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

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Summary

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 18 sites in France and England with contrasting soils and climates. Leaf area and leaf number can be predicted by the cane length. Leaf inclination distribution was planophile. There was a good relationship between light interception and 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 increased logarithmically with light availability to reach 30% cover at only 5 to 7 % light. 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 will 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. Whilst this will improve growth of regenerating trees it will also promote development of understorey vegetation which can induce severe competition for main growing resources with tree seedlings (Balandier *et al.*, 2006). Generally, research has focused on the effect of understorey vegetation through belowground resource availability (Nambiar and Sands, 1993; Casper and Jackson, 1997; Coll *et al.*, 2003, 2004) whereas less attention has been given to the effect of understorey vegetation on light competition (Comeau *et al.*, 1993, Aubin *et al.*, 2000). However some works reported the high light interception potential of different species and pointed out the differences of light interception capacity between different understory vegetation types (Aubin *et al.*, 2000; Balandier *et al.*, 2006; Balandier *et al.*, 2009; Gaudio et al., 2011a and b; Provendier and Balandier, 2008; Shropshire *et al.*, 2001).

Bramble (*Rubus fruticosus* L. agg.) is a polymorphic species grouping numerous taxa that are difficult to differentiate (Rameau *et al.*, 1989). 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 Europe (Willoughby *et al.*, 2009) but also in many countries where it was introduced and is an invasive species (Amor, 1973; Groves, 1998). It is able to rapidly invade new areas because it produces large quantities of seeds (Amor, 1974) and also able to rapidly colonize available space by vegetative reproduction (Gama *et al.*, 2006). Hence it can establish readily following opening of the overstorey and sometimes has adverse competitive effects on both the native flora and tree seedlings (Davies, 1998; Fotelli *et al.*, 2001; Frochot et al., 2002; Harmer *et al.*, 2005; Mountford *et al.*, 2006). 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 (Jensen et al., 2012a and b; Kuiters and Slim, 2003; Wehrlen, 1985). However this last point is debated because some grazing mammals, especially deer, are very fond of the leaves (Kirby, 2001). Although bramble can compete efficiently for water during drought (Fotelli *et al.*, 2001), or for soil nitrogen (Fotelli *et al.*, 2002) 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 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 places 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 (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 ratio C/N between 11.0 and 28.8 (NF ISO 10694 and 13878), indicating that the soils had very different fertilities. 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. The subspecies of *Rubus 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: firstly to measure bramble architecture and light attenuation according to their LAI or cover (Experiment 1); and secondly to determine bramble leaf area index (LAI) or cover relative to available light above the bushes (Experiment 2).

Experiment 1 – Bramble architecture and light interception

Sixteen bramble thickets distributed on 7 sites were used for this experiment. A surface of 1 m^2 of ground was delimited by 4 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 (Sinoquet and Rivet, 1997). The digitising 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 100 leaves 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 to 3) were counted and their length (L_l), width (W_l) and petiole length (L_p) 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).

Photosynthetically Active Radiations (PAR, 400-700 nm) transmitted at soil level beneath the bramble thickets were measured using two linear ceptometers 0.8-m long (Decagon device, Pullman, WA, USA). The two ceptometers, parallel and separated by a distance of approximately 0.5 m, were horizontally slipped into the vegetation, a few centimeters above the soil. Measurements were taken every 15 minutes 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 minutes. The transmittance (*T*) was then calculated as the mean PAR measured beneath the bramble thicket / the mean PAR measured above the thicket for the 24h period.

All measurements were made between May and September 2005.

Experiment 2- Bramble cover and LAI relative to light availability

Forty-four transects distributed on 11 sites 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, Figure 1). 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 5 and 8 measurement points were established along the transect depending on variability of bramble cover. At each point, light availability above the bramble, and bramble cover and LAI were determined.

Bramble cover was quantified both by the vertically projected point technique using 6 rods (Photograph 1) and by visual assessments of the vertical projection onto the soil of the whole foliage. 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 30 thickets from which the foliage was also collected to measure leaf area and calculate true LAI (Figure 2). The relationship was tested using only hits with canes, only hits with leaves, and both; the best relationship was given when using both leaves and canes (R^2 = 0.85). 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.

Light in the understorey was measured for a 24h period using point sensors (Solems^{TM}) at a height of about 1.5 m (i.e. above the bramble thicket) for each point of bramble cover measurement along the transect. As in experiment 1 transmittance was calculated as PAR measured under tree canopy / incident PAR measured with a point sensor (Solems^{TM}) 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, the LAI relative to cover and light interception law. This latter was analysed by analogy to a turbid medium with the Beer-Lambert law:

$$T = \exp(-k\ LAI) \qquad \text{(Eq. 1)}$$

with k the apparent light extinction coefficient linked to leaves and canes.

