieved for the sand scale

Sites/year	Species ^a	Thinning ^b	Date	n	LAI	LAI composition	CI ^c	CV _{LAI} (%)
Lam_Oak	AP, HO	BT	01/06	49	3.9	2.2 (HO), 1.7 (AP)	0.62	16
Lam_Oak	HO	AT	02/06	49	2.2	2.2 (HO)	0.63	29
Lam_Pine	AP + HO	BT	01/06	49	3.5	2.4 (AP), 1.1 (HO)	0.56	14
Lam_Pine	AP	AT	02/06	49	2.4	2.4 (AP)	0.50	45
Lam_control	AP + HO		06/06	64	3.5	Undetermined	0.64	11
Ventoux	B + P	BT	10/05	148	4.1		0.64	19
Ventoux	B + P	AT	04/06	148	1.2	1.2 (P)	0.52	48
Ventoux	B + P	AT	08/06	148	1.7	1.2 (P), 0.5 (B)	0.56	55
Ventoux	B + P	AT	02/07	148	1.1	1.1 (P)	0.56	39
Ventoux	B + P	AT	08/07	148	1.8	1.1 (P), 0.7 (B)	0.55	58
La Tillaie	B		08/01	99	6.2		0.60	20
La Tillaie	B		08/02	99	7.6		0.62	24

^a AR: Aleppo Pine, HO: Holm Oak, B: beech, P: Austrian Pine.

^b BT, Before thinning and AT, after thinning.

^c LAI, Leaf Area Index; CI, clumping index; CV, coefficient of variation.

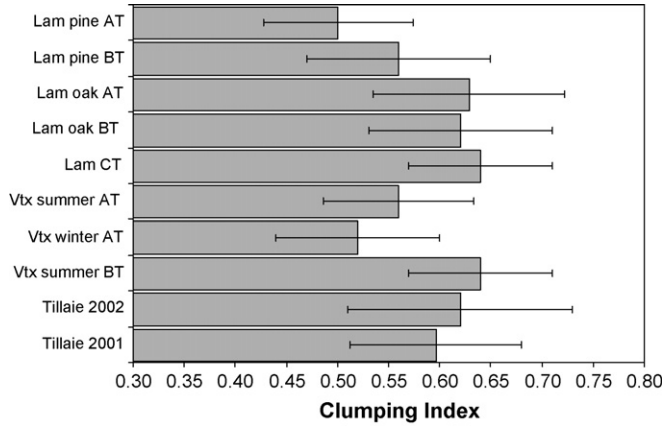


Fig. 4. Mean CI estimated by hemispherical photographs in 10 situations on three different ecosystems: “Tillaie”, a wild beech forest; Vtx, a beech regeneration under pine trees in mountain area; Lam, a Mediterranean oak-pine forest. In Lam and Vtx, AT means after thinning and BT means before thinning. Error bars represent the standard deviation.

removing pines (“oak” plot in Lamanon) did not change CI. This last result was expected since “pine” stands appear to have lower CI than “oak” stands.

In Ventoux, CI decreased in winter 2006 just after the thinning (Fig. 5) and then remained stable, but at a lower level. Note that S thinning treatment led to more clumped canopies with CI close to 0.5.

3.1.3. Variability of LAI at the stand scale

When no thinning occurred, CV_{LAI} of LAI_{AE} varied from 11% to 24% (Figs. 2 and 6). Without thinning, CV_{LAI} was positively correlated to the LAI (Fig. 6; $r^2 = 0.8$) with smaller values in Lamanon (13%) than in La Tillaie or Ventoux (21%) where higher levels of natural disturbances such as windfall were observed. However, these variations were small with regards to anthropogenic disturbance effects due to thinning (Fig. 6). Indeed, CV_{LAI} increased greatly after thinning in Ventoux (55%), Lamanon Oak (45%) and Lamanon Pine (29%). CV_{LAI} after thinning matched closely the fraction of LAI removed for these three plots (respectively, 60%, 44% and 33%). Variability in thinning techniques conducted in Ventoux led to different CV_{LAI} in 2006 (Fig. 7): 31%, 52% and 58%, respectively, for S, G and S + G cut. In this case, CV_{LAI} followed neither the relative LAI decrease nor that of the basal area. CV_{LAI} was actually driven by the heterogeneity of the cut. Indeed, the S cut was conducted homogeneously on the area while G cut was achieved by creating several square gaps each one covering

