

Architecture, cover and light interception by bramble (*Rubus fruticosus*): a common understorey weed in temperate forests

Philippe Balandier^{1*}, André Marquier², Eric Casella³, Andrea Kiewitt⁴, Lluís Coll⁵, Léon Wehrlen⁶ and Ralph Harmer⁴

¹Irstea, Research Unit on Forest Ecosystems (EFNO), Domaine des Barres, F-45290 Nogent-sur-Vernisson, France

²INRA, UMR547 PIAF, F-63100 Clermont-Ferrand, France

³Forest Research, Centre for Forestry and Climate Change, Farnham, Surrey GU10 4LH, UK

⁴Forest Research, Farnham, Surrey GU10 4LH, UK

⁵CTFC, Forest Functioning and Dynamics Team, SP-25280 Solsona, Spain

⁶INRA, UMR1092 LERFOB, MGVF, F-54280 Champenoux, France

*Corresponding author Telephone: +33 238950351; Fax: +33 238950346; philippe.balandier@irstea.fr

Received 31 January 2012

Bramble (*Rubus fruticosus* L.) is a common weed in temperate forest and also in other world ecosystems where it is recorded as an invasive plant. Although it has been described to efficiently compete for water and nutrients, little is known on its competitive ability for light. We described bramble canopy architecture, cover relative to light availability and light interception ability in 60 areas of bramble thicket at 17 sites in France and 1 in England with contrasting soils and climates. The leaf area and leaf number can be predicted by the cane (shoot) length. The leaf inclination distribution was planophile (i.e. leaf laminae distributed in the horizontal plane). There was a good relationship between light interception and leaf area index (LAI) of the different bramble thickets, with no significant site influence, meaning that a single model can be used to predict light interception by bramble in different conditions. Bramble LAI and cover rapidly increased with light availability in the understorey to reach almost 20% cover at only 5–7% light availability above the thicket. Consequently, bramble is able to tolerate deep shade, which is not in accordance with its reputed moderate to high light requirement reported in the literature and suggests that it is difficult to control this species by manipulating tree canopy. This would have adverse consequences on tree regeneration.

Introduction

Overstorey canopy opening, either by partial cutting (e.g. shelterwood or group selection) or clear-cutting, will increase light transmission to the forest floor. Although this will improve the growth of regenerating trees, it will also promote development of understorey vegetation which can induce severe competition for main growing resources with tree seedlings.¹ Generally, research has focused on the effect of understorey vegetation through belowground resource availability^{2–5} whereas less attention has been given to the effect of understorey vegetation on light competition.^{6,7} However, some works reported the high light interception potential of different species and pointed out the differences in light interception capacity between different understorey vegetation types.^{1,7–13}

Bramble (*Rubus fruticosus* L. agg.) is a polymorphic species grouping numerous taxa that are difficult to differentiate.¹⁴ It is a cosmopolitan species that will grow on a wide variety of soil types (with a preference for acid soils) and although it is generally regarded as a light-requiring species it can tolerate partial shade. It is widely distributed in the forest understorey and in

open fields, not only in Western Europe¹⁵ but also in many countries where it was introduced and is an invasive species.^{16,17} It is able to rapidly invade new areas because it produces large quantities of seeds¹⁸ and also able to rapidly colonize available space by vegetative reproduction.¹⁹ Hence it can establish readily following opening of the overstorey and sometimes has adverse competitive effects on both the native flora and tree seedlings.^{20–24} However, when its leaf density is low relative to tree regeneration, it has been considered as a facilitative species that protects young trees against adverse climate or herbivores.^{25–28} However, this last point is debated because some grazing mammals, especially deer, are very fond of the leaves.²⁹ Although bramble can compete efficiently for water during drought,²¹ or for soil nitrogen,³⁰ little is known about either its development relative to light availability or its influence on light attenuation in the understorey.

To get a better understanding of the competitiveness of bramble regarding light and to provide foresters with adequate recommendations on the need or not for its control to ensure tree seedling establishment and growth by natural regeneration or planting, we performed a wide study in bramble-dominated

areas of France and England. More specifically, the objectives of the study were: (i) to characterize the bramble canopy structure at plant and organ scale, (ii) to evaluate its development and cover relative to available light in the understorey and (iii) to assess the light interception capacity of bramble relative to its architecture. The study took place at different locations which had a wide variety of soils, climates and forest stand structures, with measurements made both in the understorey of adult stands and in open field conditions.

Materials and methods

Study sites

A total of 60 areas of bramble thicket were sampled in 18 different contrasting sites (17 in France and 1 in the UK, Table 1). The sites were selected so that the widest range of ecological conditions and stand structures can be explored. Bedrocks varied from granite, sandstone, alluvium, volcanic to limestone. Most soil textures were represented (Table 1). Soil pH ranged from 4.5 to 8.2 (NF ISO 10390) and the C/N

ratio ranged between 11.0 and 28.8 (NF ISO 10694 and 13878), indicating that the soils had very different fertilities (measurements in the first 0–20 cm mineral layer). The bramble thickets were growing either in the forest understorey beneath overstorey trees which cast differing amounts of shade or in large gaps within woodlands or open fields where there was full daylight during the whole year. The subspecies of *R. fruticosus* as well as their age were not determined and hence not taken into account for the sampling.

