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Asymmetric competition increases leaf inclination effect on light absorption in mixed canopies

Guillaume Simioni · Marion Durand-Gillmann · Roland Huc

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Abstract

• **Context** The effects of leaf inclination on plant light capture, growth, and water balance of monospecific canopies are well documented, but we still lack information on such effects in the case of multispecific canopies.

• **Aims** We investigated the effects of leaf inclination on the absorption of photosynthetically active radiation (PAR) of a mixed forest.

• **Methods** We ran a 3D mechanistic radiation transfer model for a Mediterranean forest where *Pinus halepensis* makes the upper strata while *Quercus ilex* occupies the lower strata. As factors, we included (1) the distributions of leaf inclinations that ranged from vertical to horizontal (including the actual inclinations), (2) the fraction of diffuse light, sun position, and leaf area index (LAI), and (3) the *Pinus/Quercus* LAI ratio.

• **Results** Simulated PAR absorption was more than twice as sensitive to leaf inclination in oaks than in pines because oaks depended on PAR transmitted below the pine layer. The extent of the effect depended on season, fraction of diffuse light, LAI, and vegetation spatial structure. None of the observed inclinations maximized PAR absorption, suggesting a trade-off with water economy.

• **Conclusion** Erroneous assumptions about leaf inclination lead to larger errors when modelling heterogeneous, mixed canopies. This also highlights potential caveats when using models that do not account for the spatial structure of canopies.

Keywords 3D modelling · Leaf angle distribution · Mixed forests · Radiation absorption

1 Introduction

The importance of leaf inclination on plant light interception, carbon gain, and water relations is well established. In the following, leaf inclination is defined as the angle between the vector normal to the leaf plane and the horizon. Through a strong impact on light interception, leaf inclination affects plant carbon gain (Baldocchi et al. 2002; Falster and Westoby 2003; Werner et al. 2001a), water economy (King 1997), and the risk of damage due to excessive irradiance (Werner et al. 1999).

All those effects, however, do not mean that there is a unique optimal leaf inclination distribution for all plants. Rather, studies show that the optimum leaf inclination distribution is the result of trade-offs between the various effects of leaf angle, and that the extent of those effects actually depends on many factors, such as climate, latitude, season, and position in the canopy (e.g., over- versus understorey). Light capture is maximized by vertical leaves when the sun is at low angles, as in winter or at high latitudes, and by horizontal leaves when the sun is at high angles, as in summer or at low latitudes (Falster and Westoby 2003). But light capture does not directly transfer into carbon gain. Although horizontal leaves allow to capture more light in summer, vertical leaves can minimize summer photoinhibition and increase carbon gain (Werner et al. 2001a). Maximizing light capture can also increase water loss.

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Contribution of the co-authors G. Simioni supervised the field measurements, did all the modelling work (setting up simulations, running the model and analysing model outputs), made the figures and wrote the article. M. Gillmann, as part of her bachelor project, conducted the leaf inclination measurements on *Pinus halepensis*, did part of the literature review on leaf orientation, and contributed to the interpretation of the results. R. Huc contributed to the overall experimental design and to the interpretation of the results.

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Ehleringer (1988) interpreted steep leaf inclinations in desert plants as an adaptation to reduce water loss. Also, plants adapted to low light environments tend to have more horizontal leaves, which enhance photosynthesis, than plants growing in sunlight, for which more vertical leaves increase leaf cooling under high solar radiation (McMillen and McClendon 1979).

So it is not surprising that leaf inclination displays a remarkable diversity, for which de Wit (1965) defined broad categories: erectophile, plagiophile, planophile, spherical, uniform, and extremophile. Generic mathematical formulations have since been proposed to better represent this diversity (Campbell 1986; Wang et al. 2007). Real cases have been described for all inclination types (e.g., Wang et al. 2007) with the exception of the extremophile.

Still, two aspects have been overlooked. First, the light interception efficiency of any leaf inclination distribution in relation to the proportion of diffuse radiation has scarcely been investigated. Yet diffuse radiation reduces shading within canopies compared to direct sunlight and affects plant productivity (Roderick et al. 2001). The alternation of cloudy and sunny days could thus affect the light interception efficiency at any given leaf inclination. The second aspect is competition for light within multispecific canopies. Mixed canopies are widespread, and mixed forests are being increasingly encouraged as an alternative to monospecific plantations. The effort involved in measuring leaf angles of all species that constitute a mixed forest is only worth doing if leaf inclination plays a significant role in the light absorption of each species.