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

For a same value of light availability in the understorey a large variation of LAI was observed due to site influences ($p = 0.002$), independently of light. Therefore the influence of light on LAI was not analyzed by regression but by ANOVA with site and transmittance as factors after transformation of transmittance values in classes. The different classes have not the same amplitude to balance for 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). Means were then separated by an LSD test at 95%.

Results

Bramble canopy architecture, site effects and allometric relations

In experiment 1 leaf area index (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 cm^2. Site had no effect on A_l ($P = 0.16$, table 2). In general leaf inclination angles was 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, 1993). 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 was better with cane length (L_c):

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

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 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:

Leaf Number = $2.20 + 9.66\ L_c$; $R^2 = 0.44$; $P < 0.0001$ (Eq.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 order branches. Again this relationship varied among sites ($P < 0.0001$, R^2 ranging from 0.14 to 0.63) but none of the ecological 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), but also with visual assessment, although for a same cover estimated LAI varied significantly (Figure

3). LAI was significantly related to light availability in the understorey measured just above bramble thickets ($p < 0.0001$; Figure 4), with a logarithmic increase for very low values of transmittance. Bramble height relative to light showed the same pattern, i.e. a logarithmic increase with light, with already a height of 40 cm for only 5% light ($P < 0.0001$; data not shown). Beyond 20% light bramble height was over 60 cm in mean.

Light interception by bramble

Light transmitted by the bramble thicket decreased exponentially with increasing LAI (Figure 5) or, by applying the relationship between cover and LAI (Figure 3), with increasing cover:

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

$T = \exp(-0.074\ Cover)$; $R^2 = 64.2$; $P < 0.0001$ (Cover expressed in %, Eq. 5)

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

Discussion

Bramble is a very common plant in forest understorey or in gaps, with a strong colonising capacity, dominance over herbaceous vegetation and competitive traits, so that it is often considered as a weed and controlled as such. Bramble competitiveness for water and nitrogen has been assessed in previous studies (e.g. Fotelli *et al.*, 2001, 2002), whereas little was known about its capacity to compete for light. We studied here bramble canopy architecture, LAI and cover relative to light 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 the taxonomic complexity of the species and the difficulty in identification of individual microspecies (Edees and Newton, 1988), 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 (Falster and Westoby, 2003; Sonohat *et al.*, 2002). 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°) whatever the considered thicket or 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 leaf area index (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. Indeed bramble has a leaf inclination angle very low in comparison with many other species (Falster and Westoby, 2003). For example Sonohat *et al.* (2002) reported some leaf inclination angles from 25 to 50° for *Trifolium repens* and more than 65° 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. It gives also a higher competitiveness relative to light in comparison with many other plants that could explains that bramble was often reported like having adverse effects on both plant diversity and tree regeneration.

Estimating 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 leaf area or LAI. They can be used to rapidly assess bramble competitiveness in the field, especially competitiveness for light (see below). Bramble leaf number and leaf area can be estimated from cane lengths. Site influenced the slope of the relationships. This effect could be due to a slight higher leaf area for a same cane length in more acid soil conditions (bramble is known to prefer acid conditions, Grime et al., 1988; Rameau *et al.*, 1989) but this effect is not very pronounced. The site effect may perhaps reflect more a sub-species effect. Cane diameter was not a good predictor of leaf number or leaf area for bramble unlike many other woody species such as trees of 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

Using rods and the number of hits between rods and the vegetation to estimate cover is a well recognised technique (Wilson, 2011) and it gave good results to estimate bramble LAI (Figure 2) and can be easily applied in the field with high reliability. Visual assessment of bramble cover by two people correctly trained gave also 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 (Wilson, 2011), which is not the case when using rods. Observer training and a calibration of cover scores with true value of cover or LAI by harvesting the leaves and measuring leaf area in the laboratory is 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 easier such visual assessments.

Within the European context bramble is generally regarded as a light-requiring species which is able to tolerate partial shade (Rameau *et al.*, 1989) and Ellenberg *et al.* (1992) gave this species a light requirement index of 8 on a scale of 9 (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 (Hill *et al.*, 1999) indicating a greater ability to withstand shade; it has also been described a facultative shade plant (Watt, 1934) with a light compensation point estimated to be 1% of full daylight (Amor and Richardson, 1980). 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 of 1 and percentage cover increased logarithmically with light availability reaching 30% cover at only 5 to 7 % light. 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 (Grime *et al.*, 1988; Harmer, Kiewitt and Morgan, 2012).