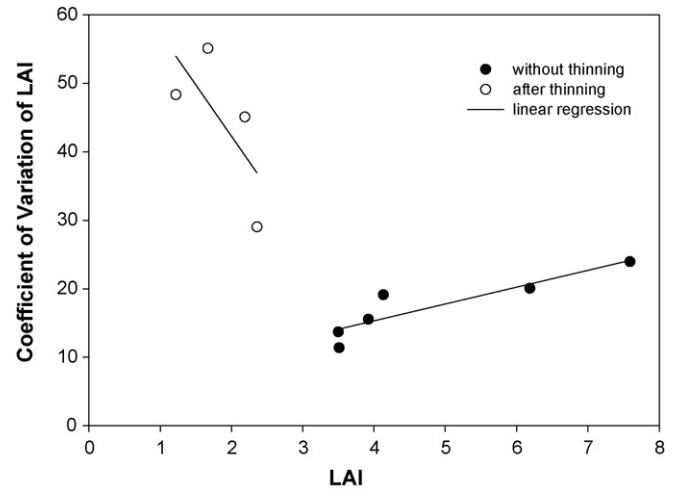


Fig. 6. Relationship between mean LAI and coefficient of variation of LAI with or without thinning in 10 cases corresponding to three sites. There are four values after disturbance: two in Lamanon (pine and oak plots) and two in Ventoux (summer and winter measurements).

400 m²: the S cut was less disturbing than G with regard to the spatial structure.

The seasonal dynamics of CV_{LAI} after thinning (Fig. 7) shows that CV_{LAI} increased in summer, after budbreak of beech leaves, due to the heterogeneous distribution of beech regeneration. On the other hand, the differences in mean CV_{LAI} between G and S + G observed in summer 2006, decreased in 2007 (Table 3; Fig. 7). This last result is due to a stronger growth of beech regeneration in the G treatment (Table 3) that led to a CV_{LAI} increase.

3.1.4. Thinning disturbance and LAI spatial pattern

The effect of thinning on LAI spatial distribution was analyzed only at the Ventoux and Lamanon sites where thinning was applied. At Ventoux, a non-selective thinning was applied: all beeches were removed on some areas and the cutting of adult trees caused also damages on beech regeneration. At Lamanon Pine and Lamanon Oak sites, a species-selective thinning of one species among the two co-dominant species was applied: all oaks and all pines, respectively, were removed. Thinning may thus impact LAI spatial pattern. This was investigated with special attention on spatial gradient by analysing the spatial correlation of LAI with X,Y coordinates using a simple linear regression model:

$$LAI(X, Y) = aX + bY + c \tag{4}$$

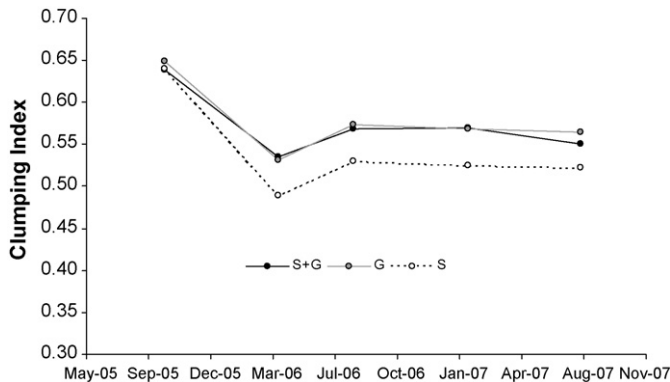


Fig. 5. Dynamics of mean CI for Ventoux site, after three thinning types: seeding cut (S), gap cut (G) and gap + seeding cut (S + G).

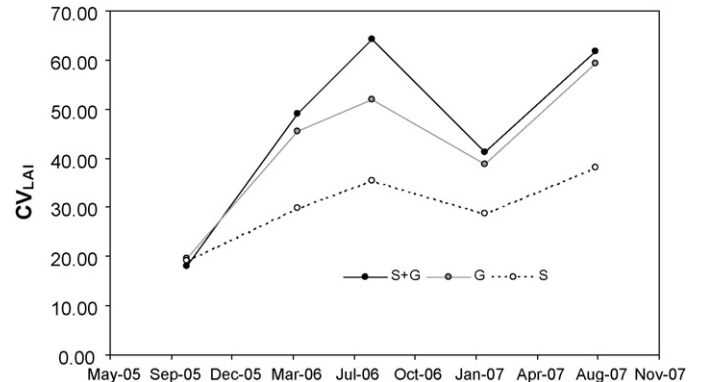


Fig. 7. In “Ventoux” site, dynamics of mean coefficient of variation of LAI (CV_{LAI}) after three types of thinning: seeding cut (S), gap cut (G), gap + seeding cut (S + G).

