PHOLIAGE

A Photosynthesis and Light Absorption model

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Introduction

Enrichment planting is the process by which desirable tree species are planted into either existing secondary vegetation, degraded forests or mono-species tree plantations. It is increasingly being used in conservation as it can both increase the ecological and economical value of forest: the first by increasing the number of plant species, hopefully resulting in an increase of animal and other species as well, and the latter by introducing a larger number and a higher diversity of economically interesting species into a certain area. Often these projects fail however, which partly can be attributed to the fact that the planted species are poorly matched to the prevailing light conditions in the forests where they are planted. If the available light is lower than the species' light requirements, growth is seriously hampered. If available light levels are too high, damage to the photosynthetic system can occur and the planted trees will suffer from more intense interspecific competition with herbaceous plants and shrubs.

Performance of plants is mainly determined by their growth and their survival and in enrichment planting studies often these two factors are evaluated to estimate optimal conditions for planted seedlings (Peña-Claros, 2001; Paquette *et al*, 2006). As light requirements are a key factor determining plant performance in enrichment planting projects, accurate assessment of light climate is very important for determining optimal growth conditions. To be able to asses light absorption and photosynthesis of these plants, mathematical models are a powerful tool, as they allow detailed prediction and comparison of plant traits under various circumstances. Currently, assessment of light climate in enrichment planting projects is usually done in rather coarse ways. At the Plant Ecology department of Utrecht University models have been developed for calculating light climate in different vegetation types. They include a model of a plant measured in layers inside a homogenous vegetation (StratiPHOLIAGE, used unnamed in Selaya, 2007) and a model of a spherical plant below a homogenous canopy layer (developed by D. van Bentum and F. Schieving, not published). Current research to individual plants within enrichment planting projects in Vietnam, however, required a model incorporating some kind of variable canopy for the surrounding vegetation, because in these projects often certain spatial cutting and planting patterns are used, e.g. line planting in clear-cut lanes.

The model described here considers the crown of a plant as an ellipsoid shaped body with a homogenous leaf area density. It is placed in a surrounding vegetation, also with a homogenous leaf area density and extending infinitely in all directions. This surrounding vegetation is limited upwards and downwards at certain heights, resulting in a flat upper and lower border, and has a circular gap around the plant's centre. The gap's radius can be smaller than the radius of the plant or even be zero, resulting in the plant being partially or completely incorporated in the vegetation.

The model is not yet complete, however: All components regarding light absorption and extinction have been left out for now. Thus actual light absorption per unit volume for any point in the ellipsoid is not calculated, but assumed to be a fixed value. The total light absorption, as an integral of the (fixed) light absorption per unit volume over the plant's crown volume, is calculated. The path lengths through crown and surrounding are calculated, necessary for calculating the light extinction in any direction, which, in turn, is not calculated.

Model description

Assume an ellipsoid-shaped plant E with origin O in a vegetation with top h_t and bottom h_b (figure 1). The path lengths of light through the plant crown and the surrounding canopy are to be calculated for any point p within the boundaries of ellipsoid E.