Experimental design

The different bramble thickets were used for two purposes: first, to measure bramble architecture and light attenuation according to their leaf area index (LAI) or cover (Experiment 1) and, secondly, to determine bramble LAI or cover relative to available light above the bushes in the understorey (Experiment 2).

Experiment 1: bramble architecture and light interception

Twenty-one bramble thickets distributed on eight sites were used for this experiment (Table 1). A surface of 1 m² of ground was delimited by four

Table 1 Forest sites used, first to measure bramble architecture and light attenuation according to their LAI or cover (Experiment 1) and, secondly, to determine bramble LAI or cover relative to available light in the understorey above the bushes (Experiment 2).

Site name	Lat. × long.	Related experiment	Number of bramble thickets	Position (in open field or in the understorey)	Overstorey composition	Bedrock	Soil texture
Cebazat	N 45° 50' × E 3° 06'	1	2	Open field		Limestone	Clay-sand
Charensat	N 45° 59' × E 2° 39'	1	1	Open field		Granite	Sandy-clay
Fontfreyde	N 45° 42' × E 2° 59'	1	5	Understorey	<i>Pinus sylvestris</i>	Volcanic	Loamy-clay
Olloux	N 45° 37' × E 3° 03'	1	3	Open field		Granite	Sandy-loam
Petite Pierre	N 48° 52' × E 7° 19'	1	4	Open field		Sandstone	Sandy
Plauzat	N 45° 37' × E 3° 9'	1	2	Open field		Limestone	Clay
Sayat	N 45° 50' × E 3° 4'	1	3	Open field		Volcanic	Loamy-sandy-clay
Theix	N 45° 42' × E 3° 2'	1	1	Open field		Volcanic	Clay-sand
Chappes	N 46° 42' × E 3° 36'	2	3	Understorey	<i>Quercus petraea</i> <i>Quercus robur</i>	Alluvium	Sandy-loam
Chiddingfold	N 51° 09' × W 0° 60'	2	7	Understorey	<i>Pinus nigra</i>	Sedimentary	Clay-loam
Comté	N 45° 38' × E 3° 18'	2	7	Understorey	<i>Pseudotsuga menziesii</i> <i>Abies alba</i> <i>Quercus petraea</i> <i>Carpinus betulus</i>	Volcanic	Loamy-clay
Ferme du Lac	N 45° 55' × E 3° 36'	2	4	Understorey	<i>Pseudotsuga menziesii</i>	Granite	Loamy-sand
Fontsalive	N 45° 39' × E 2° 52'	2	2	Understorey	<i>Picea abies</i>	Volcanic	Loam
Limoise	N 46° 40' × E 3° 03'	2	3	Understorey	<i>Quercus petraea</i> <i>Quercus robur</i>	Alluvium	Clay-sand
Lusigny	N 46° 34' × E 3° 29'	2	4	Understorey	<i>Quercus petraea</i> <i>Quercus robur</i>	Alluvium	Sandy-loam
Mareuge	N 45° 37' × E 2° 54'	2	2	Understorey	<i>Picea abies</i> <i>Abies alba</i>	Volcanic	Sandy-Loam
Montvianeix	N 45° 55' × E 3° 34'	2	5	Understorey	<i>Pseudotsuga menziesii</i>	Granite	Loamy-sand
Paslières	N 45° 54' × E 3° 30'	2	2	Understorey	<i>Pseudotsuga menziesii</i>	Granite	Sandy-loam

stakes for each thicket. Canopy architecture was assessed by direct measurements of leaf area, cane length, cane basal diameter and 3D digitizing. The position and orientation of plant organs within the thicket were recorded by using a digitising device.³¹ The digitizing device (Polhemus, USA) includes a magnetic source and a pointer. The position and orientation of the pointer in the space (x , y and z coordinates and Euler's angles, i.e. azimuth, inclination and rolling angles) are computed from the measurements of induction currents in the magnetic field. A subsample of randomly chosen leaves, 100 per bush, was digitised for leaf inclination and rolling angles measurement. Cane basal diameter (D_c) was measured in the field with a Vernier Caliper and cane length (L_c) was calculated from the digitized data.

In the laboratory, all the leaves supported by each axis, i.e. the canes (ramification order 1), and their lateral branches (ramification order 2–3) were counted and their length (L_l), width (W_l) and petiole length (L_p) were measured. The leaf area (A_l) was then computed using either a Li-3100C area meter (LI-COR device, USA) or a CI-203 (CID, USA). The total leaf area held by a cane (A_c) was then calculated.

Photosynthetically active radiation (PAR, 400–700 nm) transmitted at the soil level beneath the bramble thickets was measured using two linear ceptometers 0.8-m long (Decagon device, Pullman, WA, USA). The two ceptometers, parallel and separated by a distance of ~ 0.5 m, were slipped horizontally into the vegetation, a few centimetres above the soil. Measurements were taken every 15 min for a 24-h period to account for the daily variation in sunlight. During the same period, a PAR sensor (LI-COR device, USA) located above the thicket recorded the incident radiation every 15 min. The transmittance (T) was then calculated as the mean PAR measured beneath the bramble thicket divided by the mean PAR measured above the thicket for the 24 h period.