Table 3
Effect on LAI of three thinning types: seeding cut (S), gap cut (G), gap + seeding cut (S + G)

	S	G	S + G
CV _{LAI} summer 2005	19	20	18
CV _{LAI} summer 2006	35	52	64
CV _{LAI} summer 2007	38	59	62
LAI tot 2005	4.3	4.0	4.1
LAI tot 2006	1.5	1.9	1.6
LAI tot 2007	1.6	2.1	1.7
LAI beech 2006	0.3	0.5	0.5
LAI beech 2007	0.5	0.8	0.7

The values of *a* and *b* coefficients provides a way to show the possible gradient that occurs with LAI spatial variability. The sign of *a* and *b* gives the direction of the gradient. Results are shown in Table 4 and spatial map of interpolate LAI in Lamanon in Fig. 8.

At Lamanon Pine site, no gradient was observed before thinning (Table 4; Fig. 8). Conversely, a strong ($r = 0.7$) east to west gradient appeared after thinning. At Lamanon Oak site, the spatial structure was not significantly changed. At Lamanon, oak and pine positions were negatively correlated, which is highlighted by the strong negative correlations of LAI_{oak} and LAI_{pine}: $r = -0.80$ and $r = -0.82$, respectively, for Lamanon Pine and Lamanon Oak plots. Nevertheless, this pattern had no consequence before thinning on LAI_{tot} (= LAI_{oak} + LAI_{pine}) pattern since it was hidden for the considered variable (LAI_{tot}). However, when one species was removed, spatial pattern was revealed and a LAI gradient may appear (Lamanon Pine) after the thinning (Fig. 8). In Ventoux, thinning did not significantly change the spatial structure. But there were

Table 4
Effect of thinning on spatial correlation of LAI: gradient of increasing LAI

	<i>r</i>	<i>a</i>	<i>b</i>	<i>c</i>	
Lamanon Oak BT	0.20	3.6100	0.0110	0.0045	E gradient
Lamanon Oak AT	0.63	1.9133	0.0265	-0.0026	E gradient
Lamanon Pine BT	0.10	3.3606	0.0042	0.0028	No gradient
Lamanon Pine AT	0.72	3.0100	-0.0546	0.0220	W gradient
Ventoux BT summer	0.36	3.4054	0.0017	0.0029	NE gradient
Ventoux AT winter	0.36	1.7641	-0.0047	-0.0013	SW gradient
Ventoux AT summer	0.20	1.1546	0.0042	0.0013	NE gradient

differences between summer and winter. The gradient orientation was changed due to the position of beech regeneration. Thinning may thus induce several effects on LAI spatial pattern depending both on the original spatial pattern before thinning and the type thinning applied.

3.1.5. Regional scale

Fontainebleau will be used here to quantify the base level CV_{LAI} when few or old disturbances occurred and to show the possible effect of thinning on CV_{LAI}.

Results showed that both mean_{LAI} and CV_{LAI} varied widely (Fig. 9). There was a clear trend in decreasing CV_{LAI} when mean_{LAI} increased with, however, a large scattering for the lower mean_{LAI} values. The larger mean_{LAI} values correspond to undisturbed stands and show much more homogeneity with base level of CV_{LAI} between 10% and 20% for the four ecosystem types observed in Fontainebleau (dominant species oak, beech, mixed beech-oak and pine) in agreement with results acquired over the three previous ecosystems (La Tillaie, Ventoux and Lamanon). Part, of the CV_{LAI} value is explained by the time lag with the last thinning (Fig. 9):