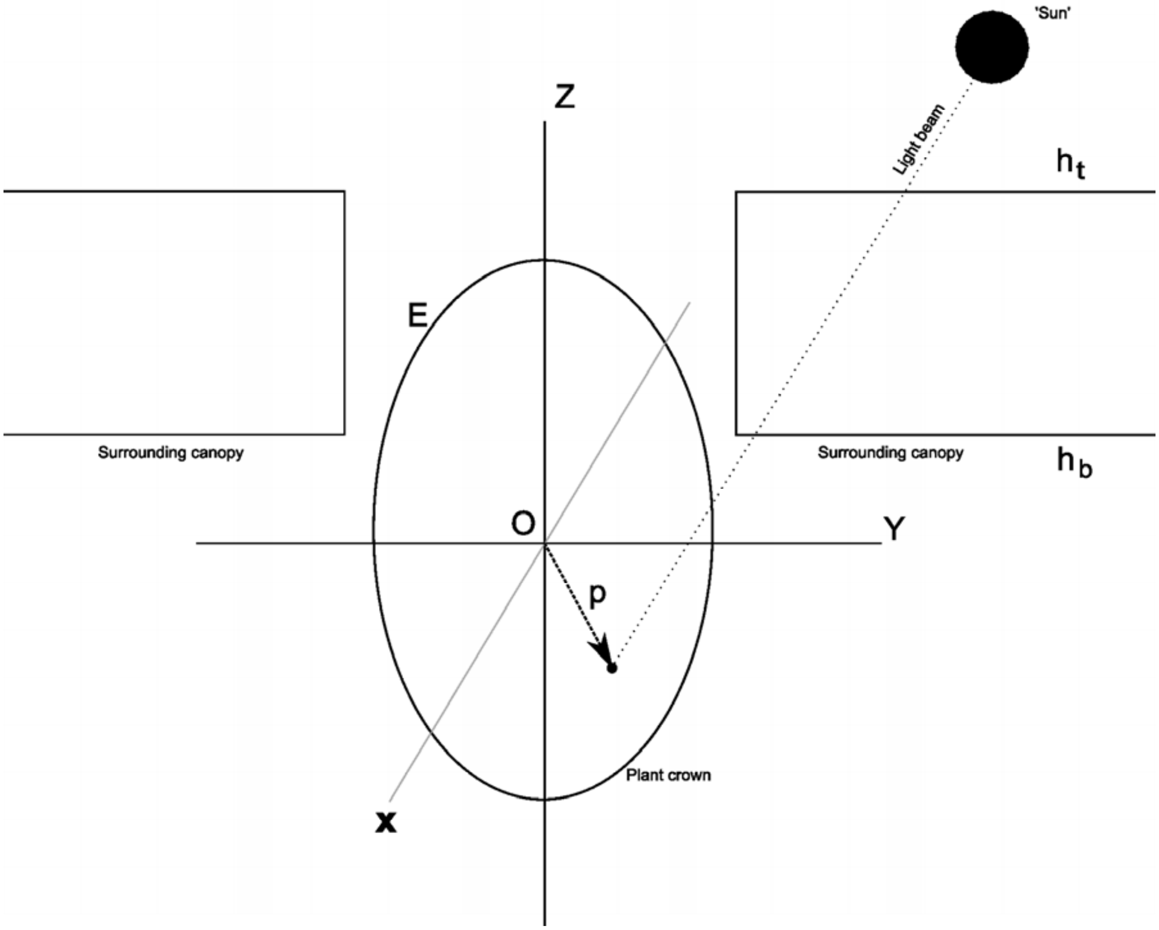

Figure 1: The model system, with plant crown, surrounding canopy, light beam and coordinate system.

Path length through the crown

Let vector d be a unit length vector pointing into the direction a beam of light is coming from. The vector from p to the boundary of E is defined as λd, so λ is the path length of light through the tree crown. Vector p is pointing from the centre of the ellipsoid to point p. Vector q is the location vector of the point where vector λd ends on the surface of the ellipsoid (figure 2).