All measurements were made between May and September 2005.

Experiment 2: bramble cover and LAI relative to light availability in the understorey

Thirty-nine transects distributed on 10 sites (Table 1) were established at the interface of a gap in the forest stand, joining a point inside the closed stand (low light availability) to a point inside the gap (high light availability). Along the transect, a gradient of bramble development (from low cover to well-developed thickets) could generally be found following the gradient of light availability. Between five and eight measurement points were established along the transect depending on the variability of bramble cover. At each point, light availability above the bramble, bramble cover and LAI were determined (see below).

The bramble cover was quantified by the vertically projected point technique using six rods (Figure 1). The cover was also determined visually by estimating the area covered by the vertical projection of the bramble foliage onto the ground and expressing this as a percentage of the total area of ground being studied. For the rod technique, the six rods were pushed into the bramble thicket and the number of hits between the rods and the bramble canes or leaves was counted. Before the experiments, the relationship between the hit number and bramble LAI was estimated on a sample of 31 thickets from which the foliage was also collected to measure the leaf area and to calculate the true LAI. The relationship was tested using only hits with canes, only hits with leaves, and both. We also tested the rod number necessary to give a good estimation of LAI whilst not increasing the time required for the job by too much; six rods were found to give a good compromise as the R^2 of the relationship did not increase much with additional rods (data tend towards an asymptote, data not shown). Visual assessments of bramble cover were made by the same two persons throughout the experiment, using classes of 2.5% cover from 0 to 10% cover and classes of 10% beyond 10% cover.

Light in the understorey was measured for a 24 h period using point sensors (Solems™) at a height of about 1.5 m (i.e. above the bramble



Figure 1 Four welded rods and two free rods (only one is shown on the photograph) were used to estimate the LAI of bramble thickets. The whole system was pushed vertically into the thicket and the number of hits between the rods and canes or leaves were counted and related to bramble LAI (Figure 2).

thicket) for each point of the bramble cover measurement along the transect. As in Experiment 1 transmittance was calculated as PAR measured under tree canopy divided by incident PAR measured with a point sensor (Solems™) in an open field location close to the forest.

All measurements were made between May and June 2010.

Data analysis

Data were analysed by Statgraphics centurion XVI (Statpoint, Inc.) using linear and non-linear regressions to establish the bramble empirical allometric relationships (total leaf area and leaf number borne by a cane according to its diameter, length and ramification order), the LAI relative to cover and light interception law (transmittance relative to LAI). This latter was analysed by analogy to a turbid medium with the Beer–Lambert law:

$$T = \exp(-k \times \text{LAI}) \quad (1)$$

where T the transmittance (range 0–1), LAI the leaf area index (m^2 leaf area m^{-2} soil) and k the apparent light extinction coefficient linked to leaves and canes.

For all relationships, the best curve was chosen according to the best model fit, highest R^2 and residuals analysis. The influences of site conditions (pH, fertility, bedrock etc.) and ramification order on the slope and intercept of the allometric relationships were tested by a general linear model.

For the same value of light availability in the understorey, a large variation in LAI was observed due to site influences ($P=0.002$),

Table 2. Bramble mean leaf area and inclination, and total leaf area and leaf number per branch as affected by branch diameter or length, site and branch order in Experiment 1 (results of general linear model or variance analysis).

Dependent variable	Independent variable	Co-factor	Mean (\pm SE)	d.f.	F	Probability
Mean surface of a leaf (A_l , cm ²)		Site	30.96 (1.71)	6	2.03	0.16
Leaf inclination angle (°)		Site	9.19 (3.22)	6	1.27	0.36
Total leaf area of a branch (A_c , m ²)	Branch diameter	Branch order	0.017 (0.0014)	3	3.40	0.017
Total leaf area of a branch (m ²)	Branch diameter	Site	0.017 (0.00056)	7	11.38	<0.0001
Total leaf area of a branch (m ²)	Branch length	Branch order	0.016 (0.0021)	3	3.66	0.012
Total leaf area of a branch (m ²)	Branch length	Site	0.019 (0.00026)	6	12.78	<0.0001
Leaf number of a branch	Branch length	Branch order	5.54 (0.448)	3	9.19	<0.0001
Leaf number of a branch	Branch length	Site	5.38 (0.081)	6	23.43	<0.0001

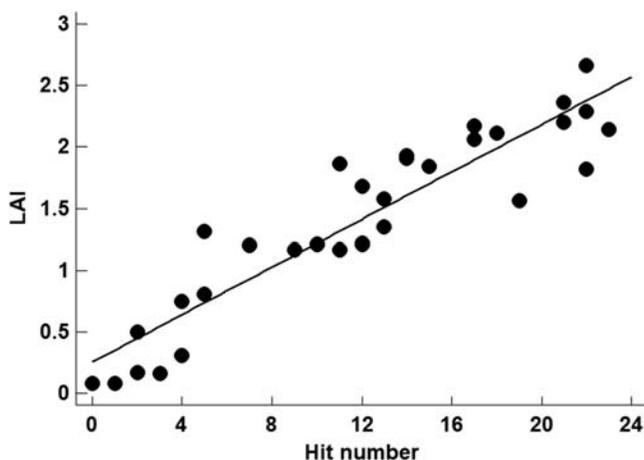


Figure 2 Bramble LAI as a function of the hit number between six rods and the bramble canes or leaves ($LAI = 0.096 \times \text{hit} + 0.256$; $R^2 = 0.85$). The relationship was used in Experiment 2 to determine LAI.