Models have been largely used to investigate leaf angle effects on plant light interception, photosynthesis, and water balance (Baldocchi et al. 2002; Falster and Westoby 2003; Werner et al. 2001b). In this study, we focused on quantifying (1) how much leaf inclination influences the partitioning of photosynthetically active radiation (PAR) between species of a mixed forest and (2) how that influence varies with the proportion of diffuse light, season, leaf area index (LAI), and the relative abundance of each species. To that end, we applied a three-dimensional (3D) individual-based radiation transfer model to simulate radiation absorption patterns of a Mediterranean mixed forest dominated by coniferous and broadleaf evergreen species.

2 Materials and methods

2.1 3D model

We used TREEGRASS (Simioni et al. 2000), a full ecosystem model designed to simulate the productivity and water balance of multispecific, heterogeneous canopies. We used only the radiation transfer component, which is an adaptation of the single tree RATP model of Sinoquet et al. (2001).

The model uses a 3D grid of cells. Each cell can contain different types of leaves (green or dead, from different species or individuals). In each cell, each leaf type is characterized by its leaf area density, inclination distribution, and optical properties. The crown of each individual tree is assumed to be cylindrical. It is assumed that leaf area density is uniform within the cylinder. Crown cylinder size does not constrain tree leaf area, only how a given leaf area translates into leaf area density. It is also assumed that trunks and branches do not contribute to radiation interception. Tree leaves are partitioned into the 3D cells according to overlaps between cylinders and cells. Radiation transfer is computed by a turbid medium analogy, which accounts for sunlit and shaded leaves, sun position, and diffuse radiation. The radiation transfer can be set up to operate at any sub-daily time step. Rays from several directions are directed into the cell grid. Sun directions vary with time of day, day of year, and latitude. The direction space is divided into solid angles, centered around representative heights and azimuths. Incident diffuse radiation is calculated assuming a standard overcast sky luminance distribution (Moon and Spencer 1942). When a ray passes through a cell, it is attenuated following Beer's law, depending on the leaf area density and on the inclination distribution of the types of leaves present in the cell. Light redistribution through reflections and transmissions is accounted for. More details can be found in Sinoquet et al. (2001).

TREEGRASS explicitly accounts for foliage clumping arising from the spatial arrangement of individual tree crowns. However, foliage clumping can also occur at fine scales, especially for conifers. We introduced a shoot clumping factor as in Chen and Black (1992): light extinction coefficients computed by TREEGRASS were multiplied by the ratio of shoot silhouette area (the effective area intercepting light) to total one-sided leaf area.

Due to lack of data at our study site, the present work could not include comparison with observations. We have no data either to assess whether the assumptions of uniform leaf area density within tree crowns, and of non-interception by woody elements, are valid at our study site. However, the accuracy of the radiation transfer model (common to TREEGRASS and RATP) has been tested and discussed in various situations: le Roux et al. (1997, grassland), Simioni et al. (2000, savanna), Sinoquet et al. (2001, walnut tree), (2005, walnut, mango, and peach trees), Combes et al. (2008, walnut and sorghum), and Massonnet et al. (2008, apple trees). These studies lend high confidence in the model's ability to simulate light absorption.

2.2 Study site

The Font-Blanche forest, in southeastern France (43°14'27" N 5°40'45" E, 420 m elevation), is composed of a top strata

of *Pinus halepensis* (Aleppo pine) reaching about 12 m, a lower strata of *Quercus ilex* (holm oak), reaching about 6 m, and an understorey strata dominated by *Quercus coccifera*. It is spatially heterogeneous: not all trees in each strata are contiguous, so trees from the lower stratas are partially exposed to direct light. This makes it a particularly well-suited forest to study the contributions of leaf inclination distribution on the ability of the different species to intercept light. The experimental site, which is dedicated to study forest carbon and water cycles, has an enclosed area of 80×80 m. For the present work, we selected three 24×24 m plots with different pine/oak ratios, for which we measured canopy structure.

2.3 Canopy structure and leaf inclination measurements

For each simulated plot, spatial coordinates, diameter at breast height, and height of each tree equal or above 2 m were measured in summer 2007. In March 2008, canopy extent of each recorded tree was measured in four directions from the trunk, following the normal and the orthogonal vectors to the direction of trunk inclination. The projected crown area of each individual tree canopy was estimated assuming it was composed of four ellipsoidal sections. This area defined the radius of the corresponding cylinder. Crown asymmetry was common, but is not a feature of the model. To minimize discrepancies between asymmetric crowns and symmetrical cylinders, the spatial positions of each tree were redefined as the barycentre of the four measurements of canopy extension. The resulting maps are presented in Fig. 1.