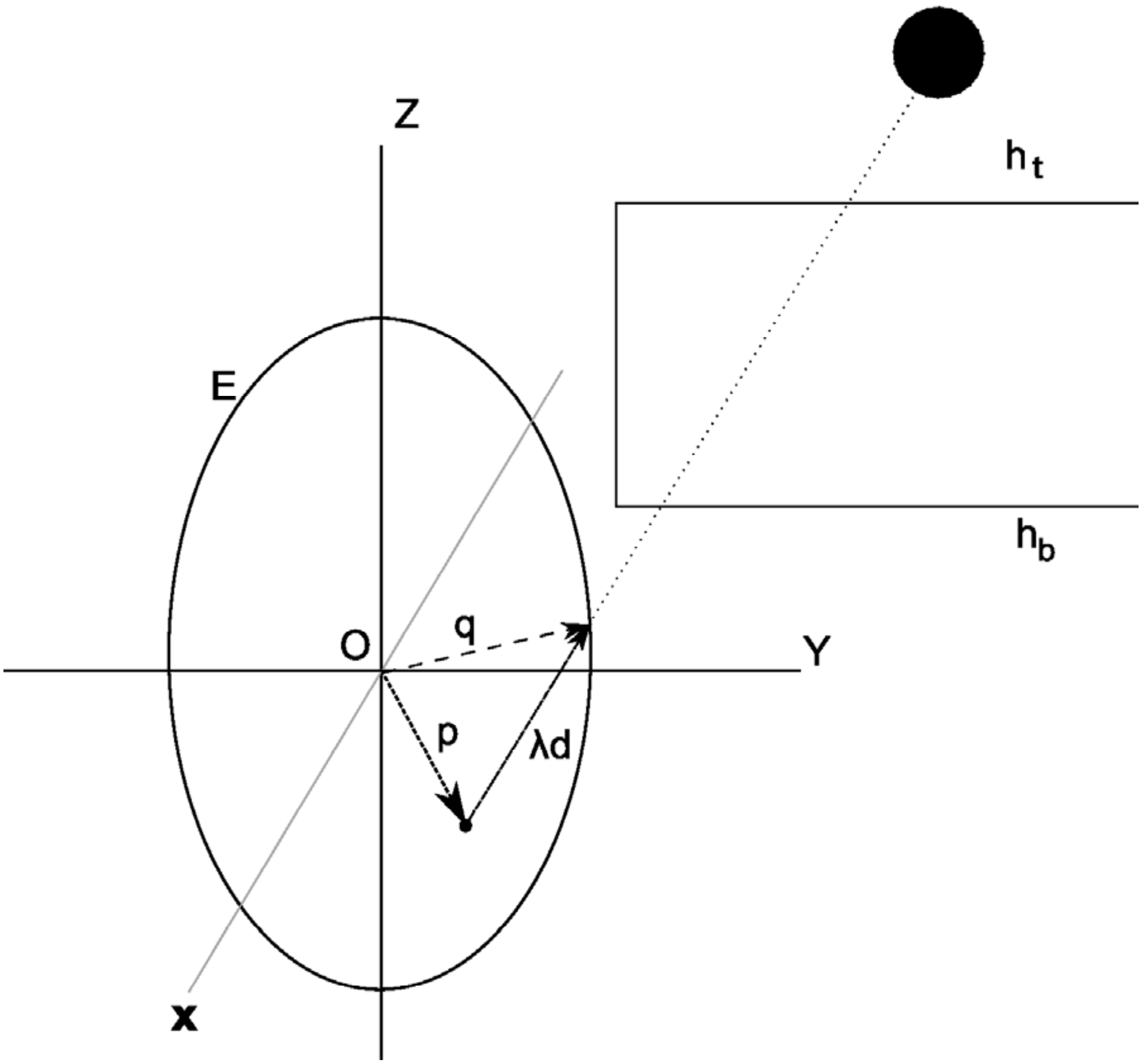

Figure 2: The model system, with vectors for calculating the path length through the crown.

Vector q has to satisfy (be an element of the ellipsoid surface ∂E):

$$\vec{q} \in \partial E \tag{1}$$

The set of vectors must satisfy this equation:

$$\vec{p} + \lambda \vec{d} = \vec{q} \tag{2}$$

Which can be rewritten as:

$$[p_x, p_y, p_z] + \lambda [d_x, d_y, d_z] = [q_x, q_y, q_z] \tag{3}$$

Which we can split to

$$p_x + \lambda d_x = q_x \tag{4a}$$

$$p_y + \lambda d_y = q_y \tag{4b}$$

$$p_z + \lambda d_z = q_z \tag{4c}$$

And as this has to satisfy the equation of ∂E (with a, b and c the axes of E)

$$\frac{x^2}{a^2}+\frac{y^2}{b^2}+\frac{z^2}{c^2}=1 \tag{5}$$

We can substitute formulas 4a, b and c into formula 5:

$$\frac{(p_x+\lambda d_x)^2}{a^2}+\frac{(p_y+\lambda d_y)^2}{b^2}+\frac{(p_z+\lambda d_z)^2}{c^2}=1 \tag{6a}$$

$$\frac{d_x{}^2\lambda^2+2d_xp_x\lambda+p_x{}^2}{a^2}+\frac{d_y{}^2\lambda^2+2d_yp_y\lambda+p_y{}^2}{b^2}+\frac{d_z{}^2\lambda^2+2d_zp_z\lambda+p_z{}^2}{c^2}=1 \tag{6b}$$

$$\frac{d_x{}^2}{a^2}\lambda^2+\frac{2d_xp_x}{a^2}\lambda+\frac{p_x{}^2}{a^2}+\frac{d_y{}^2}{b^2}\lambda^2+\frac{2d_yp_y}{b^2}\lambda+\frac{p_y{}^2}{b^2}+\frac{d_z{}^2}{c^2}\lambda^2+\frac{2d_zp_z}{c^2}\lambda+\frac{p_z{}^2}{c^2}=1 \tag{6c}$$