independently of light. Therefore, the influence of light on LAI was not analysed by regression but by ANOVA with site and transmittance as factors after transformation of transmittance values into classes. The different classes do not have the same amplitude which balances the number of observations in each class. LAI values were square-root transformed to have equal variances (but Figure 5 presents non-transformed values for convenience). The means were then separated by a least significant differences (LSD) test at 95% confidence.

Results

Bramble canopy architecture, site effects and allometric relations

In Experiment 1, LAI of our sampled bramble thickets ranged from 0.70 to 3.75. The number of leaves ranged from 195 to 1283 m⁻² and the mean area of a single leaf (A_l) from 21.8 to 44.2 cm². The site had no effect on A_l ($P = 0.16$, Table 2). In general, leaf inclination angles were normally distributed with a mean angle of 10.3° and a standard deviation of 24.4°, meaning that bramble had a planophile distribution of leaf inclination angles (i.e. leaves tend towards the horizontal, with the mean inclination angle <27°, de Wit (1965) cited in Sinoquet

and Andrieu).³² The site had no significant effect ($P = 0.36$) on the mean leaf inclination angle (Table 2).

Cane basal diameter (D_c) was not a good predictor of the total leaf area borne by a cane (A_c ; $R^2 = 0.33$, $P < 0.0001$). The prediction of A_c (m²) was better with cane length (L_c , m):

$$A_c = 0.054(L_c)^{1.29}; \quad R^2 = 0.64; \quad P < 0.0001 \quad (2)$$

The cane volume ($L_c \times D_c^2$) was also tested but was a poorer predictor than L_c alone. The branch order had a slight significant effect ($P = 0.012$, Table 2) on the slope of the relationship between A_c and L_c , with A_c decreasing with an increasing branch order and the relationship between A_c and L_c was significantly influenced by site ($P < 0.0001$) with the quality of the relationships varying between sites (R^2 ranging from 0.37 to 0.91). The site-dependent slope of the relationship between A_c and L_c decreased with increasing pH of the soil.

L_c was by far the best predictor of leaf number:

$$\text{Leaf number} = 2.20 + 9.66L_c; \quad R^2 = 0.44; \quad P < 0.0001 \quad (3)$$

The branch order had a significant effect on the relationship between leaf number and L_c ($P < 0.0001$, Table 2), the slope of the relationship being greater for the first- and second-order branches than for the third- or fourth-order branches. Again this relationship varied among sites ($P < 0.0001$, R^2 ranging from 0.14 to 0.63) but none of the soil characteristics recorded were significant explanatory variables.

Bramble cover and LAI relative to light availability

Bramble LAI was estimated with a good accuracy with the rod technique (Figure 2), the best relationship being given when using hits with both leaves and canes ($R^2 = 0.85$), but also with visual assessment, although for a same cover the estimated LAI varied significantly (Figure 3). The LAI was significantly related to light availability in the understorey measured just above bramble thickets ($P < 0.0001$; Figure 4), with a doubling of LAI values for very low values of transmittance from 3–5 to 5–7%. Bramble height relative to light showed the same pattern with already a height of 40 cm for only 5% light ($P < 0.0001$; data not shown). Beyond 20% light, the mean bramble height was over 60 cm.

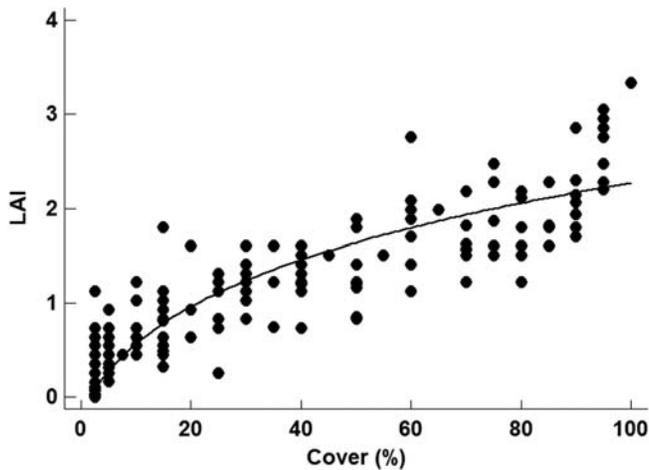


Figure 3 Bramble LAI estimated by the rod technique and related to the visual assessment of bramble bush cover (percentage of soil occupied by the visual projection onto the soil of the whole foliage) for different sites in France and England ($LAI = (0.327 \ln(\text{cover}))^2$; $R^2 = 0.96$; $P < 0.0001$).