Light attenuation by bramble

A good relationship which followed the Beer-Lambert's law was established between transmittance and LAI or cover for the different bramble 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 transmittance for small values of LAI. For example Gaudio *et al.* (2011a) found some *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 (Sonohat *et al.*, 2002). This trait combined with a planophile distribution of leaf inclination angles provides bramble with good characteristics for light interception. As observed for other species, bramble may also adjust the position of its leaves to fill the gaps in the canopy which would further optimize light interception capacity (Galvez and Pearcy, 2003).

Consequences for tree regeneration

By 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 reduction of 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. The results described are consistent with observations by Harmer, Kiewitt and Morgan (2012) who concluded that retention of overstorey cover to suppress bramble whilst promoting tree seedling growth may not be successful. 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.

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Table 1. Site description

Site name	Lat. × Long.	Number[a]	Position[b]	Bedrock	Soil texture	Total $CaCO_3$ (g/kg)	N (g/kg)	C/N	pH_{water}
Cebazat	N 45°50’ × E 03°06’	2	Open field	Limestone	Clay-sand	27	1.8	13.1	8.1
Chappes	N 46°42' × E 03°36'	3	Understorey *Quercus petraea* *Quercus robur*	Alluvium	Sandy-loam	-[c]	-	-	-
Charensat	N 45°59’ × E 02°39’	1	Open field	Granite	Sandy-clay	0	3.5	22.4	4.6
Chiddingfold	N 51°09' × W 0°60'×	7	Understorey *Pinus nigra*	Sedimentary	Clay- loam	-	-	-	4.5-5.2
Comté	N 45°38' × E 03°18'	7	Understorey *Pseudotsuga menziesii* *Abies alba* *Quercus petraea* *Carpinus betulus*	Volcanic	Loamy-clay	-	-	-	-
Ferme du Lac	N 45°55’ × E 03°36’	4	Understorey *Pseudotsuga menziesii*	Granite	Loamy-sand	-	-	-	-
Fontfreyde	N 45°42' × E 02°59'	5	Understorey *Pinus sylvestris*	Volcanic	Loamy-clay	0	3.5	13.9	5.9
Fontsalive	N 45°39' × E 02°52'	2	Understorey *Picea abies*	Volcanic	Loam	-	-	-	-
Limoise	N 46°40' × E 03°03'	3	Understorey *Quercus petraea* *Quercus robur*	Alluvium	Clay-sand	-	-	-	-
Lusigny	N 46°34' × E 03°29'	4	Understorey *Quercus petraea* *Quercus robur*	Alluvium	Sandy-loam	-	-	-	-
Mareuge	N 45°37' × E 02°54'	2	Understorey *Picea abies* *Abies alba*	Volcanic	Sandy-Loam	-	-	-	-
Montvianeix	N 45°55' × E 03°34'	5	Understorey *Pseudotsuga menziesii*	Granite	Loamy-sand	-	-	-	-
Olloix	N 45°37’ × E 03°03’	3	Open field	Granite	Sandy-Loam	0	2.2	11.5	5.6
Paslières	N 45°54' × E 03°30'	2	Understorey *Pseudotsuga menziesii*	Granite	Sandy-loam	-	-	-	-
Petite Pierre	N 48°52’× E 7°19’	4	Open field	Sandstone	Sandy	0	0.7	16.1	4.5
Plauzat	N 45°37' × E 03°09'	2	Open field	Limestone	Clay	285	1.9	28.8	8.2
Sayat	N 45°50’ × E 03°04’	3	Open field	Volcanic	Loamy-sandy-clay	0	1.4	11.2	6.0
Theix	N 45°42’ × E 03°02’	1	Open field	Volcanic	Clay-sand	0	3.0	11.0	6.3

[a] Number = number of bramble thickets studied

[b] Position = position of bramble thickets, in open field or in the understorey, and in this last case, species included in the overstorey.