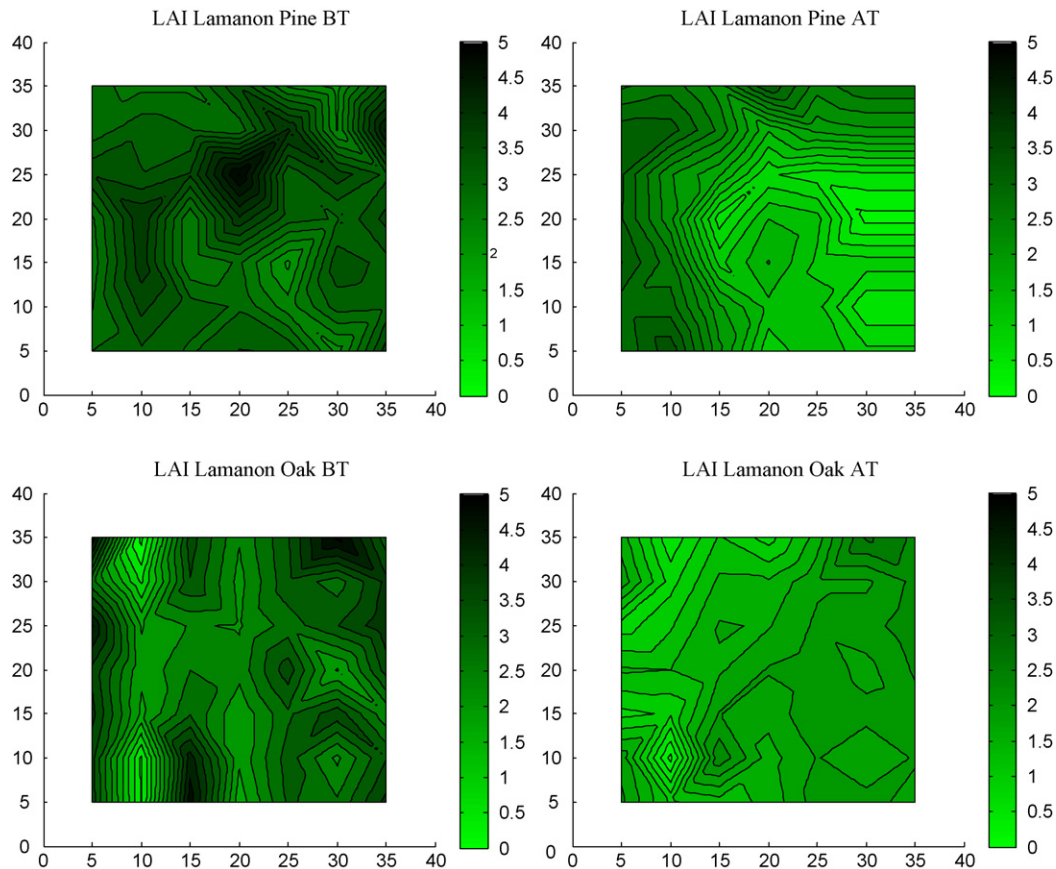


Fig. 8. Comparison of LAI spatial pattern in Lamanon Oak (top) and on Lamanon Oak (bottom) before (left) and after (right) thinning.

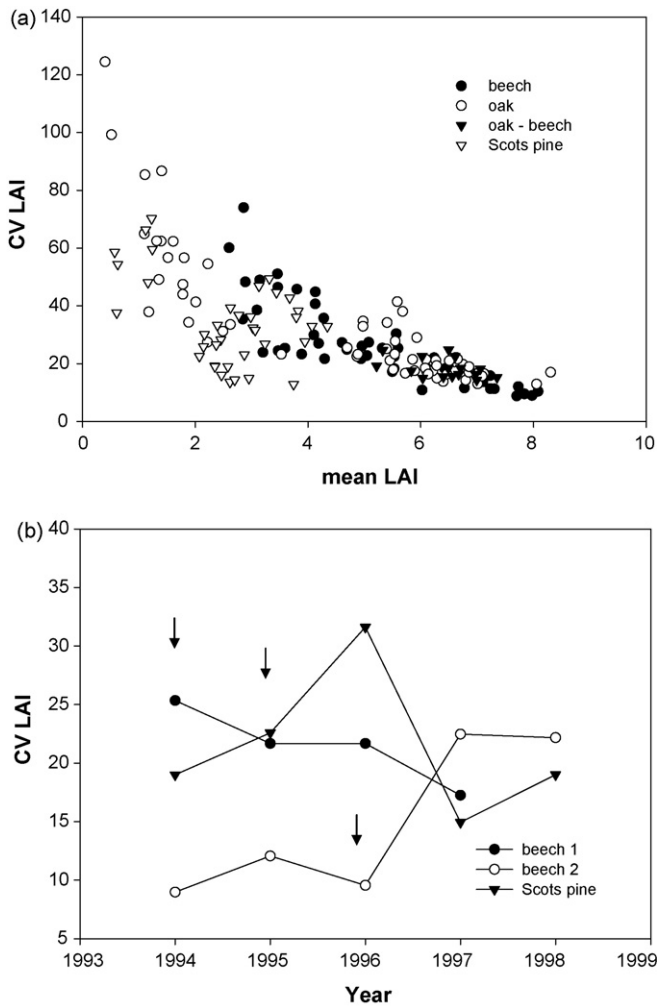


Fig. 9. (a) Coefficient of variation of LAI (CV_{LAI}) versus mean LAI measured in 40 plots of Fontainebleau forest from 1994 to 1998. (b) Temporal evolution of CV_{LAI} on three plots, the date of thinning is indicated by an arrow for the three plots.