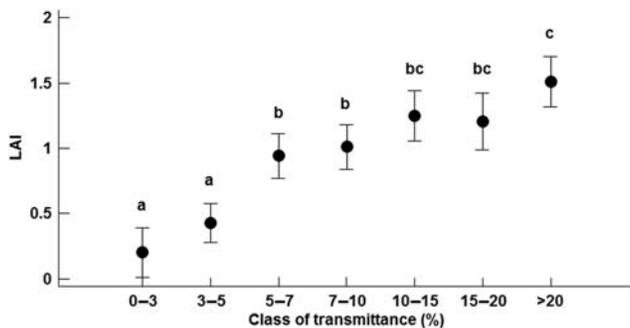


Figure 4 Bramble LAI relative to light availability in the understorey (above bramble thickets), mean and confidence interval at 95% from Fisher LSD. Different letters indicate significant different means at $\alpha = 0.05$.

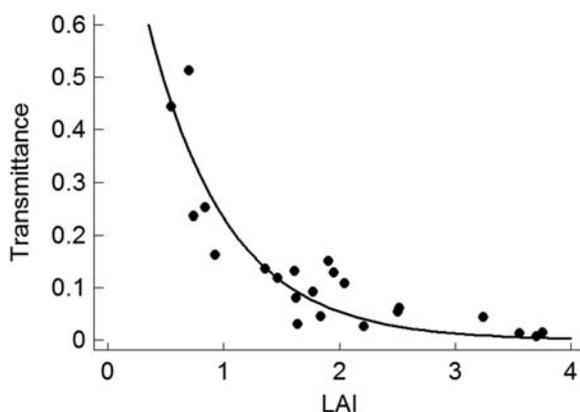


Figure 5 Transmitted light under bramble bushes relative to their LAI ($T = \exp(-1.457 \times LAI)$; $R^2 = 0.80$; $P < 0.0001$).

Light interception by bramble

Light transmitted by the bramble thicket decreased exponentially with increasing LAI (Figure 5) and consequently with increasing cover:

$$T = \exp(-1.457 \times LAI); R^2 = 0.80; P < 0.0001 \quad (4)$$

$$T = \exp(-0.074 \times \text{cover}); R^2 = 0.64; P < 0.0001 \quad (5)$$

where cover is expressed in % and deduced from the relationship presented in Figure 3.

A single relationship explained the dependence of the bramble transmittance on LAI with the extinction coefficient k (1.46) influenced neither by site ($P = 0.06$) nor whether the bramble was positioned in open field or in the forest understorey ($P = 0.20$).

Discussion

We studied here bramble canopy architecture, LAI and cover relative to light availability in the understorey and light intercepting properties in 60 areas of bramble at 18 sites with different soil, climates and forest stand structures. Bramble includes many sub-species some of which are associated with different types of habitat, but due to the taxonomic complexity of the species and the difficulty in identification of individual micro-species,³³ the exact identity of the bramble present at each site was not determined.

Bramble canopy architecture

Leaf orientation is a fundamental trait linked to light interception ability. Plants with low leaf inclination angles (horizontal leaves) intercept more light than plants with higher inclination angles, particularly when the sun is high in the sky.^{34,35} This ability is of primary importance when plants are in light-limited understorey. The bramble leaf orientation was recorded as planophile (horizontal leaves with a mean elevation angle ranging from -20 to $+20^\circ$) whatever the considered site. It means that the planophile character of bramble is very conservative across different ecological conditions and sub-species. According to the considered bramble bush, LAI varied from 0.7 to 3.75 (i.e. from little to fully developed thickets) but again this trait did not influence leaf distribution ($P = 0.93$). Indeed, bramble has a leaf inclination angle very low in comparison with many other species.³⁴ For example Sonohat *et al.*³⁵ reported some leaf inclination angles from 25 to 50° for *Trifolium repens* and $>65^\circ$ for an erectophile species such as *Festuca arundinacea*. Of course, the very planophile leaf distribution of bramble confers to this species a high ability to intercept light, which is of great interest in light-limited environment like forest understorey in terms of photosynthesis and growth.^{36,37} It gives also a higher competitiveness relative to light in comparison with many other plants that could explain why bramble is often reported like having adverse effects on both plant diversity and tree regeneration.

Estimating the leaf area and LAI in the field is generally very time consuming and often needs the harvest of the whole foliage for subsequent laboratory analysis, which also precludes studies needing non-destructive permanent bramble plots. Here

we established allometric relationships from simple bramble attributes such as cane length that allow non-destructive assessment and prediction of the leaf area or LAI. They can be used to rapidly assess bramble competitiveness in the field, especially competitiveness for light (see below). The bramble leaf number and leaf area can be estimated from cane lengths. Although these relationships are influenced by site and pH the effects are not very pronounced and may be related to bramble's preference for more acidic soil conditions.^{14,38} The site effect may also reflect a difference in the sub-species present. Cane diameter was not a good predictor of leaf number or leaf area for bramble unlike many other woody species such as trees or shrubs for instance. This may be due to the liana-like form of bramble canes, i.e. canes with the same diameter could have very different lengths.