For each species, we tested five typical inclination distributions proposed by de Wit (1965) that range from mostly vertical to mostly horizontal leaves (Fig. 2). They cover the existing range that have been observed in plants, from distributions dominated by erect leaves to those dominated by horizontal leaves. This allows to explore the full influence of leaf inclination on light absorption. We used functions from Wang et al. (2007) to compute fractions of leaf surface in each 10° leaf inclination class used in our simulations. In addition, two measured leaf inclination distributions were used for *Q. ilex*. One was derived from Gratani and Bombelli (2000) by combining their summer and winter

data. The second was measured at the Puechabon forest in southern France (Davi, unpublished). Gratani and Bombelli (2000) found steeper leaf inclinations than Davi, and even steeper than the ones we measured for *P. halepensis*. As leaf inclination usually tends to be steeper in the upper canopy and more horizontal in the lower canopy (McMillen and McClendon 1979; Utsugi et al. 2006), data from Davi seemed more appropriate for the Font-Blanche site. We nonetheless included both inclination distributions in our simulation design in order to assess their impact on light absorption.

At the time of the experiment, to our knowledge, no data were available for *P. halepensis*, so we carried out measurements. Most existing methods were not designed for multi-specific canopies, such as gap fraction inversion techniques (Chen et al. 1997) and the multiband vegetation imager (Kucharik et al. 1998), not practical (point quadrat), or not finalized (stereo photography for conifers, Biskup, personal communication). Had it been published prior to our measurements, we would probably have considered the photographic method of Ryu et al. (2010). Instead, we opted for the basic protractor and compass method, which is tedious and time-consuming, but relies on simple instruments that can be easily carried within tree canopies.

In spring 2009, whole needle groups corresponding to growth units were sampled within the upper and lower half of tree crowns. At each height, six needle groups were chosen following a similar method as that described in Girard et al. (2011): one on a dominant axis, one on a strong second-order axis, one on a weak second-order axis, and three on axes of third order or above, which make most of the canopy. Difficulty in accessing canopies meant that not all unit types could be sampled on the same trees, but we kept a balance between the types of growth units sampled. Forty-eight units were sampled from 13 trees.

Strong wind was a major issue, so measurements were done in two steps. The spatial orientation of the axis supporting a growth unit was measured in situ. Axis inclination was measured using a protractor fitted with a bubble level, with marks for every half grad. Axis azimuth was measured with a magnetic compass. When the compass reading would be compromised by metallic scaffoldings, the azimuth was

Fig. 1 Maps of the 24×24-m simulated forest plots. Circles represent individual tree canopies of *P. halepensis* (red) and *Q. ilex* (black). Other species (other colors) were simulated as *Q. ilex*. Contributions of *Q. ilex* to total leaf area index are indicated

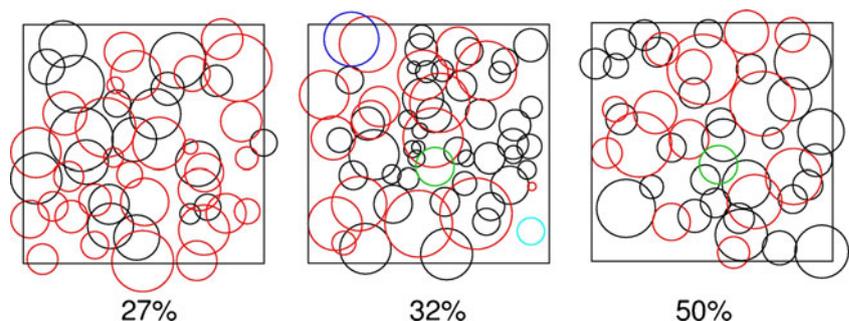
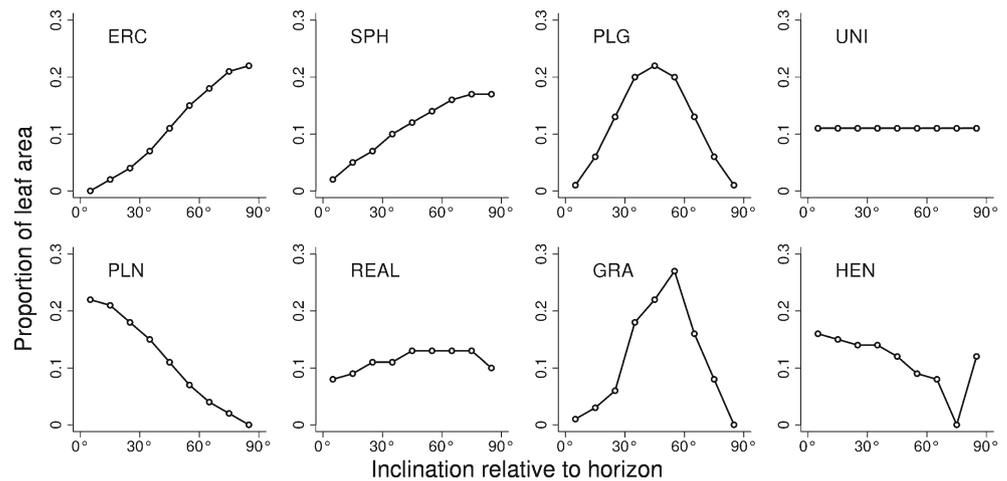