when thinning occurs in 1993, for beech 1 plot, CV_{LAI} decreased regularly with time, 25% in 1994 down to 18% in 1998. When thinning occurred in 1995 and 1996 (respectively, beech 2 and pine plots), CV_{LAI} strongly increased the year after the thinning. This confirms our conclusions developed in the first part. The return to “normal values” of CV_{LAI} after thinning takes more or less time, more than 2 years for the beech stands and just 1 year for the Scots Pine stands.

4. Discussion

4.1. CI and CV_{LAI} measurements

The indirect assessment of LAI in canopies is a major scientific issue, studied by several authors with different theories and techniques (Nilson, 1971, 1999; Lang and Xiang, 1986; Chen and Cihlar, 1995; Kucharik et al., 1999; Gardingen et al., 1999; Walter et al., 2003; Nilson and Kuusk, 2004; Leblanc et al., 2005; Chen et al., 2006). As expected, CI was lower (i.e., higher clumping) in pine ecosystems than in broadleaved or mixed forest. Values found in this study of 0.5 in pure Scots Pine (*P. sylvestris*) to 0.62 in pure Holm Oak (*Q. ilex*) stand were in the range than found in many other studies: Cescatti (2007) gave an average of 0.58 for Italian pure beech (*F. sylvatica*) to pure Norway spruce (*Picea abies*), Kucharik et al. (1999) found 0.45 and 0.4, respectively, for Jack Pine

(*Pinus banksiana*) and black spruce (*Picea mariana*), and Gardingen et al. (1999), showed a range between 0.58 and 0.83 for Downy Oak (*Quercus pubescens*). On contrary, Chen et al. (2006) found higher values with their method but their estimate, which is based on gap sizes, and not on gap fractions, is not theoretically equivalent. As clumping of needles is not properly accounted for, further work is required using photos with much better resolution.

Conversely to CI, little attention has been paid to LAI variability (Walter and Grégoire, 1996; Trichon et al., 1998; Montes et al., 2007) and no study concerns CV_{LAI} . This parameter was shown to be quite constant across natural stands, while thinning resulted in a strong increase in CV_{LAI} . The main problem of using CV_{LAI} is its potential sensitivity to the spatial sampling scheme used that depends on: (i) the sampling frequency (in our case, grid spacing) and (ii) the footprint of individual photos that varies with the range of zenith angles used and canopy height. Small effects of grid sampling interval and marginal effect of zenith angles were found in comparison with the changes induced by thinning.

4.2. Synthesis of the thinning effects on LAI

This study demonstrated that thinning led to a LAI decrease varying from 60% to 33% matching very closely the basal area decrease. Leaf clumping may increase (CI decrease) with thinning or may keep steady in other circumstances. A modification of the possible LAI spatial pattern was also shown depending of the initial spatial structure and type of thinning.

Interestingly, three modes of thinning were further studied in Ventoux site with various effects on regeneration. The LAI decreased more in “seeding plus gap cut” (S + G) and in “seeding cut” (S) than in “gap cut” (G). Clumping increased more in S than in G or S + G treatments. Finally, CV_{LAI} increased more in S + G than in G and more in G than in S treatments. Consequently, thinning led to a higher increase of light transmitted by the canopy in “seeding cut” (higher LAI decrease and higher clumping increase). However, there were more points with very low LAI (extreme values) and consequently much more light available above regeneration, in points where gap cuts were conducted (G and S + G). The consequences on the regeneration, where beech and pines are in competition, depend on the light optimum of the two species.

The main result was a strong increase of CV_{LAI} after thinning, while CV_{LAI} showed little variation across stands. It is necessary to take into account this outcome in process based models simulating dynamics or carbon sequestration. First the response of photosynthesis is not linearly related to LAI. Consequently, use of the average value can cause some bias when the variability strongly increases (Davi et al., 2006b). In this case, the estimation of the LAI variability is important to correct these possible biases. Second, the response of tree regeneration (germination and growth) is not linearly related to light under a mature canopy. For that reason, it is also interesting to quantify the effect of thinning on light regime variability, which is directly linked to LAI variability.