Bramble cover and LAI relative to light availability in the understorey

Using rods and the number of hits between rods and the vegetation to estimate cover is a well-recognized technique³⁹ and it gave good results to estimate bramble LAI (Figure 2) and can be easily applied in the field with high reliability. The visual assessment of bramble cover by two people correctly trained also gave good results (Figure 3) which were less variable than rods, the standard deviation of residues being 0.207 for the visual assessment of LAI and 0.288 for the rod technique. However, the visual assessment can be highly subjective,³⁹ which is not the case when using rods. Observer training and a calibration of cover scores with a true value of cover or LAI by harvesting the leaves and measuring leaf area in the laboratory are recommended for visual assessment of cover (note that this should also be recommended for the rod technique). Unlike plants with erectophile leaf distribution, the planophile distribution of leaves in bramble probably makes such visual assessments easier.

Within the European context, bramble is generally regarded as a light-requiring species which is able to tolerate partial shade¹⁴ and Ellenberg *et al.*⁴⁰ gave this species a light requirement index of eight on a scale of nine (full light). However, precise light requirements for individual species may vary with location and in Great Britain bramble has been assigned a corrected Ellenberg value of 6,⁴¹ indicating a greater ability to withstand shade; it has also been described a facultative shade plant⁴² with a light compensation point estimated to be 1% of full daylight.⁴³ If we consider bramble LAI or percentage cover, then our data would support the idea that bramble is much more tolerant of shade than is generally accepted. At about 5% of daylight leaf cover was high with an LAI value close to 0.8 and a percentage cover from 15 to 20%. Consequently, bramble is able to tolerate deep shade, which is not consistent with its reputed moderate to high light requirement reported in some literature. Whilst bramble may grow under shaded conditions, it may not flower or fruit successfully.^{38,44}

In addition, bramble cover or LAI was only measured during the growing season (summer). Obviously, one could expect different bramble development in the understorey of either deciduous or coniferous forests, the latter providing shade the whole year, whereas a sunny understorey could be expected in the winter-spring season under deciduous species. Whether or not

bramble took advantage of that additional light is beyond the scope of this experiment; it was not designed to answer such a question, but we recorded a trend towards more developed bramble thickets at a given light availability (in summer) under deciduous tree species in comparison with coniferous species ($R^2=0.32$; $P<0.0001$). Therefore, this question would be worthy of further developments.

Light attenuation by bramble

A good relationship which followed Beer-Lambert's law was established between bramble transmittance and LAI or cover for the different thickets (Figure 5). No significant effects of site or position of the thicket either in open conditions or in forest understorey were found, indicating that a single law can be used to predict light interception by bramble in different conditions. The apparent extinction coefficient k (1.46 when considering LAI or 0.074 with cover) is particularly high in comparison with other species reflecting a strong decrease in bramble transmittance for small values of LAI. For example Gaudio *et al.*¹⁰ found values of k (calculated with cover) between 0.0004 and 0.012 for *Calluna vulgaris*, 0.017 for *Molinia caerulea*, a typical erectophile species, and between 0.022 and 0.029 for *Pteridium aquilinum*, a species reputed to intercept a great amount of light. Extinction coefficients with such a value of 0.074 are characteristic of species with very regular leaf distribution and very small overlapping of leaves.³⁵ This trait combined with a planophile distribution of leaf inclination angles provides bramble with good characteristics for light interception, a fundamental trait in shady environment.⁴⁵ As observed for other species, bramble may also adjust the position of its leaves and petiole length allowing leaf re-orientation to fill the gaps in the canopy which would further optimize light interception capacity and thus photosynthesis.^{36,45-47}

Consequences for tree regeneration

In contrast with common belief, bramble is able to tolerate deep shade and to create significant cover under very low light availability in the understorey (<5%). In addition, the spatial arrangement of its leaves (regular planophile distribution) confers a strong ability to intercept light. These characteristics need to be taken into account, when considering the stand management which takes place when tree regeneration is needed. This typically involves a reduction in the overstorey canopy by thinning or group felling to create gaps allowing more light to reach the forest floor in order to promote tree seedling growth. However, the partially shaded conditions created will also encourage the development of dense bramble thickets which will reduce the amount of available light beneath their canopy creating deeply shaded conditions that have adverse effects on tree seedling growth. Some data reported that under dense bramble thickets oak (*Quercus robur*) seedlings may die within the first year and totally disappear the second year. Even a shade tolerant species such as beech (*Fagus sylvatica*) could be affected.²⁸ In the same way, Petritan *et al.*⁴⁸ highlighted the better growth of Douglas fir (*Pseudotsuga menziesii*) and beech (*F. sylvatica*) seedlings after the removal of shrubs including bramble. The results described are consistent with observations by Harmer *et al.*⁴⁴ who concluded that retention of overstorey cover to suppress

bramble whilst promoting tree seedling growth may not be successful. However, opposite effects were also reported such as a facilitation of oak (*Q. robur*) regeneration in bramble in the case of browsing.^{25,27} Therefore, in addition to known competitive effects for water and nutrients, the results presented here demonstrate that bramble has characteristics which also make it an effective competitor for light. Thus future work will need the characterization of the competition for light between bramble and seedlings of different tree species to better manage stand regeneration.⁹

Acknowledgements

Many thanks to the owners who allowed the experiments took place in their forests and also to the Regional Centre of private owners (CRPF Auvergne) and to the Office National of Forests (ONF).