Fig. 2 Leaf inclination distributions used in simulations: erectophile (*ERC*), spherical (*SPH*), plagiophile (*PLG*), uniform (*UNI*), planophile (*PLN*), and measured for *P. halepensis* (*REAL*) and for *Q. ilex* (*GRA*: Gratani and Bombelli 2000; and *HEN*: Davi, unpublished). For each distribution, values represent fractions of leaf surface per 10° class of angle above the horizon



estimated using reliable landmarks: the spatial orientation of the scaffolding itself or the markers located every 5 m over the whole experimental site following north–south and east–west directions. To prevent loss of turgor, immediately after collection, samples were kept in the dark in a cool box at around 5 °C, until placed in the dark in a cold chamber at 4 °C. Within 2 days after field sampling, needle orientation was measured in the laboratory. Each growth unit was secured on a bench vice in the same orientation as in the field. Then, the orientation of each individual needle was measured with protractor and compass. A total of 4,532 needles were measured. For each unit, needles were sorted by years of growth, and the needle area of each subsample was measured with a planimeter (WinDIAS Test Targets Type WTS Version 1, 1996), dried 3 days at 60 °C, and weighed. Defining leaf area for *P. halepensis* needles is rendered difficult because of their more or less ellipsoid section and because they are twisted. Since we were not interested in the total needle area, but only in the effective surface that intercepts light, we defined the needle area as the silhouette area of the needle (i.e., the equivalent of one-sided leaf area for broadleaf species), hence the use of a planimeter.

Estimations of needle clumping by Pimont et al. (2009) at shoot level for *P. halepensis* range between 0.175 and 0.25, but these data correspond to the ratio of total needle area (assuming pine needles to be cylinders) to shoot silhouette area. For one-sided leaf area (i.e., needle silhouette area), the corresponding numbers are 0.55 and 0.785. We used a mean value of 0.67. We assumed that *Q. ilex* leaves were not clumped at shoot level, a reasonable assumption for broad-leaved species (Bréda 2003). All inclination distributions used for the simulations are presented in Fig. 2.

2.4 Simulations

As we focused on the effect of leaf inclination on PAR partitioning between the two dominant species of the Font-Blanche forest, the understorey was not included. In

addition to the leaf inclination distributions listed above, we considered the effect of LAI, season, pine/oak ratio, and the proportion of diffuse light in incident radiation. Those factors are known to influence light absorption and vary over time and/or space. Values were chosen so as to cover a range larger than the realistic situations relevant for Mediterranean forests, in order to reveal the full extent of leaf inclination effects. Estimates of total plant area index at Font-Blanche are between 2.5 and 3, including the understorey (based on hemispherical photographs, unpublished). We used four levels of LAI: 1.5, 2, 2.5, and 3. LAI was partitioned between species according to the pine/oak ratio (see below) and, for each species, trees were given a leaf area commensurate with allometric relationships between stem diameter and leaf biomass (i.e., commensurate with tree size). The range of pine/oak ratios, with oaks contributing 27, 32, or 50 % of the total LAI, is the largest that we have observed at Font-Blanche, and for which vegetation structure has been measured. These proportions were estimated using allometric relationships between stem diameter and leaf biomass (López-Serrano et al. 2005 for pines; Miglioretti 1983 for oaks), and average specific leaf areas of 60 cm² g⁻¹ for pines (this study) and 129 cm² g⁻¹ for oaks (a conservative estimate from Niinemets et al. 2006). Using allometric relationships from other sites is not ideal but is of limited consequences in this study as they were only used to estimate the pine/oak ratio, and to partition the forced LAI among trees. We used three levels of diffuse light fraction: 0, 50, and 100 %, which is relevant given that clear sunny skies are prevalent, and overcast skies occur during rainfall. Twelve dates were chosen, corresponding to the 15th of each month. Table 1 presents other relevant model parameters used for all simulations. Simioni et al. (2000) found that a 1-m resolution was as a good compromise between accuracy, computation time, and memory requirements.

We made 1-day simulations, with five sub-daily time steps to account for daily variations in sun position. We used a complete factorial design totalling 18,144 simulations.