4.3. CV_{LAI} as indicator of past disturbance?

Identifying and quantifying how disturbances (e.g., thinning, fire, windfall, insect attacks, strong drought) influence stand structure and development is mandatory for understanding long-term dynamics of forests at the landscape scale. A sound ecological index should therefore be developed as an indicator of past disturbances. All structural disturbances (not functional as nitrogen deposition) act on LAI by leaf fall (due to some defoliation) or stem removal. Consequently, a generic ecological index of perturbation must be obviously linked to LAI, making LAI a good candidate for that purpose. LAI may strongly vary with space and

time. LAI dynamics is mainly governed by the phenology associated to each ecosystem type. It is therefore not straightforward to interpret LAI dynamics as a stand-alone index of past disturbance. In addition, measuring LAI dynamics is quite tedious from ground level, and poses specific problems when using remote sensing observations (e.g., clouds, atmosphere, directional effects and availability of images, topography). Conversely, spatial variability of LAI expressed in percentage (CV_{LAI}) as an index of past disturbances is easier to access from space since it is a relative quantity that should be less sensitive to atmospheric directional and topographic effects. Indeed, when a perturbation occurs, the gaps corresponding to tree removals have significant dimensions and are generally not homogeneously distributed across space. Consequently, a disturbance mechanically produces an increase in LAI variability that can be measured by its coefficient of variation. The validity of this approach was demonstrated in this study across several forest ecosystems. However, many questions still remain:

- The level of LAI variation gives some insight on past perturbations, but it is difficult to differentiate a small recent disturbance from an older stronger one.
- The increase of CV_{LAI} after thinning depends both on intensity and type of the thinning. A disturbance that homogeneously affects the stand would even lead to a decrease of CV_{LAI} or at least to a lesser increase. However, very few disturbances (even thinning) act homogeneously: fire, windfall and insects attacks mainly follow specific patterns leading to an increase of spatial heterogeneity depending on the considered scale.

If the results presented in this paper are confirmed by other studies, specific methods to measure spatial variability should be developed and evaluated. High spatial resolution sensing images (5–20 m pixels) present a very practical answer to the assessment of spatial heterogeneity and derive perturbation maps. These potentials have already been demonstrated in a previous study (Stenberg et al., 2003; Davi et al., 2006a) where the standard deviation of vegetation indices (a combination of reflectances measured in several bands) was used. This result and the expected developments with remote sensing should be also useful for tropical ecosystems, where quantifying the effect of disturbance is an important objective.

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References

Aboal, J.R., Jiménez, M.S., Morales, D., Gil, P., 2000. Effects of thinning on throughfall in Canary Islands pine forest—the role of fog. *J. Hydrol.* 238, 218–230.

Asner, G.P., Scurlock, J.H., Hicke, J.A., 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecol. Biogeogr.* 12, 191–205.

Baret, F., Andrieu, B., Steven, M.D., 1993. Gap frequency and canopy architecture of sugar-beet and wheat crops. *Agric. For. Meteorol.* 65, 207–227.

Behrenfeld, M.J., Randerson, J.T., McClain, C.R., Fledman, G.C., Los, S.O., Tucker, C.J., Falkowski, P.G., Field, C.B., Fouin, R., Esaias, W.E., Kolber, D.D., Pollak, N.H., 2001. Biospheric primary production during an ENSO transition. *Science* 291, 2594–2597.

Bréda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt) Liebl.). *Tree Physiol.* 15, 295–306.

Burton, A.J., Pregitzer, K.S., Reed, D.D., 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. *For. Sci.* 37 (4), 1011–1059.

Campbell, G.S., 1986. Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination distribution. *Agric. For. Meteorol.* 36, 317–321.

Campbell, G.S., Norman, J.M., 1989. The description and measurements of plant canopy structure. In: Russell, B.M.a.P.G.J.G. (Ed.), *Plant Canopies: Their Growth, Form and Function*. Cambridge University Press, pp. 1–19.

Carlyle, J.C., 1998. Relationships between nitrogen uptake, leaf area, water status and growth in an 11-year-old *Pinus radiata* plantation in response to thinning, thinning residue and nitrogen fertilizer. *For. Ecol. Manage.* 108, 41–55.