Which can be rewritten to the traditional quadratic equation form:

$$\alpha\lambda^2+\beta\lambda+\gamma=0 \tag{7}$$

with

$$\alpha=\frac{d_x{}^2}{a^2}+\frac{d_y{}^2}{b^2}+\frac{d_z{}^2}{c^2} \tag{8}$$

$$\beta=\frac{2d_xp_x}{a^2}+\frac{2d_yp_y}{b^2}+\frac{2d_zp_z}{c^2} \tag{9}$$

$$\gamma=\frac{p_x{}^2}{a^2}+\frac{p_y{}^2}{b^2}+\frac{p_z{}^2}{c^2}-1 \tag{10}$$

For which the solutions can be calculated using the quadratic formula:

$$\lambda=\frac{-\beta\pm\sqrt{\beta^2-4\alpha\gamma}}{2\alpha} \tag{11}$$

Only the solutions for

$$\beta^2-4\alpha\gamma\geq 0 \tag{12}$$

have to be considered.
Now we can calculate q.

Exit point of light out on surrounding vegetation

To calculate whether a light beam intersects with the surrounding vegetation, and if so, where it enters the gap we define a new set of vectors, again named p, d and q. Vector d is again a unit length vector pointing into the direction a beam of light is coming from. Vector p points to the intersection of a light beam with the ellipsoid. Vector q is the location vector for the intersection with the vegetation boundary (figure 3). For this set of vectors equation 2 applies again.