Table 1 Model parameters common to all simulations

Parameter	Value
Latitude	43°
Plot size	24×24 m
Pixel size	1×1 m
Strata depth	1 m
Leaf inclination classes	9
Sun azimuth classes	12
Sun inclination classes	8
Sub-daily timesteps	5
Leaf reflectance/transmittance	0.11
Soil reflectance	0.2

3 Results

In the following, radiation absorptions are expressed as fractions of incident PAR (FPAR), i.e., the ratio of absorbed

Table 2 Analysis of variance (R standard library) of the fraction of incident photosynthetically active radiation absorbed by *P. halepensis* trees

Factor	Df	F value	Significance
Month	11	3.72e+4	*
POR	2	6.23e+5	*
D	2	1.41e+5	*
LAI	3	4.73e+5	*
PA	5	6.56e+3	*
OA	6	0.419	NS
Month×POR	22	29.3	*
Month×D	22	1.24e+4	*
Month×LAI	33	56.0	*
Month×PA	55	4.05e+2	*
Month×OA	66	1.25e−2	NS
POR×D	4	1.39e+2	*
POR×LAI	6	2.32e+3	*
POR×PA	10	1.51e+2	*
POR×OA	12	3.22e−2	NS
D×LAI	6	4.29e+2	*
D×PA	10	1.38e+3	*
D×OA	12	0.426	NS
LAI×PA	15	46.0	*
LAI×OA	18	1.23e−2	NS
PA×OA	30	3.40e−3	NS
Residuals	17793		

Factors were pine inclination distribution (PA), oak inclination distribution (OA), diffuse radiation fraction (D), pine/oak ratio (POR), month, and leaf area index (LAI)

NS not significant

**P*<0.001, significant effects

Table 3 Analysis of variance of the fraction of incident photosynthetically active radiation absorbed by *Q. ilex* trees

Factor	Df	F value	Significance
Month	11	1.46e+3	**
POR	2	9.17e+5	**
D	2	5.88e+2	**
LAI	3	4.68e+3	**
PA	5	73.6	**
OA	6	3.26e+3	**
Month×POR	22	69.0	**
Month×D	22	4.86e+2	**
Month×LAI	33	3.01e+2	**
Month×PA	55	1.40e+2	**
Month×OA	66	70.3	**
POR×D	4	2.20e+2	**
POR×LAI	6	1.40e+3	**
POR×PA	10	13.8	**
POR×OA	12	65.3	**
D×LAI	6	8.91e+2	**
D×PA	10	3.64e+2	**
D×OA	12	2.93e+2	**
LAI×PA	15	16.4	**
LAI×OA	18	17.1	*
PA×OA	30	3.92	**
Residuals	17793		

Factors were pine inclination distribution (PA), oak inclination distribution (OA), diffuse radiation fraction (D), pine/oak ratio (POR), month, and leaf area index (LAI)

NS not significant

P*<0.05; *P*<0.001, significant effects

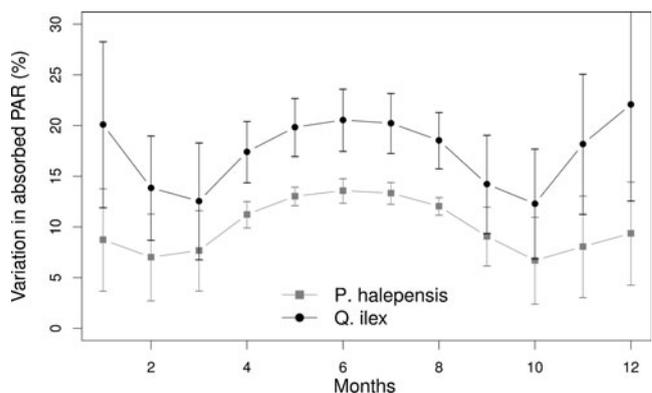


Fig. 3 Variations of simulated absorbed photosynthetically active radiation (aPAR) solely due to leaf inclination distributions. Symbols and bars represent averages and standard deviations, respectively. They were computed for each combination of date, percentage of diffuse light, leaf area index, and pine/oak ratio, as: (max aPAR−min aPAR)/max aPAR. For each species, those values integrate both oak and pine leaf inclination distributions