Cescatti, A., 2007. Indirect estimates of canopy gap fraction based on the linear conversion of hemispherical photographs: Methodology and comparison with standard thresholding techniques. *Agri. For. Meteorol.* 143, 1–12.

Chen, J.M., Cihlar, J., 1995. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *IEEE Trans. Geosci. Remote Sens.* 33, 777–787.

Chen, J.M., Pavlic, G., Brown, L., Cihlar, J., Leblanc, S.G., White, H.P., Hall, R.J., Peddle, D.R., King, D.J., Trofymow, J.A., Swift, E., Van der Sanden, J., Pellikka, P.K.E., 2002. Derivation and validation of Canada-wide coarse-resolution leaf area index maps using high-resolution satellite imagery and ground measurements. *Remote Sens. Environ.* 80, 165–184.

Chen, J.M., Liu, J., Leblanc, S.G., Lacaze, R., Roujean, J.-L., 2003. A demonstration of the utility of multi-angle remote sensing for estimating carbon absorption by vegetation. *Remote Sens. Environ.* 84, 516–525.

Chen, J.M., Govind, A., Sonntag, O., Zhang, Y., Barr, A., Amiro, B., 2006. Leaf area index measurements at Fluxnet Canada forest sites. *Agric. For. Meteorol.* 140, 257–268.

Cutini, A., 1996. The influence of drought and thinning on leaf area index estimates from canopy transmittance method. *Ann. Sci. For.* 53, 595–603.

Davi, H., Soudani, K., Deckx, T., Dufrière, E., Le Dantec, V., François, C., 2006a. Estimation of forest Leaf Area Index from SPOT imagery using NDVI distribution over homogeneous stands. *Int. J. Remote Sens.* 27 (05), 885–902.

Davi, H., Bouriaud, O., Dufrière, E., Soudani, S., Pontallier, J.Y., le Maire, G., François, C., Bréda, N., Granier, A., le Dantec, V., 2006b. Effect of aggregating spatial parameters on modelling forest carbon and water fluxes. *Agric. For. Meteorol.* 139, 269–287.

Davidson, E.A., Savage, K., Bolstad, P., Clark, D.A., Curtis, P.S., Ellsworth, D.S., Hanson, P.J., Law, B.E., Luo, Y., Pregitzer, K.S., Randolph, J.C., Zak, D., 2002. Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agric. For. Meteorol.* 113, 39–54.

Demarez, V., Duthoit, S., Weiss, M., Baret, F., Dedieu, G., 2008. Estimation of leaf area and clumping indexes of crops with hemispherical photographs. *Agric. for. Meteorol.* 148 (4), 644–655.

Dietz, J., Hölscher, D., Leuschner, C., Hendrayanto, 2006. Rainfall partitioning in relation to forest structure in differently managed montane forest stands in Central Sulawesi, Indonesia. *For. Ecol. Manage.* 237 (1–3), 170–178.

Dufrière, E., Bréda, N., 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. *Oecologia* 104, 156–162.

Dufrière, E., Davi, H., François, C., le Maire, G., Le Dantec, V., Granier, A., 2005. Modelling carbon and water cycles in a Beech forest. Part I: Model description and uncertainty analysis on modelled NEE. *Ecol. Model.* 185 (2–4), 407–436.

Gardingen, P.R., Jackson, G.E., Hernandez-Daumas, S., Russel, G., Sharp, L., 1999. Leaf area index estimates obtained for clumped canopies using hemispherical photography. *Agric. For. Meteorol.* 94, 243–257.

Gash, J.H.C., 1979. An analytical model of rainfall interception by forests. *Q. J. R. Meteorol. Soc.* 105, 43–55.

Gower, S.T., Norman, J.M., 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology* 72, 1896–1900.

Granier, A., Lousteau, D., Bréda, N., 2000. A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann. For. Sci.* 57, 755–765.

Grier, C.C., Running, S.W., 1977. Leaf area of mature Northwestern coniferous forests: relation to site water balance. *Ecology* 58, 893–899.

Hebert, M.T., Jack, S.B., 1998. Leaf area index and site water balance of loblolly pine (*Pinus taeda* L.) across a precipitation gradient in East Texas. *For. Ecol. Manage.* 105, 273–282.