[c] Non determined

504 Table 2. Results of the GLM or ANOVA on the main variables tested.

Variable to explain	Explanatory variable	Source of variability	ddl	F	Probability
Mean surface of a leaf		Site	6	2.03	0.16
Leaf inclination angle		Site	6	1.27	0.36
Total leaf area of a branch	Branch diameter	Branch order	3	3.40	0.017
Total leaf area of a branch	Branch diameter	Site	7	11.38	< 0.0001
Total leaf area of a branch	Branch length	Branch order	3	3.66	0.012
Total leaf area of a branch	Branch length	Site	6	12.78	< 0.0001
Leaf number of a branch	Branch length	Branch order	3	9.19	< 0.0001
Leaf number of a branch	Branch length	Site	6	23.43	< 0.0001

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Legend captions

Photograph 1. Four welded rods and two free rods are used to estimate the LAI of bramble bushes. The whole system is pushed vertically into the bush and the number of hits between the rods and canes or leaves are counted and related to bramble LAI (Figure 3).

Figure 1. Schematic design of understorey light and bramble cover measurements along a transect at the stand – gap interface.

Figure 2. Bramble LAI as a function of the hit number between six rods and the bramble canes or leaves (LAI = 0.096 × Hit + 0.256; $R^2 = 0.85$).

Figure 3. 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 ($LAI = (0.327 \ln(Cover))^2$; $R^2 = 0.96$; $P < 0.0001$).

Figure 4. Bramble LAI relative to transmittance (percentage of light transmitted in the understorey above bramble thickets, mean and confidence interval at 95% from Fisher LSD). Different letters indicate significant different means at $\alpha = 0.95$.

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

Photograph 1

Figure 1.

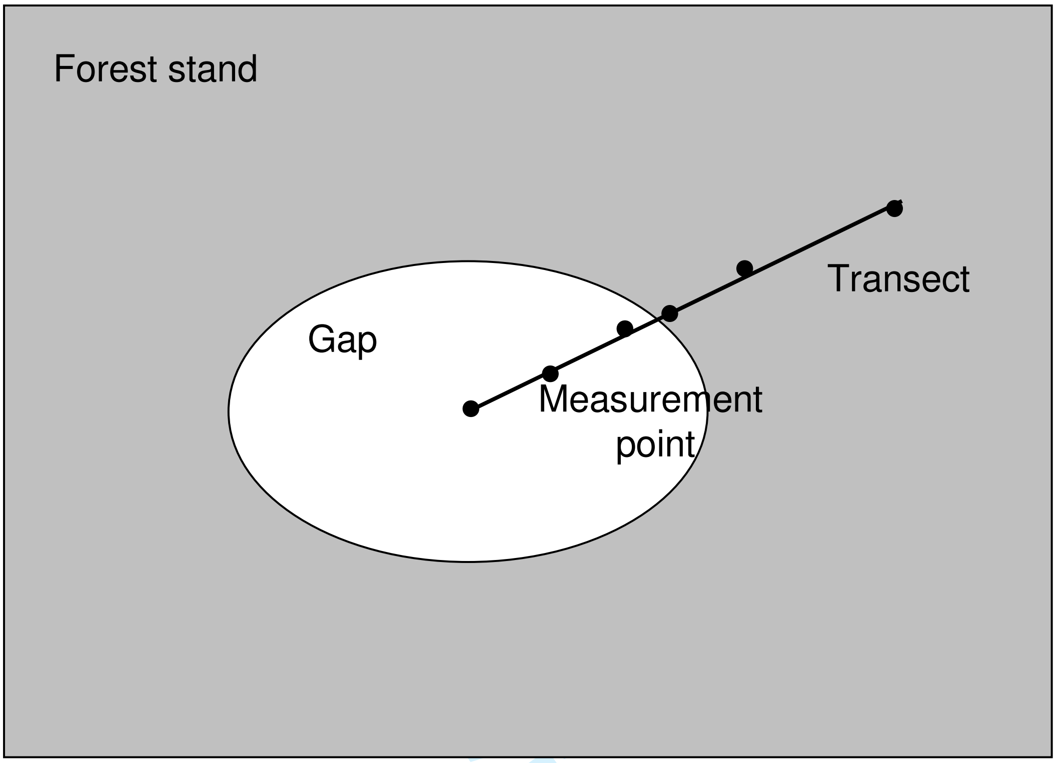


Figure 2.