Funding

This research was partly funded by grants from the National ECOGER program and the international COST Action E47.

Conflict of interest statement

None declared.

References

- Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E. and Zedacker, S.M. 2006 Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry* **79**(1), 3–27.
- Nambiar, E.K.S. and Sands, R. 1993 Competition for water and nutrients in forests. *Can. J. For. Res.* **23**, 1955–1968.
- Casper, B.B. and Jackson, R.B. 1997 Plant competition underground. *Ann. Rev. Ecol. Syst.* **28**, 545–570.
- Coll, L., Balandier, P., Picon-Cochard, C., Prévosto, B. and Curt, T. 2003 Competition for water between beech seedlings and surrounding vegetation in different light and vegetation composition conditions. *Ann. For. Sci.* **60**, 593–600.
- Coll, L., Balandier, P. and Picon-Cochard, C. 2004 Morphological and physiological responses of beech seedlings to grass-induced belowground competition. *Tree Physiol.* **24**, 45–54.
- Comeau, P.G., Braumandl, T.F. and Xie, C.-Y. 1993 Effects of overtopping vegetation on light availability and growth of Engelmann spruce (*Picea engelmannii*) seedlings. *Can. J. For. Res.* **23**, 2044–2048.
- Aubin, I., Beaudet, M. and Messier, C. 2000 Light extinction coefficients specific to the understorey vegetation of the southern boreal forest, Quebec. *Can. J. For. Res.* **30**, 168–177.
- Balandier, P., Marquier, A., Dumas, Y., Gaudio, N., Philippe, G. and Da Silva, D. et al. 2009 Light sharing among different forest strata for sustainable management of vegetation and regeneration. In *Forestry in Achieving Millennium Goals*. Orlović, Saša (ed.). Institute of Lowland Forestry and Environment, Novi Sad, Serbia, pp 81–86.
- Balandier, P., Marquier, A., Gaudio, N., Wehrle, L., Casella, E. and Coll, L. et al. 2009 Methods for describing light capture by understorey weeds in temperate forests: consequences for tree regeneration. In *Forest Vegetation Management – Towards Environmental Sustainability*. Bentsen, N.S. (ed.), Proceedings from the final COST E47 Conference, Vejle, Denmark, 2009/05/5–7, Forest and Landscape Working Papers 35-2009, Forest and Landscape Denmark, Horsholm, pp. 73–75.
- Gaudio, N., Balandier, P., Dumas, Y. and Ginisty, C. 2011 Growth and morphology of three forest understorey species (*Calluna vulgaris*, *Molinia caerulea* and *Pteridium aquilinum*) according to light availability. *For. Ecol. Manage.* **261**, 489–498.
- Gaudio, N., Balandier, P., Philippe, G., Dumas, Y., Jean, F. and Ginisty, C. 2011 Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. *Eur. J. For. Res.* **130**, 77–89.
- Provendier, D. and Balandier, P. 2008 Compared effects of competition by grasses (Graminoids) and broom (*Cytisus scoparius*) on growth and functional traits of beech saplings (*Fagus sylvatica*). *Ann. For. Sci.* **65**, 510, 9 p.
- Shropshire, C., Wagner, R.G., Bell, F.W. and Swanton, C.J. 2001 Light attenuation by early successional plants of the boreal forest. *Can. J. For. Res.* **31**, 812–823.
- Rameau, J.C., Mansion, D. and Dumé, G. 1989 *Flore forestière française, guide écologique illustré*. IDF, Paris, France, Tome 1, 611 p.
- Willoughby, I., Balandier, P., Scott Bentsen, N., McCarthy, N. and Claridge, J. (eds) 2009 *Forest Vegetation Management in Europe: Current Practice and Future Requirements*. COST Office, Brussels, 156 p.
- Amor, R.L. 1973 Ecology and control of blackberry (*Rubus fruticosus* L. agg.). I. *Rubus* spp. as weeds in Victoria. *Weed Res.* **13**, 218–223.
- Groves, R.H. 1998 Towards an integrated management system for blackberry (*Rubus fruticosus* L. agg.). *Plant Protect. Q.* **13**, 151–152.
- Amor, R.L. 1974 Ecology and control of blackberry (*Rubus fruticosus* L. agg.). II. Reproduction. *Weed Res.* **14**, 231–238.
- Gama, A., Dumas, Y. and Frochet, H. 2006 *Utilisation des herbicides en forêt et gestion durable*. Edition Quae, Paris, France, pp. 220–221.
- Davies, R.J.-P. 1998 Regeneration of blackberry-infested native vegetation. *Plant Protect. Q.* **13**, 189–195.
- Fotelli, M.N., Geßler, A., Peuke, A.D. and Rennenberg, H. 2001 Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and $\delta^{13}\text{C}$ composition. *New Phytol.* **151**, 427–435.
- Frochet, H., Armand, G., Gama, A., Nouveau, M. and Wehrle, L. 2002 La gestion de la végétation accompagnatrice: état et perspective. *Rev. For. Fr.* **54**(6), 505–520.
- Harmer, R., Boswell, R. and Robertson, M. 2005 Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood. *Forestry* **78**, 1, 21–32.
- Mountford, E.P., Savill, P.S. and Bebb, D.P. 2006 Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry* **79**(4), 389–408.
- Jensen, A.M., Götmark, F. and Löf, M. 2012 Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: a field experiment. *For. Ecol. Manage.* **266**, 187–193.
- Jensen, A.M., Löf, M. and Witzell, J. 2012b Competition and indirect facilitation from shrubs on *Quercus robur* seedlings during establishment. *Plant Ecology* (In Press). DOI: 10.1007/s11258-012-0019-3.
- Kuiters, A.T. and Slim, P.A. 2003 Tree colonisation of abandoned arable land after 27 years of horse-grazing: the role of bramble as a facilitator of oak wood regeneration. *For. Ecol. Manage.* **181**, 239–251.
- Wehrle, L. 1985 La ronce (*Rubus fruticosus* L. agg.). *Rev. Forest. Fran.* **37**(4), 288–304.