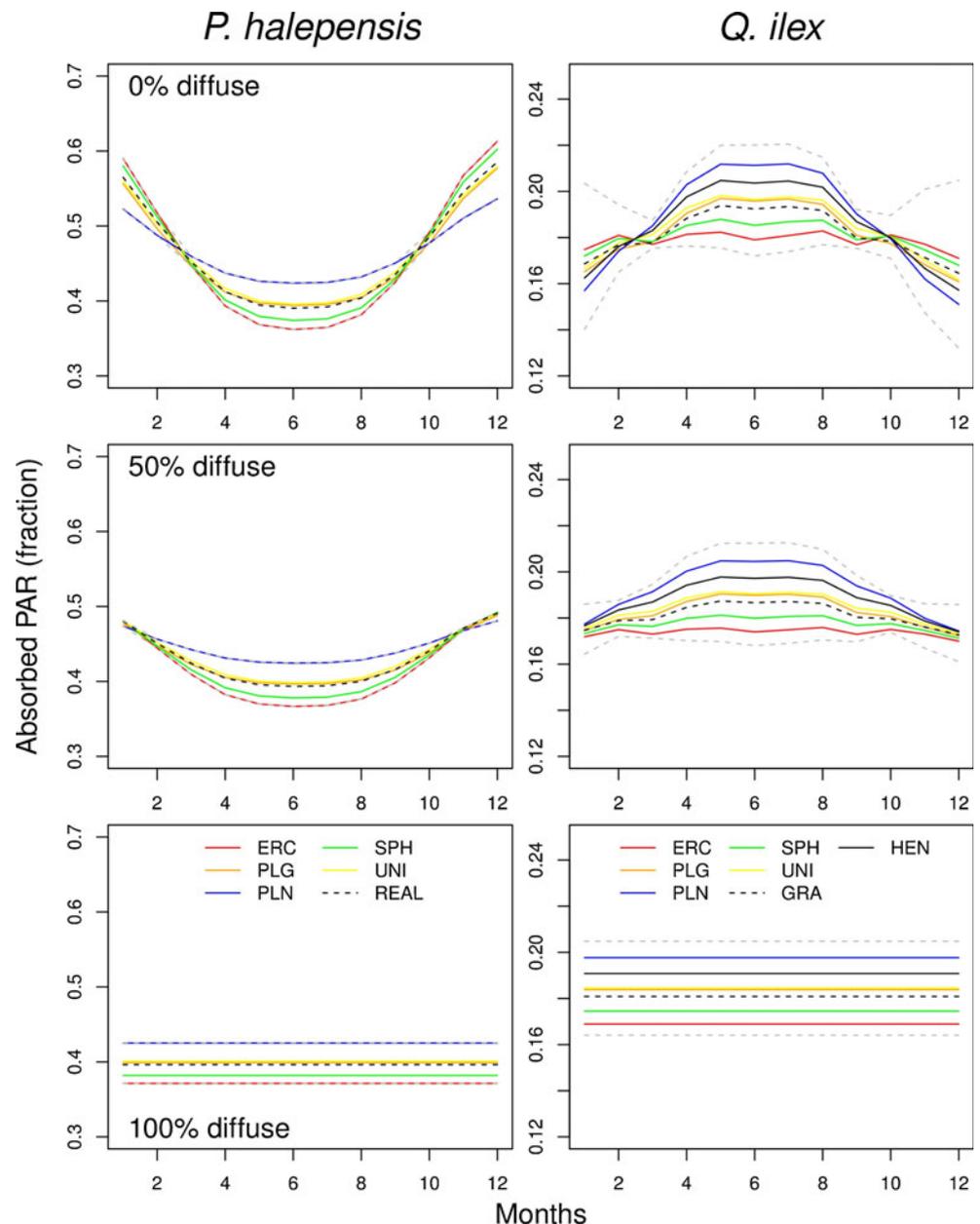
PAR to incident PAR above the canopy. They are easier to interpret than absolute PAR absorptions, which depend on available energy, which itself varies with season and cloudiness.

All factors had significant effects on pine FPAR, except for oak leaf inclination (Table 2). All factors had significant effects on oak FPAR, including pine leaf inclination (Table 3). That pine leaf inclination influenced oak FPAR and that oak leaf inclination had no effect on pine FPAR highlights the asymmetry of the competition for light. Pines occupy the upper strata and are thus insensitive to oak foliage properties. On the other hand, oaks are at least temporarily in the shade of pines. The variation in FPAR solely due to leaf inclinations (maximum minus minimum

absorptions divided by maximum absorption, for each combination of date, pine/oak ratio, LAI, and percentage of diffuse light) was highest in summer when it reached about 13 % for pines (Fig. 3). For oaks, it was around 20 % in summer, but topped in winter at around 40 %. The higher sensitivity to leaf inclination for oaks reflects the fact that the amount of light reaching the oak strata depends on pine leaf inclination. The standard errors displayed in Fig. 3 show the effects of the other factors (percentage of diffuse light, LAI, and pine/oak ratio).