Jose, S., Gillespie, A.R., 1997. Leaf area-productivity relationships among mixed-species hardwood forest communities of the central hardwood region. *For. Sci.* 43 (1), 56–64.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004. Review of methods for in situ leaf area index determination. Part I. Theories, sensors and hemispherical photography. *Agric. For. Meteorol.* 121, 19–35.

Kucharik, C.J., Norman, J.M., Gower, S.T., 1999. Characterization of radiation regimes in nonrandom forest canopies: theory, measurements, and a simplified modeling approach. *Tree Phys.* 19, 695–706.

Lang, A.R.G., Xiang, Y., 1986. Estimation of leaf area index from transmission of direct sunlight in discontinuous canopies. *Agric. For. Meteorol.* 37, 229–243.

Leblanc, S.G., Chen, J.M., Fernandes, R., Deering, D.W., Conley, A., 2005. Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. *Agric. For. Meteorol.* 129, 187–207.

Le Dantec, V., Dufrière, E., Saugier, B., 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. *For. Ecol. Manage.* 134, 78–81.

- Long, J.N., Smith, F.W., 1990. Determinant of stemwood production in *Pinus contorta* var. *latifolia* forest: the influence of site quality and stand structure. *J. Appl. Ecol.* 27, 847–856.
- Miller, J.B., 1967. A formula for average foliage density. *Aust. J. Bot.* 15, 141–144.
- Montes, F., Pita, P., Rúbio, A., Cañellas, I., 2007. Leaf area index estimation in mountain even-aged *Pinus silvestris* L. stands from hemispherical photographs. *Agric. For. Meteorol.* 145, 215–228.
- Nilson, T., 1971. A theoretical analysis of the frequency of gaps in plant stands. *Agric. Meteorol.* 8, 25–38.
- Nilson, T., 1999. Inversion of gap frequency data in forest stands. *Agric. For. Meteorol.* 98/99, 437–448.
- Nilson, T., Kuusk, A., 2004. Improved algorithm for estimating canopy indices from gap fraction data in forest canopies. *Agric. For. Meteorol.* 124, 157–169.
- Nouals, D., Jappiot, M., 1996. Les stations forestières des plateaux et monts du Vaucluse et des versants sud des montagnes de Lure et du Ventoux. Cemagref Aix-en-Provence, 280 pp. (annexes).
- Paruelo, J.M., Jobbagy, E.G., Sala, O.E., 2001. Current distribution of ecosystem functional types in temperate South America. *Ecosystems* 4, 683–698.
- Sellers, P.J., Dickinson, R.E., Randall, D.A., Betts, A.K., Hall, F.G., Berry, J.A., Collatz, G.J., Denning, A.S., Mooney, H.A., Nobre, C.A., Sato, N., Field, C.B., Henderson-Sellers, A., 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* 275, 502–509.
- Stenberg, P., 2006. A note on the G-function for needle leaf canopies. *Agric. For. Meteorol.* 136, 76.
- Stenberg, P., Rautiainen, M., Manninen, T., Voipio, P., Smolander, H., 2003. Reduced simple ratio better than NDVI for estimating LAI in Finnish pine and spruce stands. *Silva Fennica* 38, 3–14.
- Trichon, V., Walter, J.-M.N., Laumonier, Y., 1998. Identifying spatial patterns in the tropical rain forest using hemispherical photographs. *Plant Ecol.* 137, 227–244.
- Turner, P.D., Cohen, W.B., Kennedy, R.E., Fassnacht, K.S., Briggs, J.M., 1999. Relationships between Leaf Area Index and Landsat TM spectral vegetation indices across three temperate zone sites. *Remote Sens. Environ.* 70, 52–68.
- Vose, J.M., Allen, H.L., 1988. Leaf area, stemwood growth and nutrition relationships in loblolly pine. *For. Sci.* 34, 546–563.
- Walter, J.M., Fournier, R.A., Soudani, K., Meyer, E., 2003. Integrating clumping effects in forest canopy structure: an assessment through hemispherical photographs. *Can. J. Remote Sens.* 29, 388–410.
- Walter, J.-M.N., Grégoire, C., 1996. Spatial heterogeneity of a Scots pine canopy: an assessment by hemispherical photographs. *Can. J. For. Res.* 26, 1610–1619.
- Watson, D., 1947. Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot.* 11, 41–76.
- Weiss, M., Baret, F., Smith, G.J., Jonckheere, I., Coppin, P., 2004. Review of methods for in situ leaf area index determination. Part II. Estimation of LAI, errors and sampling. *Agric. For. Meteorol.* 121, 37–53.