- 29 Kirby, K.J. 2001 The impact of deer on the ground flora of British broadleaved woodland. *Forestry* **74**, **3**, 219–229.
- 30 Fotelli, M.N., Rennenberg, H. and Gessler, A. 2002 Effects of drought on the competitive interference of an early successional species (*Rubus fruticosus*) on *Fagus sylvatica* L. seedlings: ^{15}N uptake and partitioning, responses of amino-acids and other N compounds. *Plant Biol.* **4**, 311–320.
- 31 Sinoquet, H. and Rivet, P. 1997 Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitising device. *Trees* **11**, 265–270.
- 32 Sinoquet, H. and Andrieu, B. 1993 The geometrical structure of plant canopies: characterization and direct measurement methods. In *Crop Structure and Light Microclimate*. Varlet-Grancher, C., Bonhomme, R. and Sinoquet, H. (eds). INRA, Versailles, France, pp. 131–158.
- 33 Edees, E.S. and Newton, A. 1988 *Brambles of the British Isles*. The Ray Society, London, UK.
- 34 Falster, D.S. and Westoby, M. 2003 Leaf size and angle vary widely across species: what consequences for light interception? *New Phytol.* **158**, 509–525.
- 35 Sonohat, G., Sinoquet, H., Varlet-Grancher, C., Rakocevic, M., Jacquet, A. and Simon, J.C. *et al.* 2002 Leaf dispersion and light partitioning in three-dimensionally digitized tall fescue – white clover mixtures. *Plant Cell Environ.* **25**, 529–538.
- 36 Pearcy, R.W. and Yang, W. 1998 The functional morphology of light capture and carbon gain in the Redwood forest understorey plant *Adenocaulon bicolor* Hook. *Funct. Ecol.* **12**, 543–552.
- 37 Takenaka, A., Takahashi, K. and And Kohyamas, T. 2001 Optimal leaf display and biomass partitioning for efficient light capture in an understorey palm, *Licuala arbuscula*. *Funct. Ecol.* **15**, 660–668.
- 38 Grime, J.P., Hodgson, J.G. and Hunt, R. 1988 *Comparative Plant Ecology. A Functional Approach to Common British Species*. Chapman and Hall, London, UK, pp 494–495.
- 39 Wilson, J.B. 2011 Cover plus: ways of measuring plant canopies and the terms used for them. *J. Veg. Sci.* **22**, 197–206.
- 40 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 1992 *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica, Göttingen, Germany, 258 p.
- 41 Hill, M.O., Mountford, J.O., Roy, D.B. and Bunce, R.G.H. 1999 *Ellenberg's Indicator Values for British Plants*. ECOFACT Volume 2, Technical Annex. ITE Monkswood, Huntingdon, UK.
- 42 Watt, A.S. 1934 The vegetation of the Chiltern Hills with special reference to the beechwoods and their seral relationships part II. *J. Ecol.* **13**, 445–507.
- 43 Amor, R.L. and Richardson, R.G. 1980 The biology of Australian weeds 2. *Rubus fruticosus* L. agg. *J. Austral. Inst. Agric. Sci.* **46**, 87–97.
- 44 Harmer, R., Kiewitt, A. and Morgan, G. 2012 Can overstorey retention be used to control bramble (*Rubus fruticosus* L.agg.) during regeneration of forests? *Forestry* **85**, 135–144.
- 45 Pearcy, R.W., Muraoka, H. and Valladares, F. 2005 Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytol.* **166**, 791–800.
- 46 Casella, E. and Sinoquet, H. 2007 Botanical determinants of foliage clumping and light interception in two-year-old coppice poplar canopies: assessment from 3-D plant mock-ups. *Ann. For. Sci.* **64**, 395–404.
- 47 Galvez, D. and Pearcy, R.W. 2003 Petiole twisting in the crowns of *Psychotria limonensis*: implications for light interception and daily carbon gain. *Oecologia* **135**, 22–29.
- 48 Petritan, I.C., von Lüpke, B. and Petritan, A.M. 2012 Response of planted beech (*Fagus sylvatica* L.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) saplings to herbaceous and small shrubs control on clearcuts. *J. For. Res.* **17**, 164–174.