In winter, without any diffuse radiation, vertical type leaves were the most efficient, the best being the erectophile and the worst being the planophile (Fig. 4). This hierarchy was reversed in summer. This is in accordance with

Fig. 4 Effects of the proportion of diffuse radiation on the fraction of incident photosynthetically active radiation (PAR) absorbed by *P. halepensis* and *Q. ilex* trees. Lines represent averages per leaf inclination distributions (legend as in Fig. 2). Dashed grey lines represent maximum and minimum values of all combinations of inclination distributions. Results are for a total leaf area index (LAI) of 2, and with *Q. ilex* trees contributing 32 % of total LAI. Trends were similar with other LAI and pine/oak ratio combinations



previous studies (e.g., Falster and Westoby 2003) that showed that vertical leaves perform better at low solar angles, and horizontal leaves perform better at high solar angles.

Logically, because of the longer path length through the canopy of sun rays coming from low angles, pines had a higher FPAR in winter than in summer. However, oaks displayed the opposite pattern (Fig. 4). This is another consequence of the asymmetric competition for light between the two species. As pine FPAR was lower in summer compared to winter, oaks received a larger fraction of incident light in summer than in winter and that greatly affected their seasonal absorption pattern.

With 50 % diffuse light, the period during which distributions with more vertical leaves performed better was shorter than with direct light only, and the differences with more horizontal distributions were smaller (Fig. 4). Sun rays corresponding to diffuse radiation have on average shorter path lengths through the canopy than sun rays coming from low solar angles. Thus, diffuse light led to a reduction in winter FPAR for pines, which in turn increased oaks FPAR. At 100 % diffuse light, there was no seasonal variations as the directions of incoming radiation did not change with time. These effects of diffuse light are in accordance with Kim et al. (2011), who compared the absorbed light of vertical-, spherical-, and horizontal-type inclinations between clear and cloudy days.

While oak FPAR depended on the light not absorbed by pines, the relationship between FPAR values of the two species varied with the pine/oak ratio (Fig. 5). The real forest plots we used for our simulations presented different pine/oak ratios, but also different spatial structures. The two are connected. The site was initially a pure *Q. ilex* coppice stand, pines developed in the spaces not already occupied by

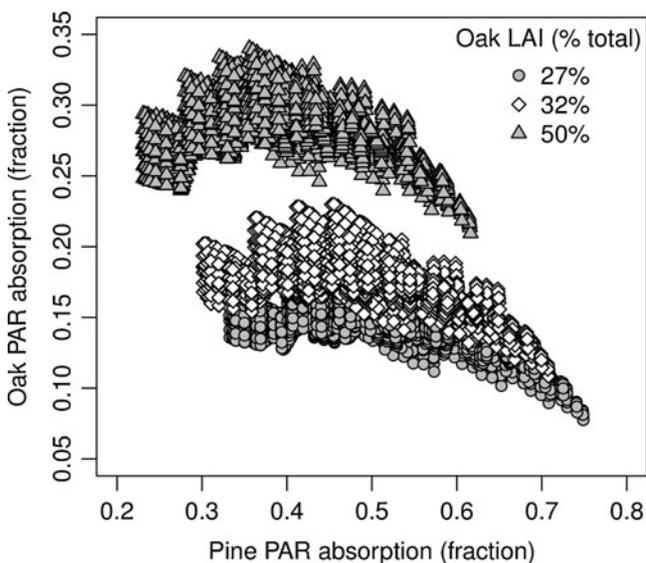


Fig. 5 Effect of the pine/oak ratio on the relationship between *Q. ilex* and *P. halepensis* ratios of absorbed to incident photosynthetically active radiation (PAR). All simulations were combined

oaks. Therefore, the lower the pine/oak ratio, the larger the gaps in the pine strata. For plots where oaks contributed 27, 32, and 50 % of total LAI, the corresponding fractions of oak canopies not directly under pine canopies was 49, 51, and 69 %, respectively. Therefore, the lower the pine/oak ratio, the less oaks were dependant on the pine strata for accessing light. This means that the spatial structure of the canopy did play a role in the light partitioning between the two coexisting species. Incidentally, Fig. 5 could give the impression that the relationship between pine and oak FPAR is not monotonic, although it actually is if the only factor considered is leaf inclination. On this figure, all treatments were plotted together and increasing total LAI, for instance, enhanced both pine and oak FPAR.