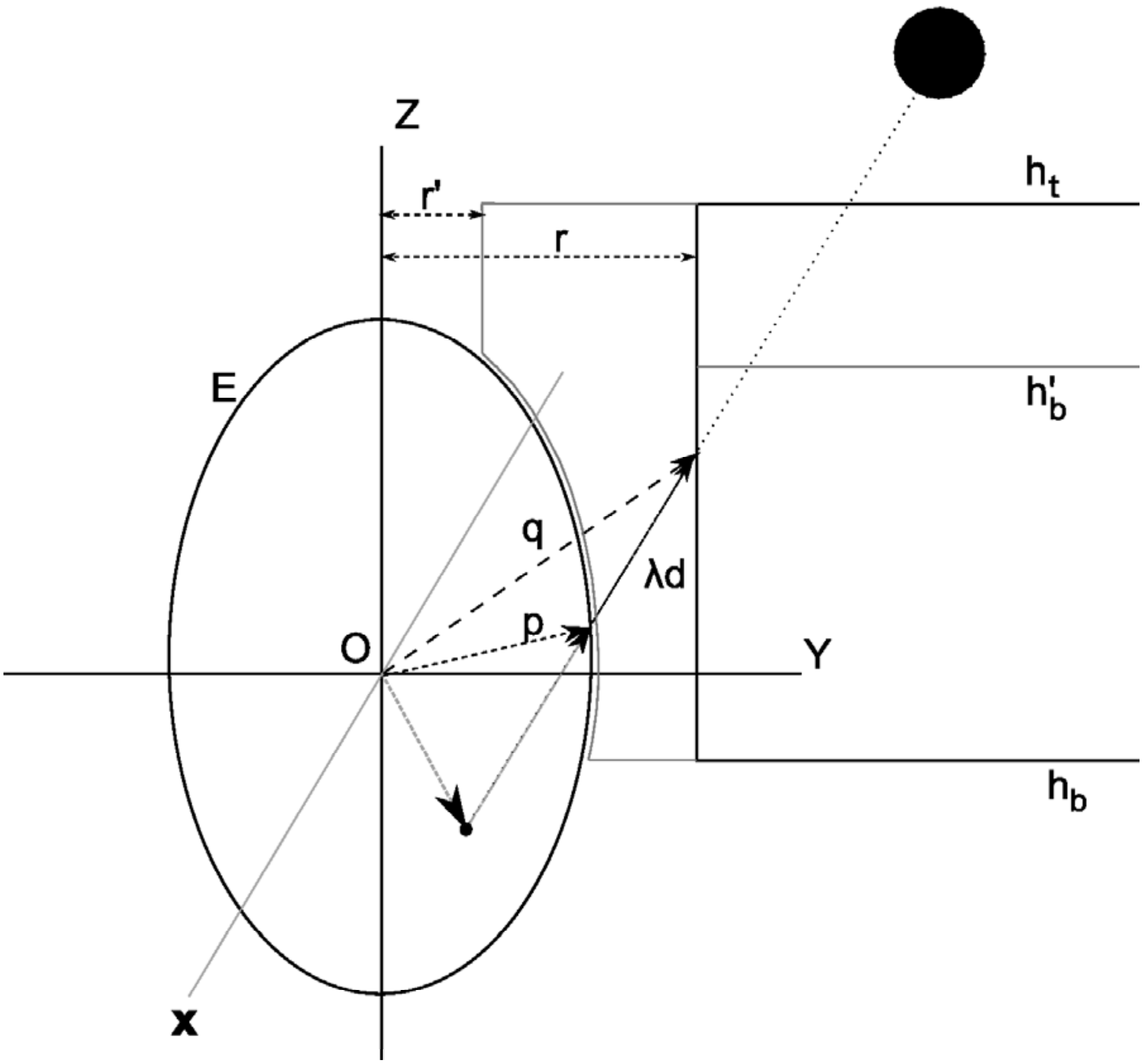

Figure 3: The model system, with vectors for calculating the intersection with the surrounding vegetation. Some alternative vegetation configurations are also shown: r' and h'_b

We can distinguish 5 situations:

1) $p_z \geq h_t$: the beam passes over the vegetation

2) $p_z < h_t$, $p_z \geq h_b$, $\sqrt{p_x^2 + p_y^2} \geq r_{gap}$: Plant joins the vegetation (as with gap diameter r' in figure 3).

3) $p_z < h_t$, $p_z \geq h_b$, $\sqrt{p_x^2 + p_y^2} < r_{gap}$: Light intersects with side boundary, or passes over.

4) $p_z < h_t$, $p_z < h_b$, $\sqrt{p_x^2 + p_y^2} \geq r_{gap}$: Light intersects with lower boundary.

5) $p_z < h_t$, $p_z < h_b$, $\sqrt{p_x^2 + p_y^2} < r_{gap}$: Light intersects with lower or side boundary (as with lower boundary h'_b in figure 3).

Which are solved as follows:
1) No intersection.
2) λ=0, so point q is point p.
3) Point q has to be on the cylinder wall formed by the gap:

$$q_x{}^2 + q_y{}^2 = r^2 \tag{13}$$

We substitute using formula 4:

$$(p_x + \lambda d_x)^2 + (p_y + \lambda d_y)^2 = r^2 \tag{14}$$

Which we can rewrite:

$$(d_x{}^2\lambda^2 + 2d_x p_x\lambda + p_x{}^2) + (d_Y{}^2\lambda^2 + 2d_Y p_Y\lambda + p_Y{}^2) = r^2 \tag{15a}$$

$$(d_x{}^2 + d_y{}^2)\lambda^2 + (2d_x p_x + 2d_y p_y)\lambda + p_x{}^2 + p_y{}^2 - r^2 = 0 \tag{15b}$$

Yielding the quadratic equation form of formula 7, with:

$$\alpha = d_x{}^2 + d_y{}^2 \tag{16}$$

$$\beta = 2p_x d_x + 2p_y d_y \tag{17}$$

$$\gamma = p_x{}^2 + p_y{}^2 - r^2 \tag{18}$$

This can be solved using the quadratic equation, yielding λ, and we can calculate point q. If $q_z \geq h_t$ there is no intersection.
4) Using formula 4c

$$p_z + \lambda d_z = h_b \tag{19a}$$

$$\lambda = \frac{h_b - p_z}{d_z} \tag{19b}$$

In this case the path length through the surrounding vegetation can be calculated without knowing point q (see next section), so in fact we can skip these calculations.
5) To find the intersection with either the lower or the side boundary we calculate λ using sections 3 (side boundary) and 4 (lower boundary) above and use the longest λ. With λ known we can calculate all coordinates of point q.