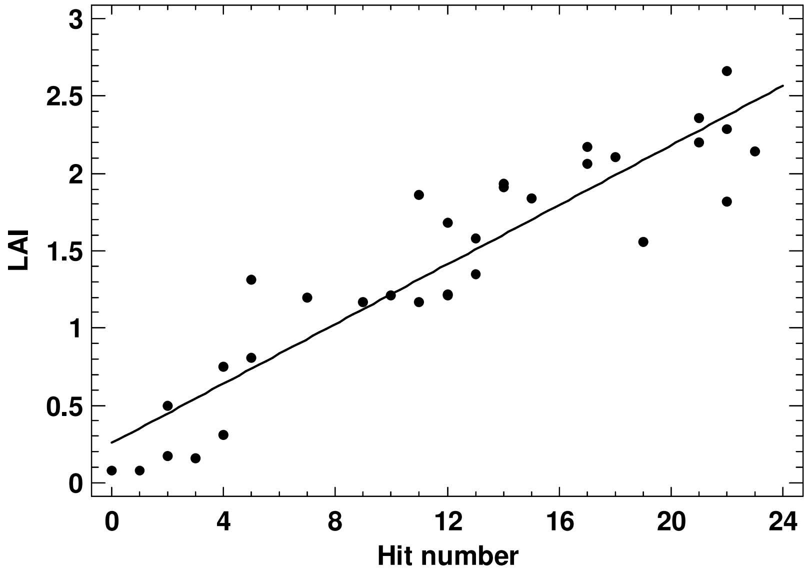


Figure 3.

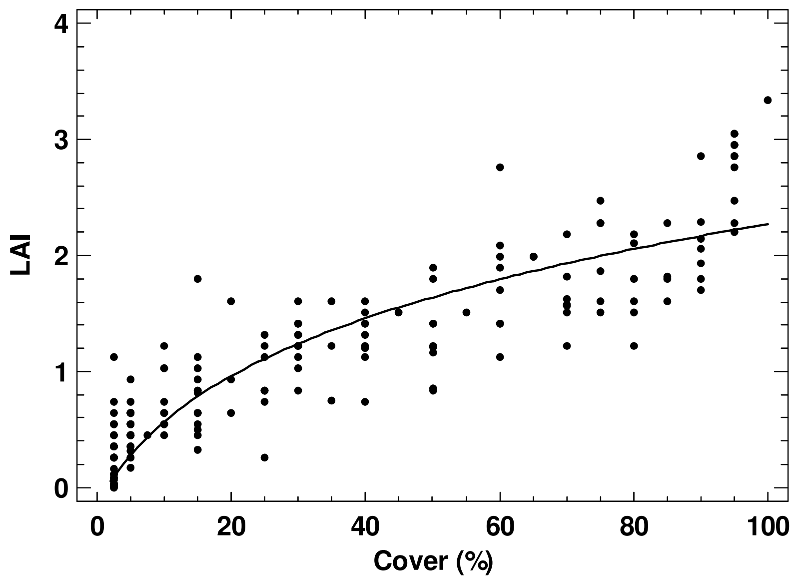
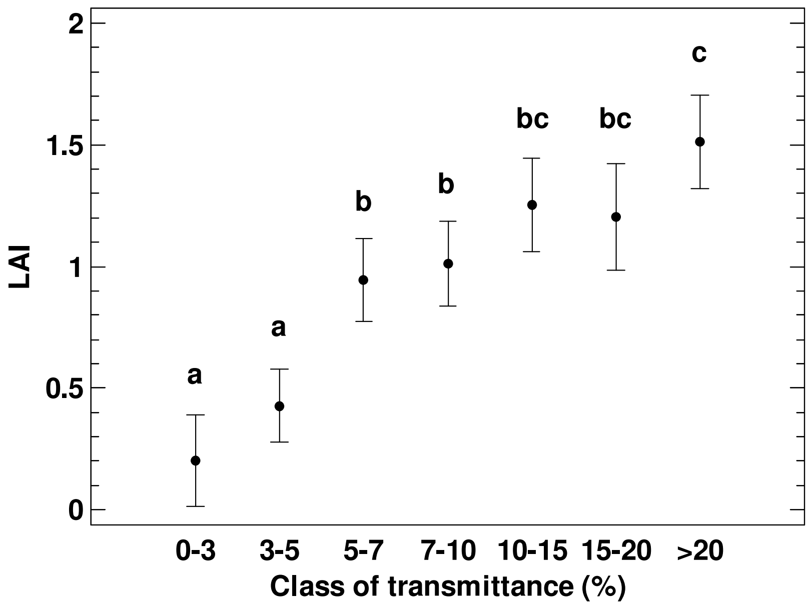


Figure 4.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1.5
1
0.5
0
LAI
a
a
b
b
bc
bc
c
0-3
3-5
5-7
7-10
10-15
15-20
>20
Class of transmittance (%)

Figure 5.