On the other hand, FPAR per unit leaf area decreased with increasing LAI for both species (Fig. 6), i.e., the increase in light absorption at the canopy level did not increase linearly with LAI. At high LAI, even with leaf inclinations that allow light to penetrate deeper in the canopy (e.g., vertical leaves under direct midday sun), most of the PAR will still be absorbed, so the effect of leaf inclination on the FPAR of a species decreases. Foliage clumping was more important for pines. As a consequence, the slope of the decrease in FPAR per unit leaf area with increasing LAI was lower for pines than for oaks (Fig. 6).

4 Discussion

While some of our findings confirm those of previous studies, there are new elements that are important in the

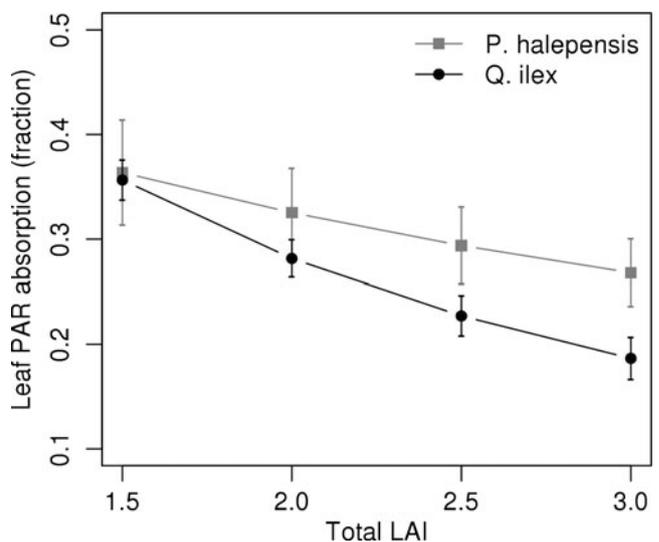


Fig. 6 Effect of leaf area index (LAI) on photosynthetically active radiation (PAR) absorption fraction at the leaf level. For each species, this was computed as the ratio of absorbed to incident PAR, divided by its LAI. Symbols represent averages and bars represent standard deviations

context of radiation transfer modelling. Measuring leaf inclination is a tedious task, let alone doing it on all species that constitute a mixed forest. In the absence of data, it is often assumed that leaf inclinations follow a spherical distribution, although measurements made on tree species can depart from it (e.g., Barclay 2001). Yet our results show that if making the wrong assumption can lead to an error in light interception for a monospecific canopy (in our case when considering the pine layer on its own), the error will increase when modelling multispecific canopies. Had we assumed leaf inclination to be spherical for both pines and oaks, the error in predicted FPAR in summer would have been around 5–7 % for pines and around 11 % for oaks (comparing the spherical and Davi distributions). In addition, in our simulated plots, oaks had partial access to direct light due to gaps in the pine layer. We should expect that, in stratified mixed canopies with no gaps, the effect would be even stronger as the dependence of the lower strata on the upper one would be total. Whether such errors are acceptable is debatable, our point is that errors increase for multispecific canopies.

We also found that vegetation spatial structure influenced the competition for light between species. This cannot be reproduced by non-spatially explicit models. Radiation transfer models ignoring the vegetation spatial structure are not designed to handle such effects, and are not recommended to predict light absorption of this type of vegetation cover, unless some form of correction to account for gaps is introduced. Plant architecture and shoot morphology are other factors that can influence light capture (e.g., Sekimura 1995). In the end, one big difficulty in modelling heterogeneous multispecific forests is the potential accumulation of small errors arising from not accounting properly for leaf inclination, leaf clumping, and vegetation structure. This accumulation could lead to large errors in predicting light absorption and other ecological processes of which light energy is the primary driver, such as photosynthesis and transpiration. This is especially true when one wants to estimate the contribution of each coexisting species.

In our simulations, the measured leaf inclinations never performed best. This probably reflects the trade-off between the various effects of leaf angle on plant biology. Erect leaves can reduce photoinhibition at high sun positions (Ryel et al. 1993; Werner et al. 1999). Werner et al. (2001a) found that vertical leaves increased whole plant carbon gain in summer. At Font-Blanche, direct sun is prevalent in summer and most precipitations occur from autumn to spring, but even then sunny days are common. In such a Mediterranean climate, it would make sense that a planophile distribution would not be beneficial in terms of water economy and carbon balance in the dry season, while in winter, having more vertical leaves would increase light absorption and benefit evergreen species. The observed inclinations could therefore represent a compromise.

Because of the trade-offs mentioned above, guessing the consequences of an inaccurate choice of leaf inclination on growth predictions is also conjectural. However, any error in light absorption will propagate to growth predictions, and those errors will be more important for the least competitive species (*Q. ilex* in our case). These issues could be tested by simulating the whole carbon and water budgets.

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