Path length through the surrounding vegetation

For the path length through the vegetation we again define a set of vectors p, d and q. Vector d again is a unit length vector pointing into the direction a beam of light is coming from, p is the location vector to the exit point of the light on the vegetation boundary and q is the location vector to the entry point of the light on the vegetation top boundary (figure 4).

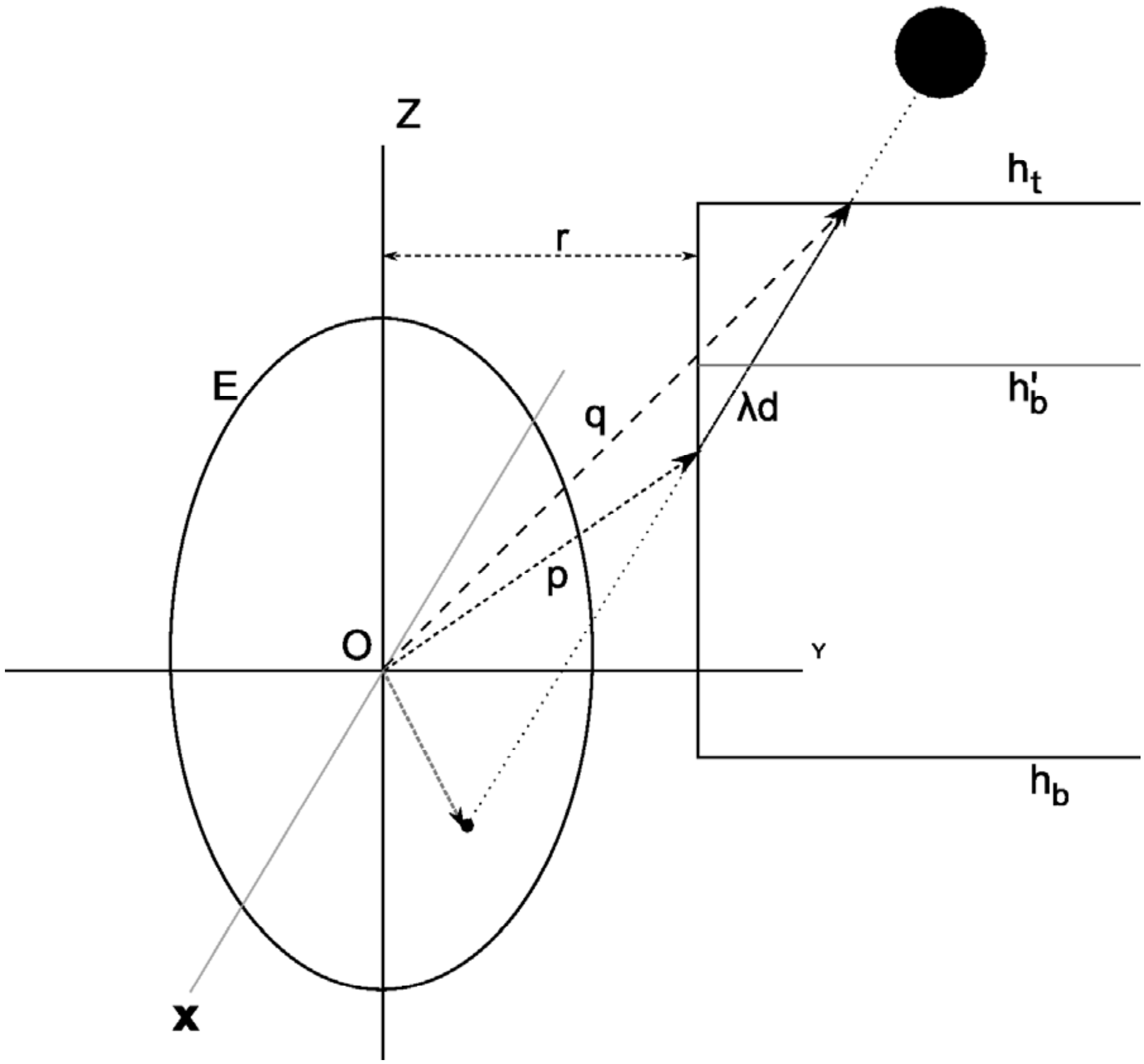

Figure 4: The model system, with vectors for calculating the path length through the surrounding canopy.

We can calculate λ analogous to situation 3 in section 'Path length through the gap', but substituting h_b with h_t.

$$p_z + \lambda d_z = h_t \tag{20a}$$

$$\lambda = \frac{h_t - p_z}{d_z} \tag{20b}$$

With λ known we can calculate all coordinates of point q. If the light beam, however, exits the vegetation through it's lower border (h'_b in figure 4), we can calculate the path length without knowing point p, using the vegetation thickness and the light polar angle:

$$\lambda = \frac{(h_t - h_b)}{\cos\theta} \tag{21a}$$

Where, because d is unit length, cosθ = d_z:

$$\lambda = \frac{(h_t - h_b)}{d_z} \quad (21b)$$

Total light capture of the ellipsoid

Now we calculate the light absorption rate for the ellipsoid. This can be done by integrating the light absorption rate per unit volume over the ellipsoid's volume. Let $p \to i(p)$ denote the light absorption rate per unit volume at each point p (this calculation is not yet specified). The total light absorption rate of an ellipsoid-shaped plant crown is then given by the integral:

$$I_{ellipsoid} = \int_{ellipsoid} i(p)dV \quad (22)$$

An ellipsoid, however, is not easy to integrate, so this integration will be transformed to the integration of a sphere.
The equation of the surface of an ellipsoid is given in formula 4. The surface of a unit sphere is given by:

$$x^2 + y^2 + z^2 = 1 \quad (23)$$

Hence each point (x,y,z) in the ellipsoid can be uniquely associated to a point (x',y',z') in a unit sphere by:

$$x' = \frac{x}{a}, y' = \frac{y}{b}, z' = \frac{z}{c} \quad (24a)$$

$$\Leftrightarrow$$

$$x = ax', y = by', z = cz' \quad (24b)$$

So each cube-shape volume element in an ellipsoid

$$\delta V = \delta x \cdot \delta y \cdot \delta z \quad (25)$$

is coupled with a volume element in a sphere

$$\delta V' = \delta x' \cdot \delta y' \cdot \delta z' \quad (26)$$

by

$$\delta V = \delta x \cdot \delta y \cdot \delta z = a\delta x' \cdot b\delta y' \cdot c\delta z' = abc\delta V' \quad (27)$$

This way we can write:

$$I_{ellipsoid} = abc \int_{sphere} i'(p')dV' \quad (28)$$

with

$$p' \to i'(p') = i(ap'_x, bp'_y, cp'_z) \quad (29)$$

We will start the integration along the z'-axis, from –1 to +1. That way we divide the sphere in 'discs' with height δz' and the radius at position z' given by:

$$R_{z'} = \sqrt{1 - z'^2} \quad 30$$

These circular discs correspond to an elliptical discs with height δz =c·δz' and with lengths of the semi-radii along the x and the y axis of $a \cdot R_z$ and $b \cdot R_z$ respectively.
The integral over an ellipse at height z can be written as an area integral over a circle at position z' in the sphere by:

$$\int_{ellipse(z)} i(p)dA = ab \int_{disc(z')} i'(p')dA' \quad 31$$

The area of the circle can be viewed as an integral over the radius of the circle ('rings') and an integral over an angle ('sectors'):

$$\int_{disc(z')} i'(p')dA' = \int_0^{R_{z'}} r' \int_0^{2\pi} i'(p')d\psi' dr' \quad 32$$

Where the integral over the angle is multiplied by r', as an angle corresponds to a distance on a unit circle (angle 2π is circumference of a unit circle), while here the circle has a radius r'. The Cartesian point p' is calculated from angular coordinates using:

$$p' = (r'\cos\psi', r'\sin\psi', z') \quad 33$$

Now we can write the initial integral over the ellipsoid as an integral over a sphere:

$$I_{ellipsoid} = abc \int_{-z}^{+z} \int_0^{R_{z'}} r' \int_0^{2\pi} i'(p')d\psi' dr' dz' \quad 34$$

Literature

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